Molt and growth of an estuarine crab, *Chasmagnathus granulatus* (Brachyura: Varunidae), in Mar Chiquita coastal lagoon, Argentina

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Summary

Juvenile and adult growth of *Chasmagnathus granulatus* was studied in the laboratory in terms of molt increment in size (MI) and the intermolt period (IP), comparing data obtained from short-term (STE) and long-term (LTE) laboratory experiments. Crabs in a pre-molt condition were collected for STE, including the entire size range of the species. Larger crabs remained in the laboratory no more than 14 days; the average time to molt was 5.8 ± 3.1 days. We registered the molt of 94 females, 64 males and 34 undifferentiated juveniles and calculated their MI. Moreover, 24 males and four females were reared in the laboratory over 3 years (LTE). Hiatt diagrams did not show sex-specific differences between juveniles of both sexes, but revealed differences between juveniles and adults in each sex as well as between adults of both sexes. The MI decreased gradually with size; this pattern was described with a quadratic model. The IP increased exponentially with size. The presence of regenerating limbs diminished the MI. The abdomen of females reached its final shape and maximum relative width at functional maturity. Growth curves for both sexes were calculated using the von Bertalanffy model, but this model yielded an underestimation of the actual maximum size of this crab.

Introduction

Growth of crustaceans appears to be a discontinuous process, as the hard exoskeleton is periodically replaced in successive molts. Each ecdysis is followed by a post-molt uptake of water and, as consequence, a rapid increase in body size during the short soft-skinned period (Hartnoll, 1982). The study of crustacean growth considers both absolute and relative growth (Kurata, 1962). Models of absolute growth in crab and crab-like species were mostly based on size increments at molt and duration of the intermolt period (IP) in laboratory-reared juvenile crabs (Botsford, 1985). In the field, absolute growth of crabs was estimated indirectly from the analysis of the size-frequency distributions, in enclosure studies, or in tag recovery surveys (see Appendix 1). In a recent review, Hartnoll (2001) showed that temperature and food are the two most important external factors influencing growth under laboratory conditions, and both vary spatially and temporally also in the field.

The relationship between post-molt and pre-molt size (Hiatt diagram) has frequently been used to estimate the average molt increment in size (MI) and the number of molts necessary to reach a given size (Hiatt, 1948). The relationship between the MI and pre-molt size was generally fitted with a linear or a log-linear model (Mauchline, 1977). However, the results are highly variable and the coefficient of determination (R^2) is often low (Tweedale et al., 1993; Gonzáles-Gurriaran et al., 1995; Lovrich and Vinuesa, 1995; Chen and Kennelly, 1999), but not always (Diesel and Horst, 1995).

The MI and IP may be affected by the artificial conditions prevailing during long-term laboratory cultivation (Hartnoll, 1982). In the present study, we thus distinguish between data obtained from short-term and long-term rearing experiments (STE and LTE, respectively). From 56 papers dealing with MI and IP (see Appendix 1), 30 were based on LTE and 10 on STE laboratory experiments (the latter measuring MI in crabs molting within a few days after capture); six of the latter covered the entire size range of the species (Hiatt, 1948; Kurata, 1962; Donaldson et al., 1981; Hines, 1989; McDermott, 1999). As further potentially confounding factors, limb autotomy and regeneration affected MI and IP (Hiatt, 1948; Spivak and Politis, 1989; Smith, 1990).

The pattern of relative growth of male chelae and female abdomen changes between immature and mature crabs (Hartnoll, 1974), thus allowing for the detection of morphometric maturity. Morphometric maturity is usually reached at a specific molt, named 'puberty molt' (Hartnoll, 1982). Moreover, the analysis of chelae and abdomen allometry has revealed three distinct developmental stages, both in males and females, in at least several spider crabs (Majoidea) (Sainte-Marie et al., 1995; Alunno-Bruscia and Sainte-Marie, 1998). These stages have received different names (reviewed by Sampedro et al., 1999). However, crabs can only successfully mate when their gonads are mature (gonadal maturity) and when they can display specific behaviours such as male combat, courtship and copulation (functional maturity) (Sampedro et al., 1999). Hence, maturity may be considered as a long process rather than a precise moment. Morphometrical, gonadal and functional maturity are not always synchronized, and each step may be achieved at a different molt (for a review see López-Greco and Rodríguez, 1999a). Morphometric maturity was studied in many crab species on the basis of field-collected samples (for a review see Fernández-Vergaz et al., 2000); whereas laboratory rearing of juveniles was less often used to study morphometric changes associated with maturity (Gonzáles-Gurriaran et al., 1995).

The intertidal zone of Mar Chiquita, Argentina, the southernmost in a series of brackish coastal lagoons extending along the coasts of southern Brazil, Uruguay and northeastern Argentina, is commonly inhabited by a grapsid crab, *Chasmagnathus granulatus* (Dana 1851). It is considered as a

key species in 'cangrejal' saltmarsh ecosystems (from Spanish, cangrejo = crab, Olivier et al., 1972; Spivak et al., 1994), where it digs semipermanent burrows in mudflats and *Spartina densiflora* grasslands (Boschi, 1964; Spivak et al., 1994; Iribarne et al., 1997). Juveniles live near conspecific adults in separate burrows, but usually juvenile and adult burrows are interconnected (Spivak et al., 1994; Luppi, 1999). Long-term laboratory rearing of crabs allowed for the estimation of MI and IP of *C. granulatus* juveniles (Rieger and Nakagawa, 1995; López and Rodríguez, 1998; Luppi et al., 2001) and adults (López-Greco and Rodríguez, 1999a). Absolute and relative growth of juveniles, as well as limb autotomy was studied in the field (Gavio et al., 1994; Ruffino et al., 1994; Luppi and Spivak, 1996; Luppi et al., 2001). López-Greco and Rodríguez (1999b) showed discrepancies between the size of morphometric, gonadal and functional maturity of this species. Despite all available information on the life history of this species, effects of long-term laboratory rearing, environmental conditions, sex and limb regeneration, on growth rates have not been evaluated, so that realistic estimates of its actual growth in the natural habitat are still not available.

In the present study, we estimated size increments at molt to adult size of *C. granulatus* in Mar Chiquita coastal lagoon, Argentina and the number of molts necessary to reach the size at morphometrical maturity. Short-term rearing experiment are compared with data obtained from individual crabs that lived in the laboratory for up to 3 years, and growth is compared between sexes, and in relation to limb regeneration.

Materials and methods

The study area

The Mar Chiquita coastal lagoon is located between 37°32′–37°45′S and 57°19′–57°26′W, 35 km NE of the city of Mar del Plata, Argentina. It covers an area of 46 km^2, a maximum depth of approximately 1.2 m at low tide (Fasano et al., 1982) and is divided into a wide northern and a narrow southern part. Water temperature and salinity show strong seasonal, daily and local variations (Anger et al., 1994; Reta et al., 2001). Semidiurnal tides (amplitude < 1 m) superimposed by variable, often strong wind stress cause an irregular pattern of influx and outflux, which is hampered by a sandbar at the entrance of the lagoon (Anger et al., 1994; Reta et al., 2001). Intertidal environments in the lagoon comprise mud flats and large surrounding cordgrass (*S. densiflora*) areas (Olivier et al., 1972; Iribarne et al., 1997).

Collection and rearing techniques

Short-term rearing experiment. Crabs representing the entire size range from 1.7 to 37 mm carapace maximum width (CW), of the species *C. granulatus* were collected in the southern part, near the mouth of the lagoon. During April 2000, late pre-molt crabs of *C. granulatus*, identified by a typical pale colour, were collected by hand from their burrows. This period was chosen because the molting frequency tends to increase at the end of the breeding season (López-Greco and Rodríguez, 1999b). Immediately after collection, the crabs were taken to the laboratory and the CW measured. They were then maintained individually in flasks with brackish water (23 psu), which represents the salinity usually found in the lagoon. The water was prepared by addition of freshwater to inshore seawater, both of which had been previously filtered (10 μm). The size of the flasks and the volume of water varied with crab size.

Undifferentiated crabs (< 4 mm CW, sex not recognized by external differences) were kept in 0.1 L, juveniles (< 15 mm CW) in 0.25 L, and adults in 1 L, containers. All crabs were kept in natural light and at ambient temperature. They were fed with *Artemia* sp. *nauplii* (undifferentiated and juveniles) or pellets for bottom fishes (adults). Food was added daily *ad libitum*, and water was changed every other day. To avoid effects of prolonged laboratory rearing, only crabs that molted within 2 (C1) to 14 days (adults) of arrival in the laboratory were used to measure MI. All individuals were checked daily for molting. The presence of regenerating chelipeds or pereiopods (injured crabs) was also registered. CW was measured in all crabs, and abdomen width (AW; 4th segment) only in females, before and after molting. Post-molt crabs were measured after their carapace hardened (12–48 h after molt). Measurements were taken using a stereomicroscope with an eyepiece micrometer (undifferentiated crabs) or a caliper (juveniles and adults) to the nearest 0.1 mm.

Long-term rearing experiment. Ovigerous *C. granulatus* were caught in Mar Chiquita in November 1991 and transported to the Helgoland Marine Biological Station (Germany) where they were maintained in local seawater (32–33 psu) at a constant 18°C, and a 12 : 12 h daylight : darkness regime until larvae hatched. Larvae and early juveniles were mass-reared under the same environmental conditions (see Anger and Ismael, 1997 for techniques of larval rearing). Twenty-eight first-stage crabs were subsequently reared individually from metamorphosis (9 January 1992) through the following 3 years. Early juveniles (< 5 mm) were fed daily with *A. nauplii*, larger specimens with pieces of isopods (*Idotea balthica*). The presence of exuviae was recorded daily. CW and length, and AW were measured in the exuviae using the same techniques as for field-caught examples (see above).

Growth models

The average size increment was estimated using the Hiatt model (Hiatt, 1948; Kurata, 1962). This describes growth as the linear equation,

$$L_{t+1} = aL_t + b$$

where, L_t is the pre-molt CW in stage t, L_{t+1} is post-molt CW in the following stage, a is the slope and b is the y-intercept of the regression line. Equations for undifferentiated, juveniles, males and females were calculated separately. The limit between immature juveniles and morphologically mature males corresponds to the size of gonadal maturation (15 mm CW) (Gavio et al., 1994). Females were considered as mature when they reached 17 mm CW, which is the size of the smallest ovigerous female found in Mar Chiquita (T. A. Luppi unpubl. data).

The regression model was used to fit the Hiatt model. Slopes and y-intercepts of regression lines were compared by means of ANCOVA (intercepts after removal of the interaction term, if slopes did not differ significantly, Zar, 1996). When slopes showed significant differences, the point of intersection for regression lines of immature and mature individuals was calculated following Comeau et al. (1998, p. 266):

$$I_{CW} = b_2 - b_1/a_1 - a_2$$

where, I_{CW} is the CW at the intersection point, b_1 and a_1 are the y-intercept and slope parameters of the first equation, b_2 and a_2 of second equation respectively. The intersection values calculated from STE data used afterwards to define the limits

between immature and mature individuals in the analysis of LTE data. The growth at molt or MI was expressed, (i) as a percentage size increment over pre-molt,

PSI = (post-molt CW − pre-molt CW)/pre-molt CW × 100

(ii) as absolute size increment at molt,

SIM = post-molt CW − pre-molt CW

The relationships between growth at molt and pre-molt CW were estimated by linear, log-linear or quadratic equations ($y = ax^2 + bx + c$), those between PSI and pre-molt CW in healthy or injured crabs (males and females pooled) with quadratic equations. The relationship between IP and pre-molt CW (LTE) were fitted with an exponential equation. The age at a given CW (LTE males and females) was described with the von Bertalanffy growth model,

$$\text{CW}_{(t)} = A[1 - (1/3e^{-k(t-j)} + 1)^{-1}]$$

where, A is the asymptotic value of CW, k is the growth constant, j is the age at CW $= 0$ and t is the time elapsed since metamorphosis.

The relationship between AW and pre-molt CW, was fitted with a logistic equation,

$$\text{AW}_{(\text{CW})} = A(e^{-k(\text{CW}-i)} + 1)^{-1}$$

where, A is the asymptotic value of AW, k is the growth constant and i is the midpoint or CW_{m}. Drawings of the abdomen of females in three developmental stages were made using a stereomicroscope with an attached *camera lucida*.

Quadratic, von Bertalanffy and logistic models were fitted to the data with a non-linear least-squares procedures using a Microsoft Excel Solver macro-complement. Differences in the parameters of the models between males and females, healthy and injured, and among different sources of data, were compared by means of 95% confidence intervals. These were calculated with a Bootstrap iteration method (macro-complements for Microsoft Excel).

Our results were compared with growth data obtained from undifferentiated, juvenile and adult crabs reared in the laboratory over long periods (Luppi et al., 2001; López and Rodríguez, 1998; López-Greco and Rodríguez, 1999b).

Results

General results

Crabs collected in the pre-molt stage of the molt cycle (STE) included 94 females (17 immature, 77 mature, i.e. >17 mm CW), 64 males (22 immature, 42 mature, i.e. >15 mm CW) and 34 undifferentiated juveniles; all of these were found in burrows. Maximum post-molt CW was 34.4 mm and 35 mm for males and females, respectively. The average time from collection to first molt in the laboratory was 5.8 ± 3.1 days, and the maximum rearing time was 14 days. Twenty-eight crabs (24 males, four females) were reared in the laboratory for 3 years (LTE). Most of them (n = 21) reached the 18–20th instars; the maximum CW reached was 27.8 and 26.6 mm for males and females, respectively.

Hiatt diagrams

STE. The relationship between pre-molt and post-molt CW (Hiatt diagrams) was calculated separately for undifferentiated crabs (Fig. 1a), immature and mature males (Fig. 1a) and immature and mature females (Fig. 1b). There were no significant differences in the slopes between undifferentiated and immature males, undifferentiated and immature females, and immature crabs of both sexes. In contrast, the slope of Hiatt lines of mature and immature males, and of mature and immature females differed significantly (ANCOVA, $F = 49.92$ and 79.22, respectively, $P < 0.001$). In addition, the slope parameter for mature females was significantly lower than that for mature males (ANCOVA, $F = 8.482$, $P = 0.004$). The lines of immature and mature crabs intersected at a size of 17.2 and 18 mm CW in males and females, respectively (Fig. 1a,b).

LTE. Hiatt diagram were again calculated for immature and mature males (Fig. 1c) and for immature and mature females
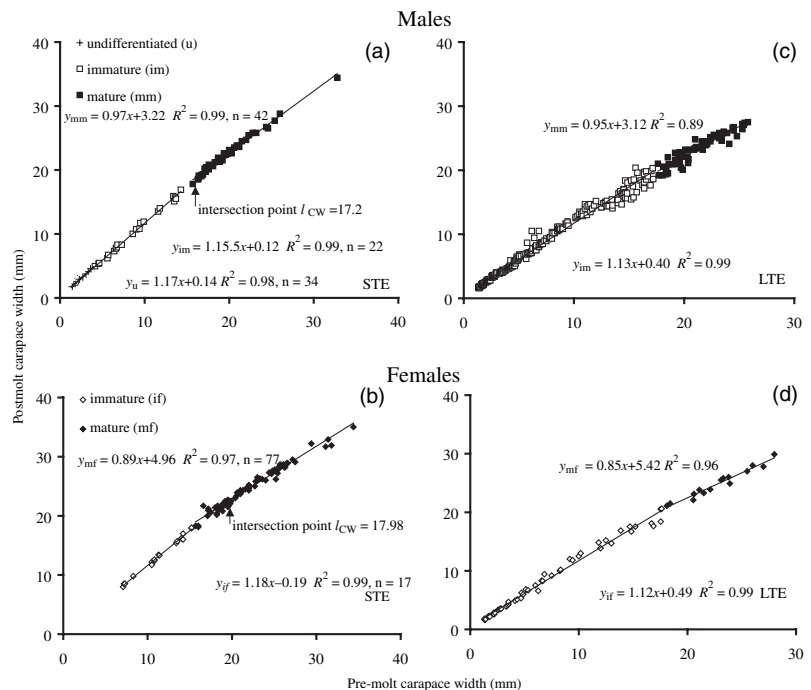

Fig. 1. *Chasmagnathus granulatus*: pre-molt and post-molt carapace width relationships (Hiatt growth models) estimated from short (<14 days, a, b) and long-term laboratory-reared crabs (approximately 3 years, c, d). (a) Undifferentiated, immature and mature males; (b) immature and mature females; (c) immature and mature males, (d) immature and mature females

(Fig. 1d). The slopes for mature and immature males and those for mature and immature females differed significantly (ANCOVA, $F = 25.0$ and 16.6, respectively, $P < 0.0001$). No significant differences were found between mature females and males, or between crabs in STE and LTE.

Molt increment

STE. Linear, log-linear and quadratic models were applied to the relationship between PSI or SIM and the pre-molt CW. The highest R^2 values were obtained with quadratic equations (Table 1); and this model was used for further analysis. Lines differed between sexes in both PSI and SIM (Fig. 2). The 95% confidence intervals of parameters a, b and c were different and did not overlap (Table 2). The CW with maximum PSI was 7.1 and 11.6 mm for males and females, respectively (Fig. 2a–c), while maximum SIM was 20.8 and 19.7 mm for males and females, respectively (Fig. 2b–d).

LTE. Linear models were applied to the relationship between PSI and pre-molt size in males and females (Fig. 3a,c respectively). Lines did not differ significantly in slope and y-intercept between sexes. Exponential equations were calculated for the relationship between the IP and CW (Fig. 3b,d). The slopes of equations for log-transformed data differed between sexes (ANCOVA, $F = 6.08$, $P < 0.05$).

Table 1

Chasmagnathus granulatus: relationship between percentage of size increment (PSI) or size increment at molt (SIM) and pre-molt carapace width, for males and females

	Males	Females
Linear model		
PSI	0.43	0.5
SIM	0.53	0.005
Log-linear model		
PSI	0.42	0.4
SIM	0.57	0.003
Quadratic model		
PSI	0.52	0.66
SIM	0.81	0.59

R^2 values of the models linear, log-linear and quadratic.

Effects of autotomy on growth

The PSI was compared between autotomized (injured) and complete (healthy) crabs that molted in the laboratory within a few days after collection (STE). PSI values of injured crabs tended to be lower along the entire size range (Fig. 4), but the differences compared with healthy crabs were statistically not significant, because of high confidence intervals for a, b and c, and fewer data for injured crabs (Table 2).

Female abdomen growth

STE. The morphometric relationship between AW and pre-molt CW (Fig. 5) was modelled with a simple logistic equation: $AW_{(CW)} = 23.3 \ (e^{-0.16(CW-19.3)} + 1)^{-1}$. The midpoint of the sigmoidal curve is $CW_m = 19.3$ mm, the constant is $k = 0.16$, and its limit AW is $A = 23.3$ mm. The AW grows from 10 to 90% of the limit value of A from 5.93 to 32.65 mm CW (Δ_{CW}).

The comparison of the AW in the same individuals before and after molting allowed us to establish four groups of females:

No. 1: The abdomen of eight immature females was narrow both before and after molting (Fig. 6a). The increment in AW (Δ_{AW}) varied from 8 to 36% (Fig. 7a).

No. 2: The abdomen of eight larger immature females was proportionally wider after molting, but not enough to reach the basis of the coxae (Fig. 6b). Six of these individuals had extraordinarily high Δ_{AW} values, varying from 40 to 80% (Fig. 7a); two others, with several autotomies, had lower Δ_{AW} values.

No. 3: The abdomen of 27 females reached its maximum relative width after molting (Fig. 6c). Before molting, the morphology of their abdomen was similar to that of post-molt no. 2 females (Fig. 6b). We considered these females as already sexually mature before molting, because one of us (T. A. Luppi, pers. comm.) observed a similar morphology in many ovigerous females in the field. The Δ_{AW} varied in this group from 15 to 40% (Fig. 7a).

No. 4: The abdomen of 28 females already reached before molting the basis of the coxae, and consequently, the maximum relative width (Fig. 6c). Their Δ_{AW} varied from 3 to 30% (Fig. 7a).
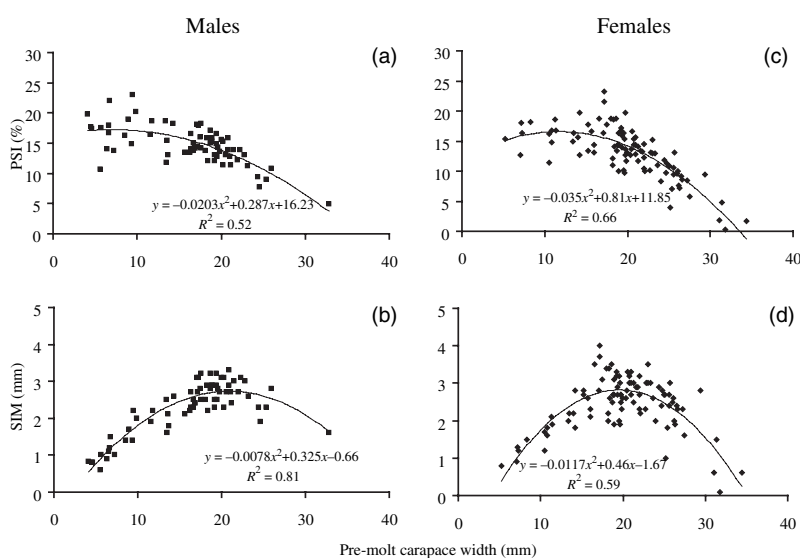

Fig. 2. *Chasmagnathus granulatus*: relationship between percentage of size increment at molt (PSI; a, c) or absolute size increment at molt (SIM; b, d) and pre-molt carapace width (CW) for males (a, b; n = 64) and females (c, d; n = 94) reared in the laboratory for a short period (see the 95% confidence limits of the a, b and c parameters of quadratic equations in Table 2)

Table 2

Chasmagnathus granulatus: relationships between percentage of size increment (PSI) or size increment at molt (SIM) and pre-molt carapace width, for males and females (Fig. 2); relationship between PSI and pre-molt carapace width, for healthy and injured crabs (Fig. 4)

	Male		Female	
	Upper limit	Lower limit	Upper limit	Lower limit
Percentage of size increment (PSI)				
a	−0.022	−0.019	−0.047	−0.025
b	0.293	0.280	1.252	0.452
c	16.22	16.21	15.15	7.73
Size increment at molt (SIM)				
a	−0.007	−0.008	−0.010	−0.014
b	0.336	0.314	0.542	0.391
c	−0.696	−0.629	−2.403	−1.159
	Healthy		Injured	
	Upper limit	Lower limit	Upper limit	Lower limit
Percentage of size increment (PSI)				
a	17.49	12.30	36.97	2.31
b	0.83	0.21	1.64	−1.59
c	−0.019	−0.036	0.017	−0.060

Confidence limits (95%) of the a, b and c parameters of quadratic equations ($y = ax^2 + bx + c$).

The relationship between pre-molt and post-molt AW was calculated separately for immature (nos 1–2) and mature (nos 3–4) females (Fig. 7b). There was a significant difference in the slope parameters obtained for immature and mature females (ANCOVA, $F = 74.5$, $P < 0, 0001$). An exponential equation (using data of groups 1, 2 and 3) related the Δ_{AW} and pre-molt CW (Fig. 7a).

LTE. The relationship between AW and pre-molt CW (Fig. 5) was also modelled with a logistic equation: $AW_{(CW)} = 19.7 (e^{-0.22(CW-16.5)} + 1)^{-1}$. Here, the fitted parameters of the sigmoidal curve are: $CW_m = 16.5$ mm, $k = 0.22$, $A = 19.7$ mm. The Δ_{CW} ranged from 6.7 to 26.4 mm. The regression lines differed significantly between the STE and LTE data, as the 95% confidence intervals for corresponding A, k and i values did not overlap (Table 3).
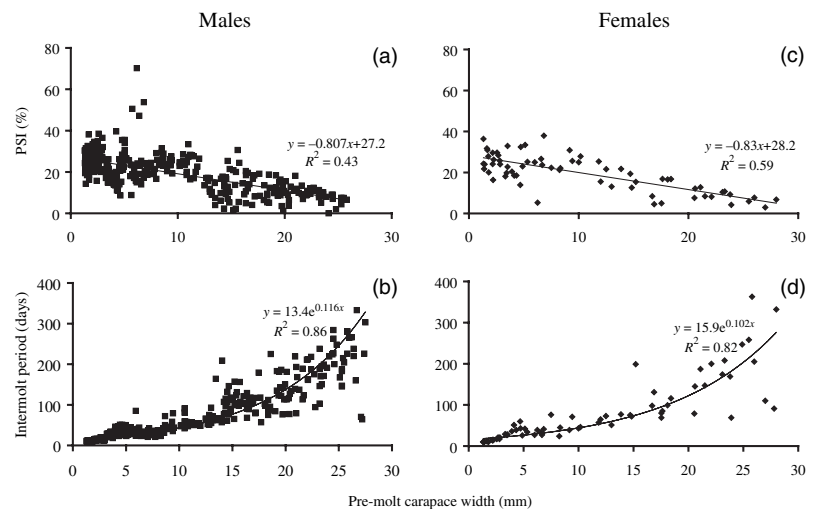
Number of molts and size increment

The Hiatt diagrams (Fig. 1) allow us to calculate the relationships between CW and instar number for STE crabs (Fig. 8). This model suggests that males and females molt 20 times before reaching adult size of 36 mm and 33 mm CW, respectively, corresponding to the largest modal classes of size-frequency distributions in field data (Luppi et al., 1997; Spivak et al., 1996). However, after molting 20 times in the laboratory (LTE), both sexes reached a smaller size (32 and 31 mm CW, respectively, Fig. 8) than those in STE. On the contrary, juvenile STE and LTE males and females reached this size at maturity after 12 or 13 molts.

Growth curves

The von Bertalanffy growth curves were calculated separately for LTE males and females (Fig. 9). The asymptotic values of CW were higher in females ($A = 34$ mm) than in males ($A = 31.7$ mm), but this difference was not significant; the 95% confidence intervals of A, k and j corresponding to females were wider and included the values of males (Table 3). This result is probably related to the small number of females available.

Discussion

Molt and growth

The growth of *C. granulatus* from two Argentine populations (Samborombón Bay and Mar Chiquita Lagoon) has been partially studied in the laboratory by López and Rodríguez (1998), López-Greco and Rodríguez (1999b) and Luppi et al. (2001), respectively. The equation of the Hiatt growth diagram for undifferentiated crabs reared in the later study was $L_{t+1} = 1.153 L_t + 0.27$. The slope of this line did not differ significantly from that obtained in the present investigation for undifferentiated STE crabs, but the *y*-intercept was different (n = 169, ANCOVA: $F_a = 0.098$, $P = 0.75$; $F_b = 3.39$, $P = 0.067$).

López and Rodríguez (1998) reared *C. granulatus* juveniles in the laboratory (initial CW approximately 12.5 mm). After four molts, males and females reached 18.8 and 19.95 mm CW, with molt increments (PSI) of 52.8 and 56.8%, respectively. On the basis of our Hiatt diagrams (Fig. 1), we estimated the corresponding PSI values as 78.2 and 88%, so that males

Fig. 3. *Chasmagnathus granulatus*: relationship between percentage of size increment at molt (PSI; a, c) or inter-molt period (b, d) and pre-molt carapace width (CW) for a group of males (a, b; n = 24) and females (c, d; n = 4) reared in the laboratory for 3 years
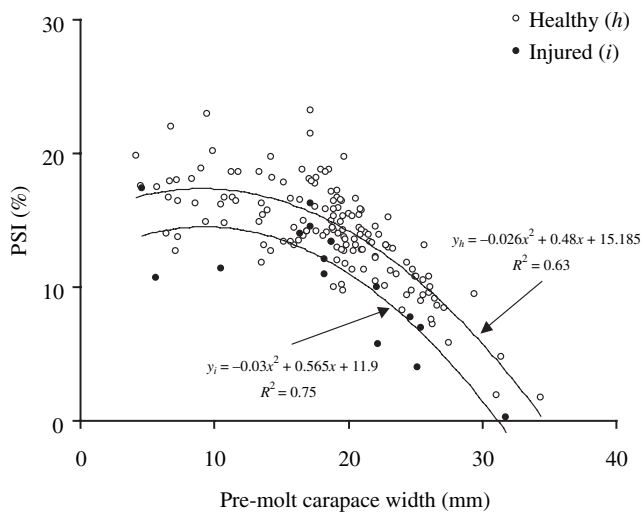
Fig. 4. *Chasmagnathus granulatus*: relationship between percentage of size increment at molt (PSI) and pre-molt carapace width (CW) for healthy (n = 149) and injured (n = 16) crabs reared in the laboratory for a short period, males and females pooled (see the 95% confidence limits of the a, b and c parameters of quadratic equations in Table 2)

$y_h = -0.026x^2 + 0.48x + 15.185$

$R^2 = 0.63$

$y_i = -0.03x^2 + 0.565x + 11.9$

$R^2 = 0.75$
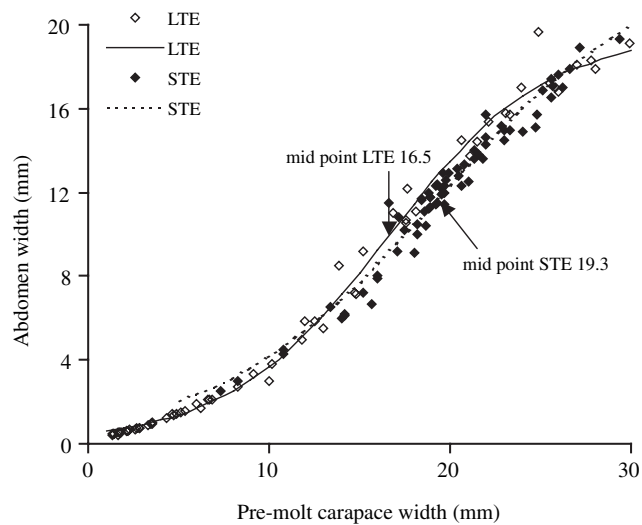

mid point LTE 16.5

mid point STE 19.3

Fig. 5. *Chasmagnathus granulatus*: relationship between abdomen width and pre-molt carapace width (CW) for females from short-term laboratory rearing (< 14 days, STE) and from long-term laboratory rearing (approximately 3 years, LTE), with a logistic model of growth superimposed (see the 95% confidence limits of the *A*, *k* and *i* parameters in Table 3)
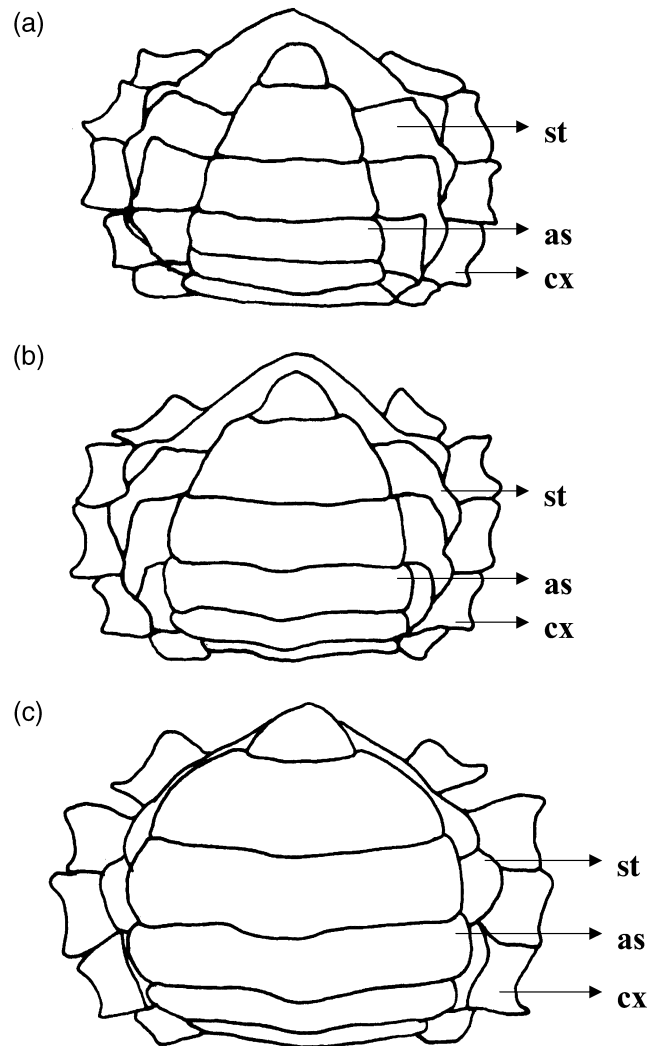

Fig. 6. *Chasmagnathus granulatus*: abdominal view of immature (a), and mature females (b, c). cx, coxae; st, sternite; as, abdominal segment. The abdomen was: (a) clearly narrow, (b) wide but without reaching the basis of the coxae, (c) wide, reaching the basis of the coxae

and females should have measured approximately 22.3 and 23.5 mm CW. The differences between these estimates from both STE and LTE crabs and the results obtained by López and Rodríguez (1998) and our estimates, ranged from 48 to 55%. On the contrary, López-Greco and Rodríguez (1999b) found in the laboratory that larger males and females (CW = 29.3 and 26.2 mm) had PSI values of 3.9 and 3.1%, respectively. In our study, the PSI of STE crabs with similar sizes was 7.1 and 8.8%, and 6.1 and 3.9% in LTE crabs (males and females respectively). Hence, our STE values were 83 and 185% higher than those calculated by López-Greco and Rodríguez (1999b), and they were 17.5 and 127.6% higher than our LTE values in males and females, respectively. These discrepancies can only to some extent be explained by regional

differences between populations. We suggest that the conditions of laboratory rearing may highly influence the size increments at ecdysis, and these artefacts may become stronger during long-term rearing experiments. On the contrary, all crabs used in STE were in advanced pre-molt and molted within a few days after their arrival in the laboratory. Consequently, we expected only a small effect of rearing conditions on their molt increment.

The average IP of juvenile (CW approximately 12.5 mm) *C. granulatus* in the laboratory was 57 days in Mar Chiquita crabs (LTE, Fig. 3) and approximately 100 days in Samborombón Bay crabs (López and Rodríguez, 1998). These differences could partially be explained by variation in life history traits of geographically distant populations and, more likely, with dissimilar-rearing conditions. Growth differences between grapsoid populations distributed along 10° of latitude were reported by Hines (1989). However, Mar Chiquita and Samborombón are only 150 km (approximately 1.4° of latitude) apart, suggesting that these populations may be genetically connected (E. D. Spivak, unpubl. data). On the other hand, the rearing techniques differed in temperature, salinity and food: López and Rodríguez (1998) maintained the crabs at 21°C and 12 psu (18°C and 34 psu in our study) and
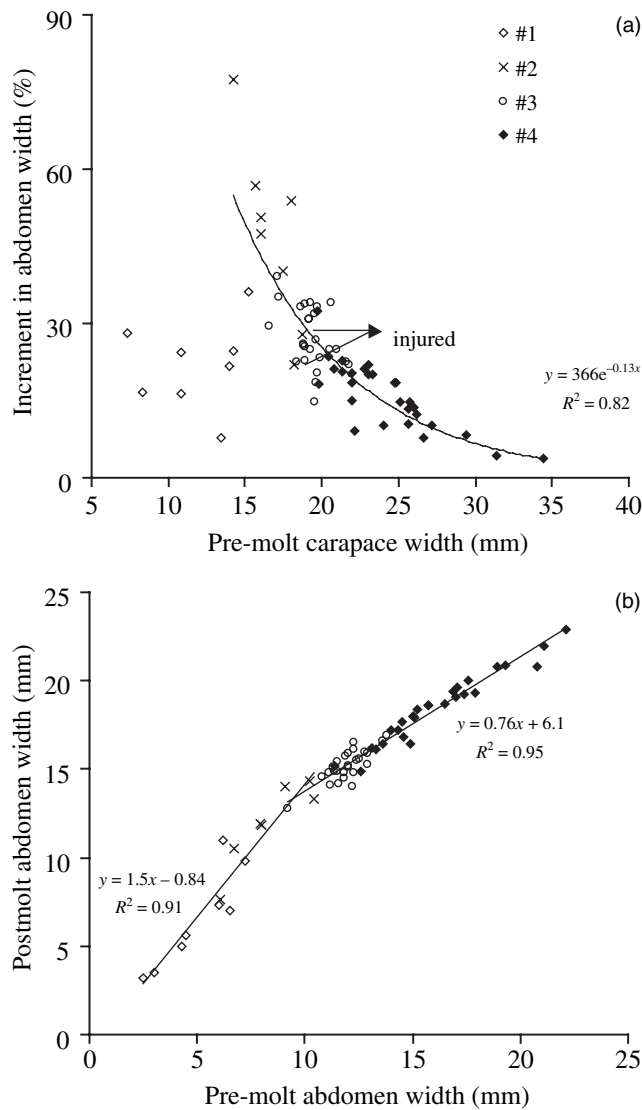
Fig. 7. *Chasmagnathus granulatus*: (a) relationship between percentage of increment in abdomen width at molt and pre-molt carapace width (CW) for four groups of females: no. 1, the abdomen was clearly narrow before and after molting (see Fig. 6a, n = 8); no. 2, the abdomen was clearly narrow before molting and wide after molting, but did not reach the basis of the coxae (see Fig. 6b, n = 8); no. 3, the abdomen reached the basis of the coxae after molting (see Fig. 6c, n = 27); no. 4, the abdomen had reached the basis of the coxae before molting (n = 28). The exponential equation was based on data from nos 2, 3 and 4, pooled. (b) Relationship between post- and pre-molt abdomen width for the same group of females. Linear equations were based on data from immature (nos 1 and 2) and mature (nos 3 and 4) females

Table 3
Chasmagnathus granulatus: relationships between abdomen width and pre-molt carapace width from long- and short-term rearing females (LTE, STE, Fig. 5) and between carapace width and rearing time from males and females (LTE, Fig. 9)

	STE		LTE	
	Upper limit	Lower limit	Upper limit	Lower limit
Logistic (abdomen growth)				
A	24	21	20.7	18.9
k	0.19	0.15	0.23	0.21
i	19.8	18.1	17.2	15.9
	Male		Female	
	Upper limit	Lower limit	Upper limit	Lower limit
von Bertalanffy (age-at-size growth)				
A	33	30.1	37.1	32.3
k	0.0016	0.0014	0.0016	0.0012
j	−24.3	−19.6	−23.2	−9.8

Confidence limits (95%) of the A, k, j and i parameters of logistic and von Bertalanffy models, respectively.
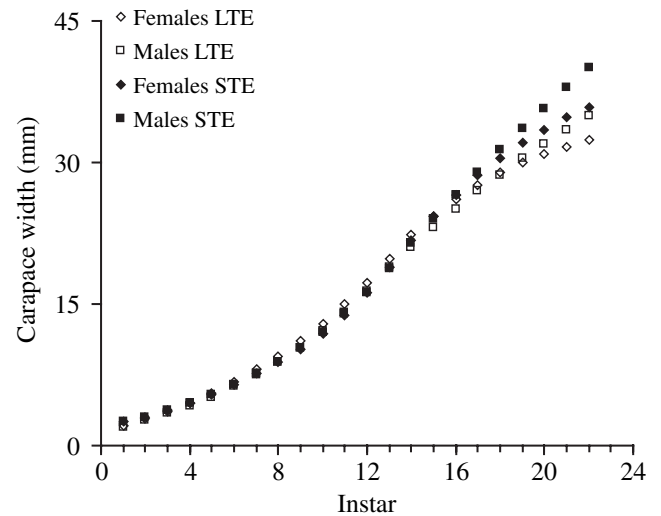

Fig. 8. *Chasmagnathus granulatus*: relationship between carapace width and the number of molts, constructed on the basis of Hiatt diagrams equations of short- (<14 days, STE) and long-term (approximately 3 years, LTE) laboratory-reared males and females

fed them with artificial pelleted rabbit food and cow liver twice a week (daily feeding with marine isopods in our study). While higher temperatures tend to shorten the IP of Crustacea (Hartnoll, 2001), the Samborombón crabs grew more slowly than those from Mar Chiquita Lagoon, despite the higher rearing temperature. On the contrary, smaller sizes and longer IPs were correlated with lower salinities in estuarine crabs reared in the laboratory (Spivak, 1999). Finally, a reduced or less suitable food supply lengthens the IP (Hartnoll, 2001). Differences in the quality and quantity of food should thus help to explain the differences in growth rates observed in these different studies.

As the methods of laboratory rearing affect growth, it may be difficult to extrapolate laboratory data to natural populations (Hartnoll, 1982, 2001). However, the significance of such artefacts may vary greatly among species. After comparing the results from laboratory observations and field enclosures with estimates from a field survey, Gonzáles-Gurriaran et al. (1995) concluded that laboratory rearing did not affect growth in *Maja squinado*.

The Mar Chiquita population of *C. granulatus* has been widely studied in the field (see Spivak et al., 2001 for recent review). The size structure of the adult crabs is usually characterized by the presence of two groups. The group formed by the large males and females averaged 36 and 33 mm CW, respectively (Spivak et al., 1996). However, crabs reared in the laboratory at constant temperature and salinity reached after 3 years only 27.8 and 26.6 mm CW, respectively (LTE,
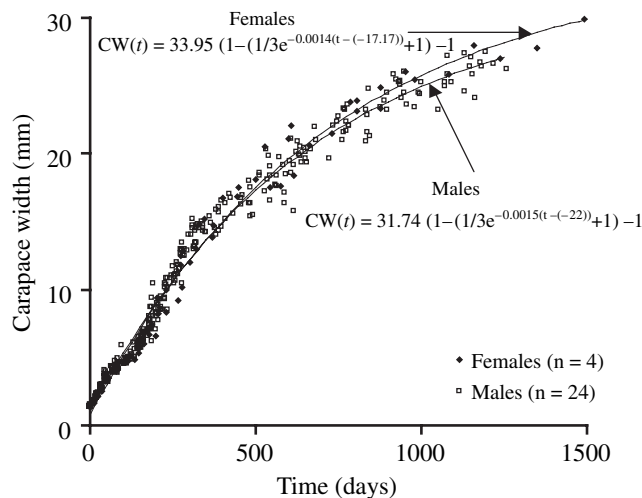
Fig. 9. *Chasmagnathus granulatus*: relationship between carapace width (CW) and age from male (n = 24) and female (n = 4) data, with a growth model of von Bertalanffy superimposed (see the 95% confidence limits of the *A*, *k* and *j* parameter in Table 3)

this study). On the basis of von Bertalanffy growth curves, females should reach approximately 33 mm CW only after 7 years, and males would never reach 36 mm CW. By contrast, Kittlein et al. (2000) modelled the growth of *C. granulatus* on the basis of field data also by means of a multivariate logistic regression and estimated that the time to reach maximal model size should be only 2.6 and 2.4 years in males and females, respectively. This estimate agrees with field observations (Spivak et al., 1996). In size-frequency distributions, the mean size of crabs belonging to the first year class ranged from 24 to 27 mm CW (both sexes), the second year class averaged 36 and 33 mm CW in males and females, respectively. On the other hand, Luppi et al. (2001) reported for *C. granulatus* recruits (field data) a linear relationship between CW and time: CW = $0.056t$ + 1.35. Hence, newly settled recruits in the field can reach adulthood after only 1 year (Luppi et al., 2001), and we can estimate a lifespan of no more than 3 years.

In contrast to the growth in juveniles and adults, laboratory conditions did not affect the growth of undifferentiated juvenile of *C. granulatus*. Luppi et al. (2001) showed that first instar crabs reached the same size after 21 days both in laboratory cultures and field enclosures, and that this size agreed with estimates from a field survey for the same period.

Relationship between growth and reproduction

As may be expected from the literature on crab growth (see Hartnoll, 1982; Botsford, 1985), Hiatt diagrams suggest two phases of growth in *C. granulatus*: a juvenile phase with a higher slope, and an adult phase. A decrease in growth per molt after reaching maturity was usually considered as a bioenergetic trade-off between growth and reproduction (Adiyodi, 1988; Nelson, 1991). In *C. granulatus* females, the discontinuity in the Hiatt diagram (CW approximately 18 mm, Fig. 1b) was within the size range of morphological maturity in the field (Gavio et al., 1994). In addition, it agreed with the size at functional maturity sensu López-Greco and Rodríguez (1999a), and with the minimum size of ovigerous females found in Mar Chiquita lagoon (17 mm, Spivak et al., 1996). However, gonadal maturity may be reached at a smaller size

(15.6 mm, Gavio et al., 1994). In males, the size of the discontinuity in the Hiatt plot (CW = 17.2, Fig. 1a) was larger than the size at gonadal maturity (CW = 15 mm, Gavio et al., 1994) but smaller than the size at functional maturity: males observed in copula in the field were always larger than females (CW > 17.8 mm, López-Greco and Rodríguez, 1999c).

In short-term experiments mature females grew less than mature males at each molt. This was observed also in other crabs (see Hartnoll, 1982; Fukui, 1988; Chen and Kennelly, 1999), although there are exceptions (Tagatz, 1968). One of the arguments used to explain this difference is that females have a higher reproductive investment than males, but this hypothesis has never been quantified in crabs (Hartnoll, 1982; Fukui, 1988). As another factor, differences in feeding activity may explain sex-specific differences, at least in some species (Chen and Kennelly, 1999). Ovigerous *C. granulatus* females were not observed feeding until egg hatching (F. Botto, unpubl. data), and most of the energy obtained when feeding is resumed should be used for producing a new egg clutch; adult males, in contrast, feed throughout the breeding season. When crabs molt at the end of the breeding season the size increment may thus be lower in females even if the reproductive investment was similar between sexes (López-Greco and Rodríguez, 1999b). In addition, females continued using energy from food for developing new ovocytes also after the breeding season has finished (López-Greco and Rodríguez, 1999b, T. A. Luppi, pers. comm.). In our long-term laboratory studies, the molt increment of adult *C. granulatus* was similar in both sexes, probably due to unlimited feeding throughout the year (Fig. 1c,d). The same was observed also by López-Greco and Rodríguez (1999b) although the molt increments measured in their study was generally smaller.

The maximum size reached by *C. granulatus* in the laboratory (this study) and in the field in Mar Chiquita (Spivak et al., 1996, this study) is smaller in females than in males. This fact may be explained with differences in the growth increments (STE, Fig. 2a,b) and IPs (LTE, Fig. 3). Since the IP, but not the growth increments, differed between sexes when food was not limited (LTE, Fig. 2c,d), we assume that the trade-off between growth and reproduction as well as foraging behaviour may be responsible. The energy allocation to reproduction should be proportionally stronger in females, because more energy is needed for the production of oocytes than spermatocytes, as was proposed by Hartnoll (1985) and demonstrated by Alunno-Bruscia and Sainte-Marie (1998). The observation that females never molted during the reproductive period should be a consequence of this strong trade-off.

Regression models applied to size increment at molt

The relationship between the growth factor and the pre-molt size was generally fitted by a linear or a log-linear model (Mauchline, 1977). Although the reported R^2 values were frequently low, PSI was negatively related with pre-molt size in *Ma. squinado* juveniles (Gonzáles-Gurriaran et al., 1995), but not in juvenile *Paralomis granulosa* (Lovrich and Vinuesa, 1995). SIM was positively and significantly related in *Menippe mercenaria* (Tweedale et al., 1993) but not in *Ma. squinado* (Gonzáles-Gurriaran et al., 1995). When the entire size range of a species was studied, the R^2 values of the PSI–CW relationship ranged from 0.7 in *Sesarma jarvisi* (Diesel and Horst, 1995) to 0.11 in *Ranina ranina* males (Chen and Kennelly, 1999). We obtained a higher R^2 value in

C. granulatus using a quadratic rather than a linear or log-linear model (Table 2). When we analysed our data in separate size groups, we found different relationships between female SIM and pre-molt CW:

CW < 15 mm, $y = 0.00005x^2 - 0.16x - 0.01$, $R^2 = 0.77$

$15 < $ CW $ < 23$ mm, $y = -0.008x^2 - 0.3x - 0.12$, $R^2 = 0.009$

CW > 23 mm, $y = -0.002x^2 - 0.104x + 6.4$, $R^2 = 0.58$

We thus suggest that the model for estimating growth increments depends on the size range and the biology of the species. Likewise, Mauchline (1977) stated that the range of sizes should be carefully taken into account for interpreting results of growth studies.

Effect of regenerating limbs on growth increments

The presence of regenerating limbs tended to reduce growth increment at ecdysis, especially at larger body sizes, indicating a trade-off between growth and regeneration. Negative effects of limb regeneration on growth were described also in other crabs (Kuris and Mager, 1975; Smith, 1990; Spivak, 1990; Lovrich and Vinuesa, 1995). This effect varied with the number of autotomies and the stage of the molt cycle when limbs were lost. In addition, autotomies could also affect feeding efficiency, decreasing the energy available for growth (Juanes and Hartwick, 1990). Limb regeneration may thus also affect the process of morphological change at the onset of maturity (T. A. Luppi, pers. comm.; Clayton, 1990). Effects of limb autotomy on growth should be important at a populational level, especially in species with high incidence of autotomies, and should be considered in crab fisheries where size at the onset of maturity is a relevant feature.

Abdomen morphometry

In most grapsoid crabs, the puberty molt of females is defined on the basis of relative AW. When the abdomen reaches the basis of pereiopod coxae (maximum AW), the female is considered morphometrically mature. The size at morphometrical maturity is used for separating mature and immature females in Hiatt diagrams. Morphometrical maturity of female crabs usually occurs at a definite molt (puberty molt or maturity molt; Ingle, 1983), which can be preceded by one or more pre-puberty molts (Marchand, 1973; Hartnoll, 1982; Sampedro et al., 1999).

In *C. granulatus* females we found that at least two molts were necessary to complete the 'morphometric maturity' of the abdomen. The first molt had a very high increment in AW, but the post-molt abdomen remained relatively narrow (i.e. not reaching the pereiopod coxae). Some of these females were functionally mature, carrying eggs (T. A. Luppi, field observ.). Although the abdomen had a smaller increment in width at the second molt, it reached the coxae, i.e. the females became morphometrically mature. These two molts defined three developmental stages in female *C. granulatus*, as was observed in several spider crabs (Alunno-Bruscia and Sainte-Marie, 1998). Following the terminology adopted by Alunno-Bruscia and Sainte-Marie (1998), we designated these stages as juvenile, adolescent and adult.

Growth curves

The maximum size of *C. granulatus* estimated on the basis of LTE data with the von Bertalanffy model (34 and 31.75 mm

CW, males and females respectively) was 15% smaller than the maximum observed size in the field (40 and 38 mm CW, Spivak et al., 1996). This may be a consequence of a prolonged culture in the laboratory, or an artefact of the model itself. Similar deviations between von Bertalanffy growth curves and actual growth were observed by Philips et al. (1992) in lobsters. The use of continuous growth models (like that of von Bertalanffy) for estimating discontinuous growth in crustaceans has thus been criticized (Philips et al., 1992; Chen and Kennelly, 1999). On the contrary, Wehrtmann and Albornoz (2003) showed that size, but also morphology, differed between laboratory reared and field collected decapod larvae.

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Appendix 1
Papers on growth in brachyuran and some anomuran crabs (excluding relative growth)

Author	Species	Type of data	Size group
Bennett (1974)	*Cancer pagurus*	TR	A
Carroll (1982)	*Cancer antennarius*	TR	A
Collier (1983)	*Cancer magister*	TR and FS	AS
Chen and Kennelly (1999)	*Ranina ranina*	TR	AS
Hill (1975)	*Scylla serrata*	FS	A
Klein and Breteler (1975a)	*Carcinus maenas*	FS	J
Paul (1982)	*Callinectes arcuatus, C. toxotes*	FS	AS
Du Preez and McLachlan (1984)	*Ovalipes punctatus*	FS and LTE	AS
Stevens and Armstrong (1984)	*Cancer magister*	FS	J
Davidson and Marsden (1987)	*Ovalipes catharus*	FS	AS
Fukui (1988)	Several species	FS and LTE	AS
Orensanz and Gallucci (1988)	*Cancer magister, C. productus, C. gracilis, C. oregonensis*	FS and LTE	J
Smith and Jamieson (1989)	*Cancer magister*	FS and TR	AS
Sastre (1991)	*Emerita portoricansis*	FS	AS
Ariyama (1992)	*Portunus trituberculatus*	FS and LTE	AS
Branco and Masunari (1992)	*Callinectes danae*	FS	AS
Donaldson et al. (1992)	*Paralithodes camtschaticus*	FS	J
Mantelatto and Fransozo (1994)	*Hepatus pudibundus*	FS	AS
Comeau et al. (1998)	*Chionoecetes opilio*	FS	AS
Luppi et al. (2001)	*Chasmagnathus granulatus, Cyrtograpsus angulatus*	FS and LTE	J
Tagatz (1968)	*Callinectes sapidus*	FE	J
De Leersnyder (1972)	*Eriocheir sinensis*	LTE	J
Turoboyski (1973)	*Rhithropanopeus harrissi*	LTE	AS
Klein and Breteler (1975b)	*Carcinus maenas*	LTE	J
Anderson and Ford (1976)	*Cancer anthonyi*	LTE	J
Miller and Watson (1976)	*Chionoecetes opilio*	LTE	AS
Nye (1977)	*Helice crassa*	LTE	A
McLay (1985)	*Pagurus traversi, P. novizealandiae*	LTE	AS
Spivak (1988)	*Cyrtograpsus angulatus*	LTE	J
Wilber and Wilber (1989)	*Mithrax spinosissimus*	LTE	J
Shirley et al. (1990)	*Paralithodes camtschatica*	LTE	A
Fitz and Wiegert (1991)	*Callinectes sapidus*	LTE	AS
Negreiros-Fransozo and Fransozo (1991)	*Eriphia gonagra, Eurypanopeus abbreviatus, Sesarma rectum*	LTE	J
Tunberg and Creswell (1991)	*Mithrax spinosissimus*	LTE	J
Wilber and Wilber (1991)	*Mithrax spinosissimus*	LTE	J
Kondzela and Shirley (1993)	*Cancer magister*	LTE	J
Tweedale et al. (1993)	*Menippe mercenaria*	LTE	J
Hoenig et al. (1994)	*Chionoecetes opilio*	LTE	AS
Diesel and Horst (1995)	*Sesarma jarvisi*	LTE	AS
Otani et al. (1996)	*Tritodynamia horvathi*	LTE	AS
Paul and Paul (1996)	*Chionoecetes bairdi*	LTE	AS
Alunno-Bruscia and Sainte-Marie (1998)	*Chionoecetes opilio*	LTE	AS
López and Rodríguez (1998)	*Chasmagnathus granulatus*	LTE	J
Zhou et al. (1998)	*Paralithodes camtschaticus*	LTE	A
López and Rodríguez (1998)	*Chasmagnathus granulatus*	LTE	A
Spivak (1999)	*Cyrtograpsus angulatus, C. altimanus*	LTE	AS
Hiatt (1948)	*Pachygrapsus crassipes*	STE and LTE	AS
Kurata (1962)	Several species	STE and LTE	AS
Gonzáles-Gurriaran et al. (1995)	*Maja squinado*	STE and LTE	A
Lovrich and Vinuesa (1995)	*Paralomis granulosa*	STE and LTE	J
Sainte-Marie et al. (1995)	*Chionoecetes opilio*	STE and LTE	AS
Warner (1967)	*Aratus pisoni*	STE	A
Hogarth (1975)	*Carcinus maenas*	STE	J
Donaldson et al. (1981)	*Chionoecetes bairdi*	STE	AS
Hines (1989)	*Hemigrapsus oregonensis, Scyra acutifrons*	STE	AS
McDermott (1999)	*Hemigrapsus sanguineus*	STE	AS

Type of data: FS, field survey; FE, field enclosure; TR, tag recovery; STE and LTE, short (< 14 days, STE) and long (several years, LTE) term laboratory-rearing experiments. Size group: A, adults; J, juveniles; AS, all sizes.