

Morphometry, sexual maturity, fecundity and epibiosis of the South American spider crab *Libidoclaea granaria* (Brachyura: Majoidea)

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Libidoclaea granaria was collected as part of the by-catch of the *Zygochlamys patagonica* (Bivalvia: Pectinidae) fishery, between 36° and 39°40'S and at 80 to 128 m depth. Crab densities ranged from 0 to 150 individuals 100 m⁻², with a mean of 9.8 ± 20.4 individuals 100 m⁻². Mature males and females ranged from 24 to 61 mm, and from 16 to 48 mm, carapace width (CW), respectively. The largest immature female measured 22.5 mm CW. The number of eggs carried by a female ranged from 1200 to 9300. Sponges were the most frequent epizoic organisms, followed by the lepadomorph cirriped *Ornatoscalpellum gibberum*, Serpulidae and Spirorbidae worms. Since all these organisms were reported on *Z. patagonica* beds, crabs are camouflaged to match their habitat. Small crabs usually had naked carapaces, indicating a high moult frequency. Larger crabs instead, had epibionts on their carapaces, suggesting a lesser moult frequency. The erosion of carapace spines and the heavy epibiosis of large specimens suggest the existence of a terminal anecdyosis.

INTRODUCTION

The diversity of spider crabs is very great (Martin & Davis, 2001). This diversity is related not only to morphology but to habitat and size: although they are all marine, they occur in shallow and deep water, even in the intertidal, and on different bottoms (Rathbun, 1925). On the other hand, adults range from 5 to 350 mm CW. In spite of their diversity, the monophyly of the superfamily Majoidea is supported by some larval characters, although the sister-group relationships within the former Majidae are uncertain (Pohle & Marques, 2000).

Nine species of spider crabs were found on the Argentine continental shelf, between 34° and 56°S (Boschi et al., 1992; Schejter et al., 2002). *Collodes rostratus* A. Milne-Edwards 1878, *Libinia spinosa* H. Milne-Edwards 1834 and *Pelia rotunda* A. Milne-Edwards 1875 are endemic to the south-western Atlantic. *Leucippa pentagona* H. Milne-Edwards 1833 is widely distributed on the Atlantic and Pacific coasts of America; *Rochinia gracilipes* A. Milne-Edwards 1875 is found both in the south-western and south-eastern Atlantic; *Pyromaia tuberculata* (Lockington, 1877) recently invaded Brazilian and Argentinian coastal waters. Finally, *Eurypodius lateillei* Guérin 1828, *Leurocyclus tuberculatus* (H. Milne-Edwards & Lucas 1842) and *Libidoclaea granaria* H. Milne-Edwards & Lucas 1842 are Magellanic species (i.e. they inhabit the Atlantic and Pacific waters of southern South America).

Libidoclaea granaria is distributed from Valparaíso, in the Pacific, and from 'off Buenos Aires', in the Atlantic, to the Beagle Channel (Boschi et al., 1992; Vinuesa et al., 1999) (Figure 1). Adults were found from 30 to 100 m depth. The morphology of larvae reared in the laboratory was

described by Fagetti (1969). Bacardit & Vera (1986) and Lovrich (1999) found *L. granaria* larvae between 37° and 46°S in the Argentine Sea and in the Beagle Channel, respectively. The systematics of spider crabs has been recently reviewed and former majid subfamilies are now considered families of the Majoidea (Martin & Davis, 2001 and the references therein). According to these authors, classification of *L. granaria* should be Majoidea: Pisidae. Since the familial and subfamilial classification of Majoidea are still controversial (Martin & Davis, 2001), we decided to mention only the superfamilial status in the title of this article.

The pattern of growth of most crustaceans involves a series of immature instars and one or several mature instars. Successive immature instars are generally of similar morphology, in spite of the size increase and subtle changes in the relative proportions of some body parts at each moult. However, the transition between immature and mature instars is achieved at a particular moult, the 'puberty moult', that is accompanied by morphological changes (Hartnoll, 2001 and the references therein). For example, the male chelae and female abdomen may enlarge disproportionately to the carapace at the puberty moult; the size at which this change occurs is the size of morphometric maturity. However, crabs can only successfully mate when also their gonads are mature (gonadal maturity) and when they can display specific behaviours (functional maturity). Morphometric, gonadal and functional maturity are not always synchronized, and in some cases each one is achieved at a different moult (López-Greco & Rodríguez, 1999).

Although many crab species growth continues indefinitely, moult ceases definitively in most spider crabs. After

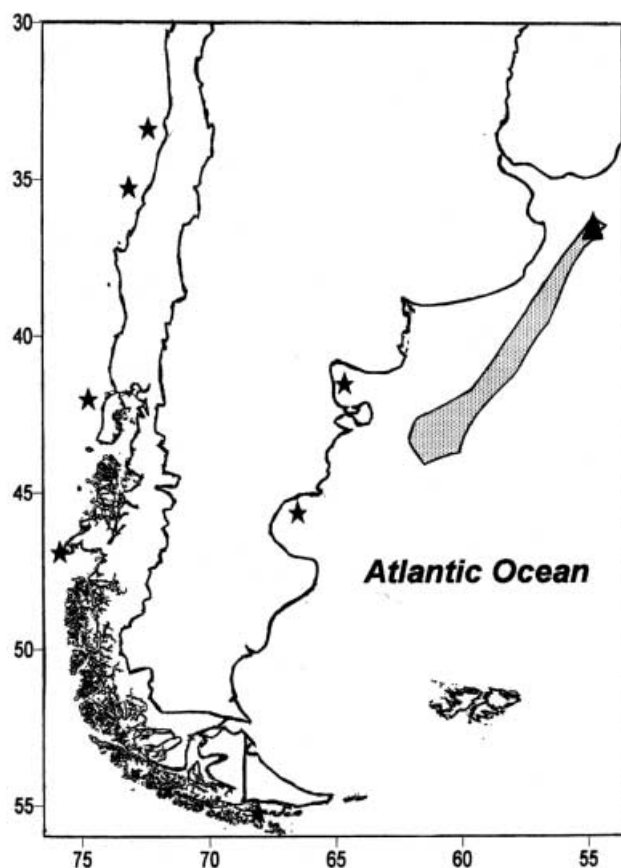


Figure 1. *Libidoclaea granaria*. Geographical distribution. ★ represent localities where adults or larvae of this crab were collected (Garth, 1958; Bacardit & Vera 1986; Boschi et al., 1992; Vinuesa et al., 1999). The shaded area illustrates the region where *Zygochlamys patagonica* beds were explored and crabs were collected; the ▲ indicates the area with the higher densities of crabs (100–150 crabs 100 m⁻²).

this terminal moult, the crab enters a so called ‘terminal anecydysis’. The puberty moult may, or may not, be the terminal moult: in spider crabs both moults ‘are one and the same’ (Hartnoll, 2001). Three life history phases have been described in males and females of various majoid species; these phases are separated by two or one ‘critical moults’; Sampedro et al. (1999) thoroughly reviewed the various terminologies used to designate phases and critical moults.

Spider crabs ‘are notable for their habit of decorating or masking themselves by placing bits of foreign substances on their backs and appendages’ (Rathbun, 1925). Algae, sponges, hydroids, alcyonarians, tunicates and other adventitious materials are held in place by the hooked setae that characterize many majoid species (Rathbun, 1925; Hartnoll, 1993). Moreover, other sessile epibionts, such as cirripeds, bivalves and polychaetes, use majid carapaces as a substrate for settlement. Finally, mobile organisms, such as amphipods, may live in this community. The slow movements, the absence of burying behaviour, and the terminal anecydysis contribute to the establishment of a complex and abundant epibiota on many spider crabs (Hartnoll, 1993).

The population biology and life history of *L. granaria* have not been studied yet. The present contribution aims to describe and quantify the morphometric changes that

take place during the ontogeny of this species, to describe its growth phases, to estimate the size-at-maturity and fecundity, and to characterize its epibiotic fauna.

MATERIALS AND METHODS

Libidoclaea granaria was collected on *Zygochlamys patagonica* (the Patagonian scallop) beds in March 2001. Crabs were part of the by-catch of the scallop fishery, and were collected between 36° and 39°40’S by the RV ‘Capitán Cánepa’ (Instituto Nacional de Investigación y Desarrollo Pesquero, Argentina) during the 2001 research cruise (Figure 1). Samples (N=120) were obtained from 80 to 128 m depth with a non-selective rectangular dredge (2.5 m mouth opening, 25 mm mesh size in the top net, 35 mm in the bottom net). Crabs were separated and counted on board; density (crabs 100 m⁻²) was calculated referring to the estimated number of crabs in the haul over the swept area. The swept area of each haul (mean area=2550 m²) was estimated using the time of the haul (10 min), the velocity of the vessel (mean velocity=3.32 knots), the width (2.5 m) and the efficiency of the dredge. The efficiency of the dredge for the Patagonian scallop fishery beds (~100 m depth) was 43% (Valero, 2002). The mean density (MD), its standard deviation (SD) and the coefficient of dispersion (CD=SD²/MD), were calculated in order to test for the type of spatial pattern; the distribution is regular if CD<<1, random if CD≈1, and aggregated if CD>>1. All the specimens from four dense samples (nos. 1: 36°52’S 54°19’W, 128 m depth; 2: 36°53’S 54°22’W, 121 m depth; 3: 36°44’S 54°14’W, 120 m depth; 4: 36°48’S 54°15’W, 124 m depth; Figure 1) were frozen on board and finally preserved in 5% formaldehyde solution in the laboratory.

Crabs from these four samples (N=266) were sexed, assigned to two categories (immature and mature) on the basis of the presence of spermatophores in the gonads (males), the abdomen morphology and the presence of eggs (females) and measured. The pleon of immature females is flat and does not reach the pereopod coxa; the pleon of mature females is domed and extends to the base of the coxae.

The following variables were measured in the laboratory to the nearest 0.1 mm using a Vernier caliper and a binocular microscope when necessary: carapace length, from the rostrum base to the posterior spine base, (CL); carapace width, between the bases of lateral spines, (CW); rostrum length (RL); lateral (LSL) and posterior (PSL) carapace spine length; pleon length (PL) and width at the broadest point (PW); cheliped length (CHL) and height (CHH); male gonopod length (GL); and merus length of the third walking leg (ML) (Figure 2). In addition, we counted the number of eggs of 14 ovigerous females.

The median size-values among samples 1–4 were compared with a Kruskal–Wallis analysis of variance (ANOVA) on ranks test. Quantitative relationships between morphometric data were described with least-square regressions (after Kolmogorov–Smirnov tests for normal distribution). The carapace width was chosen as the reference dimension for size in most relationships. Log–log regression slope values (b) between 0.9 and 1.1 were considered indicative of isometry (‘conservative definition’; Clayton, 1990: 285). Slopes and intercepts of

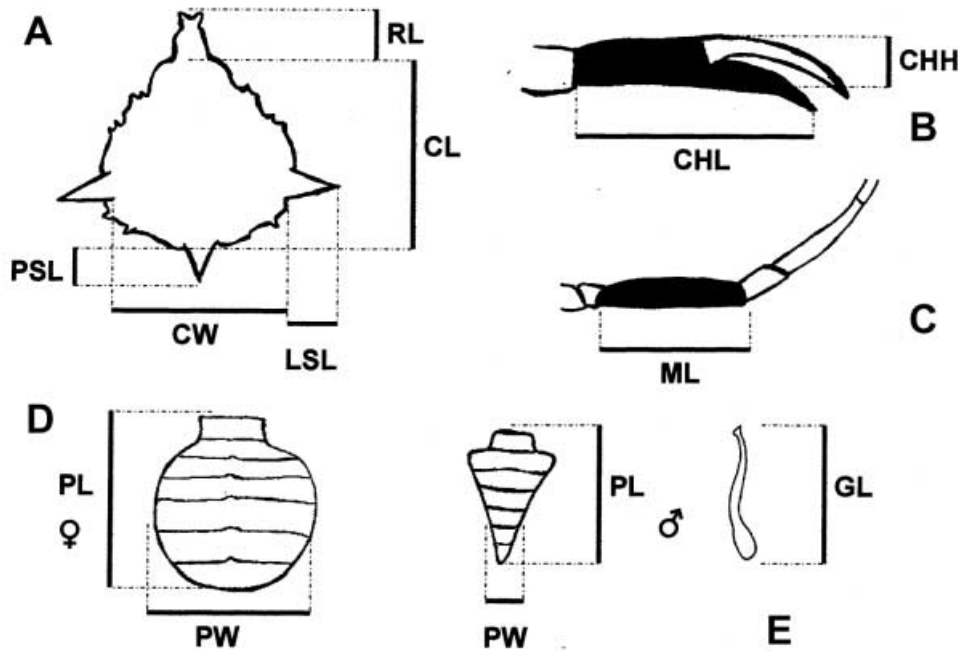


Figure 2. *Libinia granaria*. Diagrams of (A) carapace; (B) cheliped; (C) third walking leg; (D) female abdomen; and (E) male abdomen and gonopod, showing the various morphometric features measured. CL, carapace length; CW, carapace width; RL, rostrum length; LSL and PSL, lateral and posterior carapace spine length; PL and PW, pleon length and width; CHL and CHH, cheliped length and height; GL, gonopod length; ML, merus length.

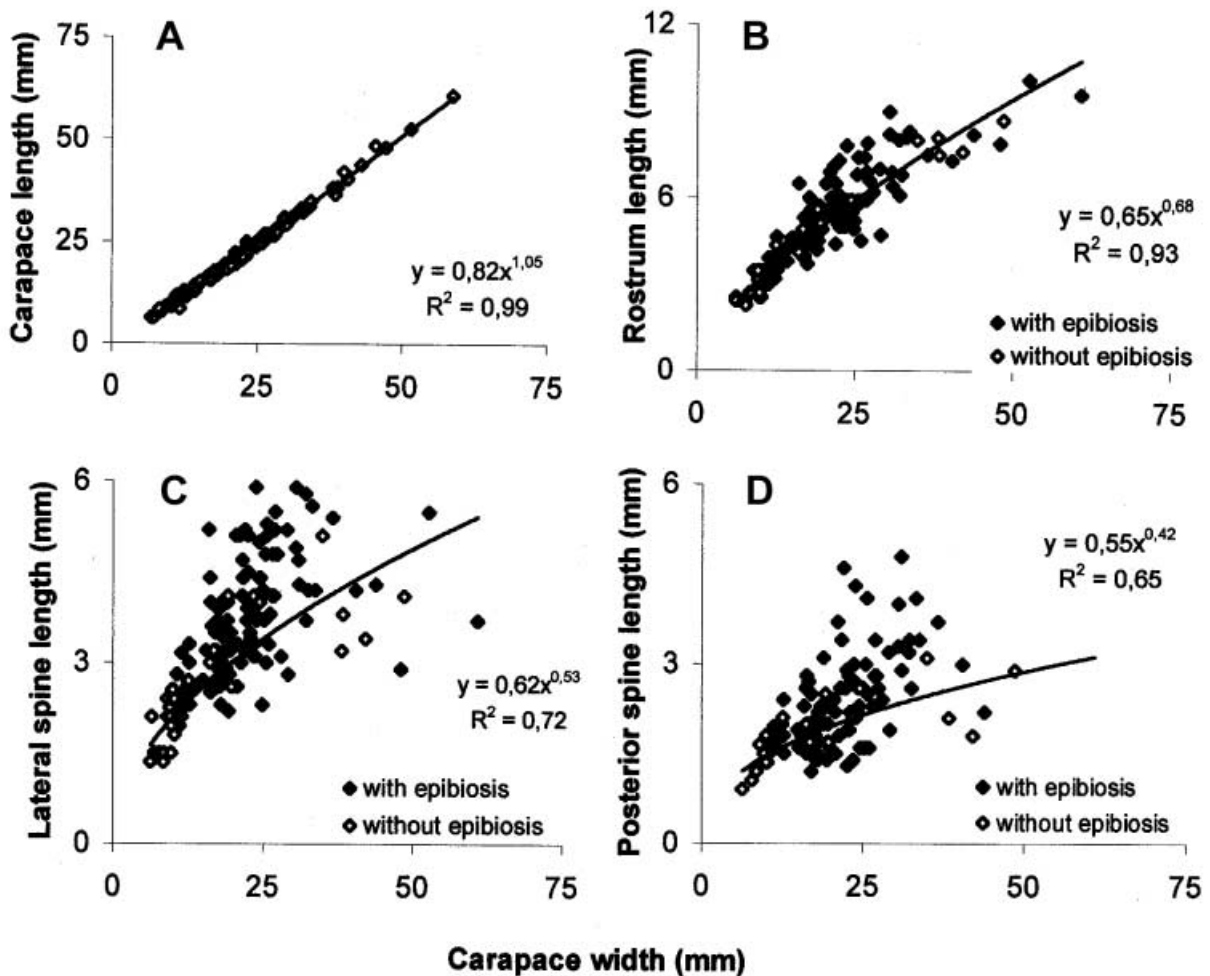


Figure 3. *Libinia granaria*. Relationships between carapace width and (A) carapace length; (B) rostrum length; (C) lateral spine length; and (D) posterior spine length. The regression lines in B, C and D were calculated using only crabs without epibiosis.

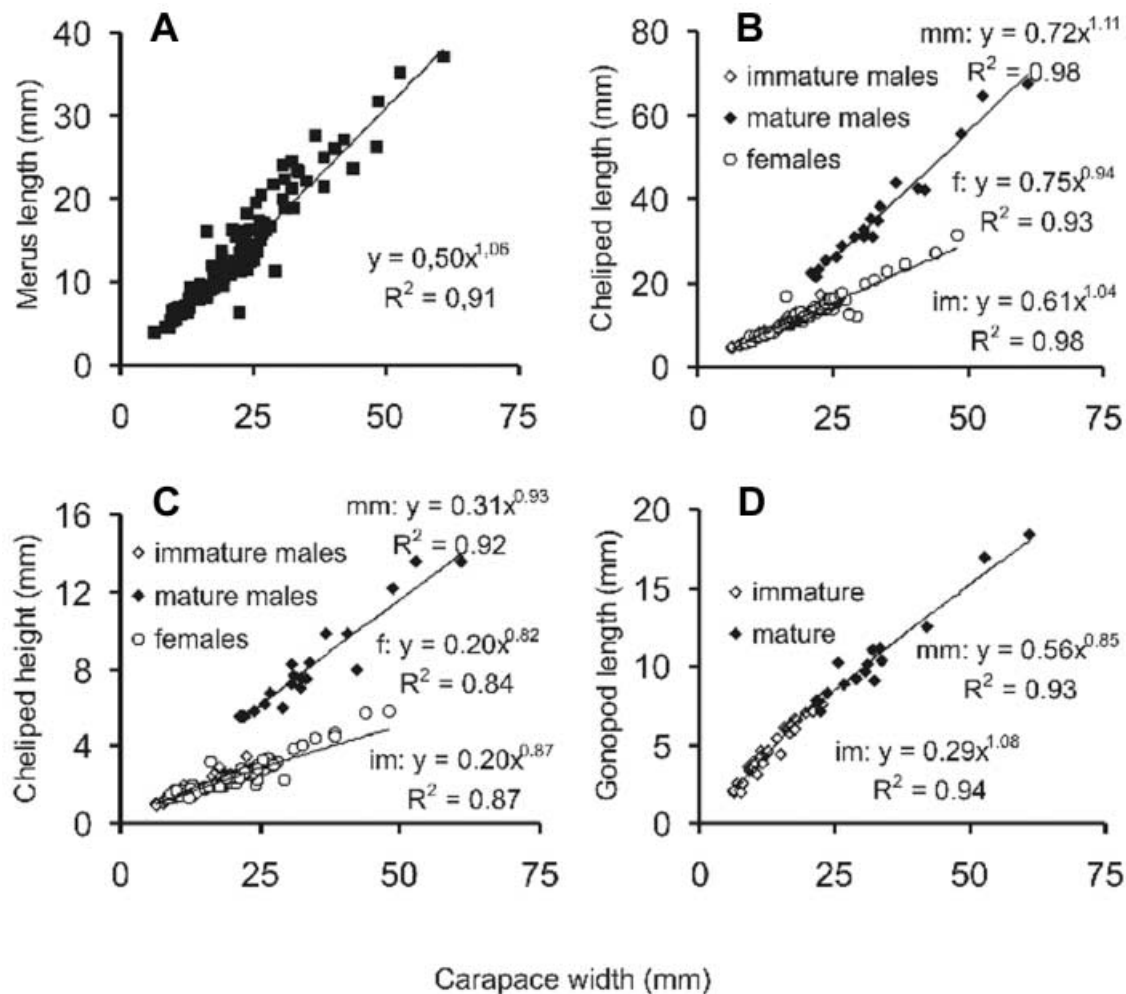


Figure 4. *Libidoclaea granaria*. Relationships between carapace width and length of the merus of (A) the third limb; (B) chela length; (C) chela height; and (D) male gonopod length. The regression lines in B and C correspond to immature and mature males (im, mm, respectively) and females (f), the regression lines in (D) correspond to immature and mature males.

different regression lines were compared with an analysis of covariance (ANCOVA). Differences were considered statistically significant when $P < 0.05$. The relative size at female sexual maturity (CW at which 50% of the females are mature) was estimated using logistic regression. The logistic equation $y = A(e^{-k(x-i)} + 1)^{-1}$, where A is the asymptotic value, k is a constant and i is the midpoint, was fitted to the data with a non-linear least-squares procedure using a Microsoft Excel Solver macro-complement. The 95% confidence intervals for the three parameters were calculated with a Bootstrap iteration method (macro-complement for Microsoft Excel).

Epibiont organisms were identified to the lowest possible taxonomic level and recorded in all the organisms found in the four high-density samples. The relationships between epibiosis, size and sex were analysed using the Mann-Whitney test or the χ^2 -test. When the power of all the statistical tests is below the desired power of 0.800, negative findings should be interpreted cautiously.

RESULTS

Densities of *Libidoclaea granaria* specimens on *Zygochlamys patagonica* beds ranged from 0 to 150 individuals 100 m^{-2} , with a mean (\pm SD) of 9.8 ± 20.4 individuals 100 m^{-2}

($N=120$). The coefficient of dispersion was $\gg 1$ ($CD=42.57$), indicating a patchy distribution. Males in samples 1 to 4 ($N=101$) ranged from 6.3 to 60.9 mm carapace width (CW), females ($N=165$) from 6.3 to 48.1 mm CW. The differences in the median size values among these samples were statistically significant in both sexes (Kruskal-Wallis ANOVA on ranks: females, $P < 0.0001$; males, $P = 0.00273$). One large male (CW=36.6 mm) with an internal carapace, indicating a premoult stage, was found. The sex ratio (samples 1 to 4 pooled) was 1.6 males:1 female, and differed significantly from the expected 1:1 ratio ($\chi^2=7.33$, $P=0.007$).

The morphological changes of the carapace during the ontogeny were described by the potential relationships between CW and carapace length (CL), rostrum length (RL), lateral spine length (LSL) and posterior spine length (PSL) (Figure 3); all regressions were significant (ANOVA, $P < 0.001$). Male and female data were pooled since their respective slopes did not differ significantly (ANCOVA, $P > 0.05$, data not shown). The CL was isometric to CW; the other three variables were negative allometric to CW. The coefficient of determination of these relationships decreased as follows, $CL > RL > LSL > PSL$ (Figure 3), even if the effect of erosion of rostrum and spine extremes was removed using only crabs

Table 1. *Libinia granaria* H. Milne-Edwards & Lucas, 1842. Statistical comparison (ANCOVA) of allometric relationships between sexes and phases of the life history.

Trait	Source of variation	N	Slope F-ratio	P	Intercept F-ratio	P
Cheliped length (Figure 4B)	Size	53	1771.63	***	1906.824	***
	Sex, phase (males, I×M)		1.002	n.s.	213.031	***
	Interaction		2.265	n.s.		
	Size	125	1603.135	***	1921.269	***
	Sex, phase (males I×females)		2.261	n.s.	8.335	**
	Interaction		3.829	n.s.		
	Size	114	946.815	***	1558.355	***
	Sex, phase (males M×females)		0.024	n.s.	570.007	***
	Interaction		0.009	n.s.		
Cheliped height (Figure 4C)	Size	53	356.825	***	398.834	***
	Sex, phase (males I×M)		2.201	n.s.	160.943	***
	Interaction		0.418	n.s.		
	Size	125	544.536	***	646.158	***
	Sex, phase (males I×females)		0.039	n.s.	10.177	**
	Interaction		0.443	n.s.		
	Size	114	356.373	***	634.828	***
	Sex, phase (males M×females)		1.708	n.s.	623.741	***
	Interaction		1.400	n.s.		
Gonopod length (Figure 4D)	Size	55	515.392	***		
	Sex, phase (males, I×M)		5.661	n.s.		
	Interaction		7.463	**		
Pleon width (Figure 5A)	Size	103	549.036	***		
	Sex, phase (females I×M)		71.499	***		
	Interaction		34.978	***		
Pleon length (Figure 5B)	Size	93	451.203	***	436.193	***
	Sex, phase (females I×M)		13.899	***	209.829	***
	Interaction		4.209	n.s.		

I, immature; M, mature (Figures 4 & 5); *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; n.s., not statistically significant; $P > 0.05$.

free of epibionts (i.e. recently moulted) for RL, LSL and PSL regressions. Merus length also was isometric to CW (Figure 4A, ANOVA, $P < 0.001$).

The relative size of male chelae differed markedly between immature and mature *L. granaria*. Although the cheliped length (CHL) was isometric to CW in immature males, mature males and females (Figure 4B), the cheliped height (CHH) was negatively allometric to CW in immature males and females, and isometric in mature males (Figure 4C). The differences in slope observed between sexes, and between immature and mature crabs, during chelae ontogeny were non-significant, whereas the differences in y-intercept were always significant (Table 1). The gonopod length was isometric to CW in immature males and positively allometric in mature males; both phases differed significantly in slope (Figure 4D, Table 1). The largest immature male measured 22.5 mm CW, and the smallest mature male measured 21.1 mm CW.

The growth of pleon width and length (PW and PL) was isometric with respect to CW in males and negatively allometric in immature and mature females (Figure 5A,B). The slopes of the regression lines differed significantly when the PW–CW relationship was compared between immature and mature females (Table 1). Although the slopes of the PL–CW relationships did not differ between female phases, differences in y-intercept were significant (Table 1).

The largest immature female measured 22.6 mm CW, and the smallest mature female measured 15.9 mm CW. The size at which 50% of the females were mature was 17.82 ± 1.35 mm CW (Figure 5C), the 95% confidence interval of this estimate was 16.54 to 19.45 mm CW. The mean values, standard deviations and 95% confidence intervals of the estimates of parameters A and k were the following: $A = 98.01 \pm 2.82$ (90.45–100) and $k = 5.88 \pm 0.46$ (4.46–6.12). The number of eggs carried by the females ranged from 1200 to 9300.

The frequency of encrusted carapaces was high: 46.6% of collected crabs in samples 1 to 4 carried at least one species of epibiont. Crabs with epibionts were significantly larger than those without epibionts (Mann–Whitney test, $P < 0.001$). Although the proportion of crabs without epibionts decreased with increasing size, some large crabs had a bare carapace (Figure 5D). Sponges were the most frequent epibiont (95.2%), followed by the lepadomorph cirriped *Ornatoscalpellum gibberum* (13.7%), and Polychaeta Serpulidae (8.9%) and Spirorbidae (5.7%). Less represented epibionts were hydrozoan polyps (2.4%), colonies of tunicates and bryozoans (2.4%), small specimens of the bivalve *Hiatella solida* (0.8%), nematoda (0.8%) and amphipods (1.6%). The surface of carapace covered by sponges was highly variable. *Ornatoscalpellum gibberum* ranged in number from 1 to 6 adults and up to 15 small, sometimes recently settled, individuals on a single carapace. The carapaces of *L. granaria* carrying *O. gibberum*

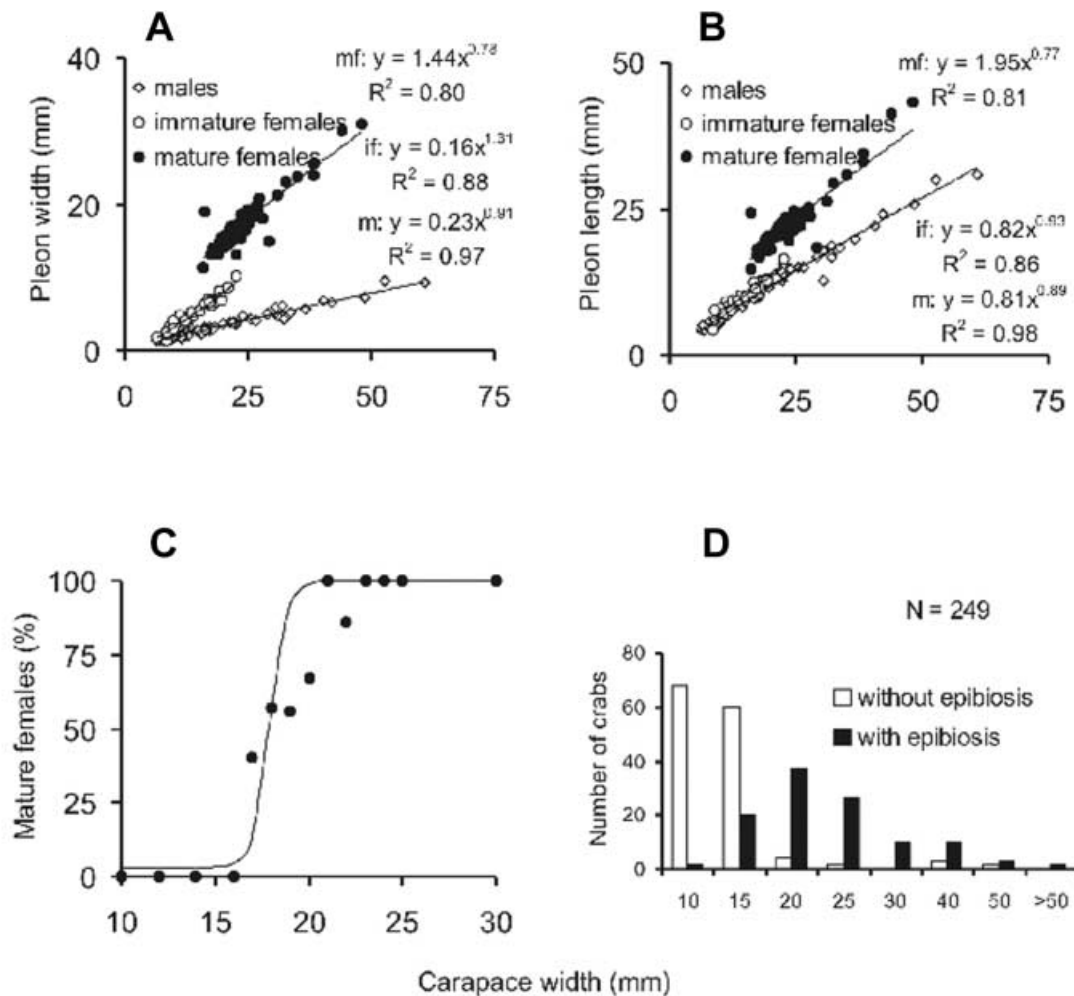


Figure 5. *Libido-claea granaria*. Relationships between carapace width and (A) pleon width and (B) pleon length; the regression lines correspond to immature and mature females (if, mf, respectively). (C) Female size at maturity; the logistic equation fitted to data was $y = 98.01(e^{-5.88(x-17.82)} + 1)^{-1}$. (D) Size-frequency distributions of crabs with and without epibiosis.

were significantly wider than those of crabs with other epibionts exclusive of the cirriped (Mann-Whitney test, $P < 0.001$). The proportion of sexes of crabs with and without epibionts did not vary significantly ($\chi^2 = 1.35$, $P = 0.246$, although the power of the performed test was low at 0.198).

DISCUSSION

The puberty moult of spider crabs generally occurs over a wide size-range, even in single populations of a species, in a limited area and over a short period (Hartnoll et al., 1993). Consequently, the size of mature crabs is highly variable. The studied population of *Libido-claea granaria* did not differ from the pattern expected for spider crabs. The size of mature males ranged from 24 to 61 mm CW. Males larger than 24 mm CW always had sperm in their ducts. Their chelae length and height were relatively larger, and the second gonopod length was relatively shorter, than in immature individuals. Mature and immature males could be distinguished by morphometric characters (Figure 5). The size of mature females ranged from 16 to 48 mm CW. However, we found large immature females, ranging from

16 to 22.5 mm CW. We do not find evidence of a prepubertal moult and a third growth phase in *L. granaria*, as was reported in other majids but this may be due to the relatively small sample sizes. The existence of a terminal anecydysis in *L. granaria* is suggested by erosion of lateral and posterior spines of many specimens > 24 mm CW and by the development of an epibiotic community on the carapace (see below).

The largest mature *Libido-claea granaria* measured during this study were 2.7 and 2.1 times wider than the largest immature crab, for males and females, respectively. These figures correspond to a size increment of $\sim 170\%$ or $\sim 112\%$, respectively, that was never observed in a single moult of a large, close to maturity, crab. Consequently, the largest immature crabs present in the population at the time of sampling cannot account for the largest mature crabs. It is possible that larger immature *Libido-claea granaria* were not found in our samples because they occur only at another time in the year or in other places. Alternatively, the puberty moult may not necessarily be the last moult in all specimens of all spider crab species, as Dawe et al. (1991) suggested. For example, a large *L. granaria* male in pre-moult stage was observed in our samples.

The fecundity of majoid species ranges from 180 (Hines, 1982) to 4,000,000 eggs per female (Haynes et al., 1976), and the carapace width (CW) of mature females ranges from 5 (Hines, 1982) to 400 mm (Haynes et al., 1976). The number of eggs carried by a female of *Libidoclaea granaria* ranged from 1200 to 9300, and agreed with the expected fecundity of a relatively small spider crab (20 to 40 mm CW).

The epizoic community of spider crabs functions primarily as camouflage (Hartnoll, 1993). Immature spider crabs usually carry material adhering to peculiar hooked setae, but post-puberty crabs also have epibionts attached to the tegument, reflecting the permanency of the substrata (Hartnoll, 1993). Our samples of *Libidoclaea granaria* were collected on beds of the scallop *Zygochlamys patagonica*. All the organisms found on *L. granaria* carapaces were also reported as common epibionts of *Z. patagonica* (Bremec & Lasta, 2002), allowing crabs to have the same appearance as their environment. Small crabs (<15 mm CW) usually had naked carapaces, indicating a high moult frequency. Larger crabs instead, had epibionts on their carapaces, suggesting a terminal anecydysis or, at least, a reduced moult frequency. Moreover, only larger crabs were colonized by *Ornatoscapellum gibberum*.

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