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Postsettlement growth of two estuarine crab species, *Chasmagnathus granulata* and *Cyrtograpsus angulatus* (Crustacea, Decapoda, Grapsidae): laboratory and field investigations

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Abstract The estuarine grapsid crabs *Chasmagnathus granulata* and *Cyrtograpsus angulatus* belong to the most typical and dominant inhabitants of brackish coastal lagoons in southeastern South America. In a combined laboratory and field investigation of juvenile growth, we measured the increase in body size in these species under controlled conditions as well as in field experiments (in Mar Chiquita lagoon, Argentina), seasonal changes in size frequency distribution of a natural population, and growth related changes in selected morphometric traits of male and female juveniles (relations between carapace width, carapace length, propodus height and length of the cheliped, and pleon width). At 24°C, *Cy. angulatus* grew faster than *Ch. granulata*; it reached the crab-9 instar (C9; 13 mm carapace width) after 92 days, while *Ch. granulata* required 107 days to reach the C8 instar (7.4 mm). At 12°C, growth ceased in both species. The pleon begins to show sexual differences in the C5 (*Cy. angulatus*) and C8 instar (*Ch. granulata*), respectively, while the chelae differentiate earlier in *Ch. granulata* than in *Cy. angulatus* (in C4 vs C6). In the field, growth was maximal in summer, and was generally faster than in laboratory cultures. However, there is great individual variability in size (about 25% even in the first crab instar) and in size increments at ecdysis, increasing throughout juvenile growth. Our data indicate that, in the field, small-scale and short-term variations in feeding conditions, temperature, and salinity account for an extremely high degree of variability in the absolute and relative rates of growth as well as in the time to sexual differentiation.

Keywords Allometry · Crab · Grapsidae · Juvenile · Sexual dimorphism

Introduction

The growth of crustaceans appears as a discontinuous process, as the hard exoskeleton is periodically replaced in successive ecdyses, followed by postmolt uptake of water and, in consequence, a rapid increase in body size during the short soft-skinned period. Hence, growth rates depend on two principal components, (1) the size increment after molting, (2) the duration of the intermolt period (Kurata 1962; Klein Breteler 1975; Hartnoll 1982; Restrepo 1989; Tweedale et al. 1993). The intermolt period usually increases with size, while the percentage increment tends to decrease.

In the field, growth is usually studied indirectly, through the analysis of size frequency distributions, assuming that no major immigrations or emigrations take place in a population during the period of investigation (Hartnoll 1982). Under controlled conditions in the laboratory, in contrast, intermolt periods and size increments can be studied in identical individuals, allowing for precise quantitative descriptions of growth. On the other hand, laboratory conditions are artificial and may thus not allow for full extrapolation of experimental data to field populations. Attempting to compensate for some of those limitations, we chose a combined approach of laboratory and field studies in this investigation.

In crabs, various morphological structures such as the carapace, claws, walking legs, or the pleon may show differential rates of growth. Changes in allometric relations between different body dimensions have extensively been studied in field-collected individuals (e.g. Kurata 1962; Mauchline 1977; Hartnoll 1982), while fewer reports deal with morphometric changes in safely identified successive instars (Anderson and Ford 1976; Yatsuzuka and Meruane 1987; Tunberg and Creswell 1991). This bias was attributed to difficulties in the collection, identification, and subsequent rearing of juve-

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niles (Hebling et al. 1982; Negreiros-Fransozo and Fransozo 1991), which render ecological research on the functional importance of juveniles in their natural habitats generally difficult (O'Connor 1990). In the present study, we measured growth in various body dimensions both in field-caught and laboratory-reared crabs, with emphasis on sexual differences in morphometric relations.

Grapsid and ocyropid crabs are characteristic and frequently dominant inhabitants of the intertidal and supratidal zones of tropical and temperate estuaries and brackish coastal lagoons (Pillay and Ono 1978; Seiple 1979; Willason 1981; Jones and Simons 1982; Seiple and Salmon 1987; Spivak et al. 1994). Representing typical examples, *Chasmagnathus granulata* and *Cyrtograpsus angulatus* (Grapsidae) are considered as key species in "cangrejal" saltmarsh ecosystems (from Spanish, *cangrejo* = crab), which are widespread along the warm-temperate southwestern Atlantic coasts (Boschi 1964, 1988). In 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, these two species co-occur with dense populations (Olivier et al. 1972; Spivak et al. 1994). Adult *Cy. angulatus* are predominantly found in the lower intertidal and the adjacent subtidal, but occur also on rocky open sea shores. *Ch. granulata* digs burrows in muddy substrates, preferably in the upper intertidal and supratidal zones fringing saltmarshes.

In Mar Chiquita, reproduction takes place from September to May in *Cy. angulatus*, and from October to March in *Ch. granulata*, with several egg clutches produced during each season (Spivak et al. 1996). According to plankton studies, newly hatched zoea-I larvae are exported from the lagoon, later zoeal development takes place in coastal marine waters, and the megalopa stage returns for settlement into the lagoon (Anger et al. 1994). Settlers and early juveniles of *Cy. angulatus* are predominantly found in crevices of sand "reefs" which are constructed by *Ficopomatus enigmaticus*, a tube-building polychaete, and in other sheltered microhabitats, e.g. under stones and between empty mollusc shells. Young *Ch. granulata*, in contrast, are frequently found on muddy bottoms, especially inside and around the burrows of conspecific adults (Boschi 1964; Spivak et al. 1994; Luppi et al. 1994).

Although ecological and physiological traits of *Cy. angulatus* and *Ch. granulata* are well documented for the larvae (Boschi et al. 1967; Anger et al. 1994; Anger and Ismael 1997; Ismael et al. 1997; Gebauer et al. 1998; Valero et al. 1999) and for the adult phase of the life cycle (Spivak and Politis 1989; Gavio and Spivak 1994; Spivak et al. 1994, 1996; Luppi and Spivak 1996; Iribarne et al. 1997; Luppi et al. 1997; Lopez Greco and Rodriguez 1998; Luppi 1999; Spivak 1999), much less information is available on the juvenile phase (Spivak 1988; Rieger and Nakagawa 1995; Anger and Ismael 1997; Lopez and Rodriguez 1998; Gebauer et al. 1999). The principal aim of the present paper is thus to quanti-

tatively describe the juvenile growth of these species. This includes (1) the absolute and relative patterns of growth under controlled laboratory conditions, (2) sexual and size-dependent changes in morphometric relations, and (3) estimates of growth in the field.

Materials and methods

Study area

Mar Chiquita lagoon (37°32'–37°45'S/57°19'–57°26'W) covers an area of 46 km². A few small rivers feed it with freshwater, while seawater enters and leaves it periodically with semidiurnal high tides. The extent of water exchange depends on the tidal amplitude and the direction and speed of winds (Olivier et al. 1972; Reta et al. 1997). Water temperature (Fig. 1) and salinity show strong seasonal, daily and local variations (Anger et al. 1994; Marcovecchio et al. 1997; Martos and Reta 1997).

Collection and rearing techniques

Megalopae of *Cy. angulatus* and *Ch. granulata* were collected during March 1996 in their respective settlement habitats and subsequently transported to the laboratory. Thirty megalopae were transferred individually to 100 ml plastic bowls with 80 ml water (23‰ salinity), which was prepared by the addition of freshwater

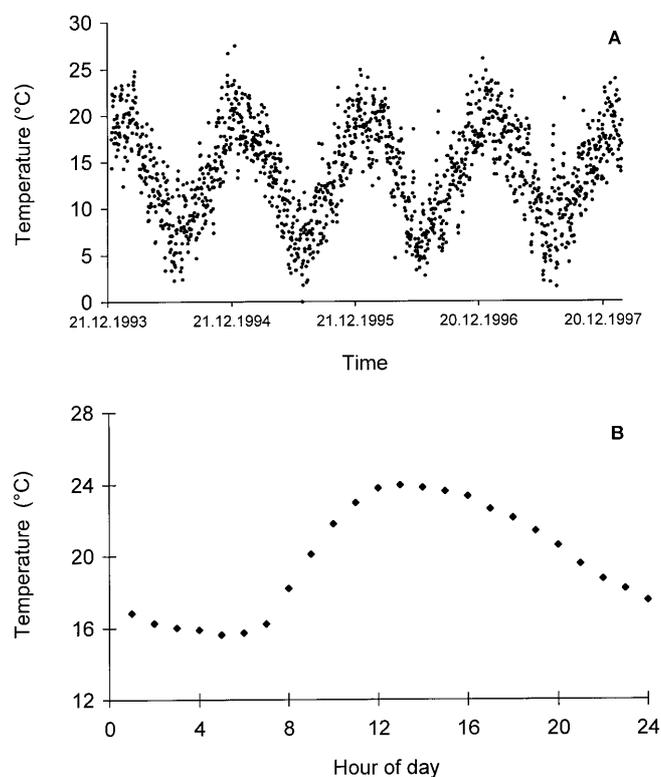


Fig. 1A, B Temperature conditions in Mar Chiquita lagoon. **A** Seasonal and interannual variations of average daily air temperatures during the study period, from 1993 to the end of the last field experiment (March 1998); the dates in the x-axis indicate the beginning of the austral summer; **B** Daily variation of air temperature (hourly mean values); data from the meteorological station at Camet airport, 30 km south of Mar Chiquita lagoon (courtesy National Meteorological Service)

to inshore seawater (34‰), both previously filtered (10 µm). The cultures were maintained at constant 24°C and a 16:8 h light:dark photoperiod. The water was changed on alternate days and nauplii of *Artemia* sp. were added as food. Juveniles with ≥5 mm carapace width were transferred to 250 ml plastic bowls. All individuals were checked daily for molting or mortality. Exuviae and dead individuals were stored individually in 4% formaldehyde.

Growth measurements

From each exuvia, the following measurements were taken using a stereomicroscope with an ocular micrometer or, in larger crabs, a caliper (0.01 mm precision): maximum carapace length (CL), maximum carapace width (CW; in *Cy. angulatus* including the lateral spines), maximum cheliped height (CHH) and length (CHL) measured in the propodus, and maximum pleon width (PW) measured in the fourth somite. From these data, percentage size increments (PSI) were calculated. Sex was determined from pleon and pleopod morphology. Successive crab instars were named C1, C2, etc. Relationships between body measurements (logarithmically transformed), PSI, and intermolt periods (IP) in successive instars were analysed with least-square regressions, and slopes of regression equations were compared using ANCOVA (Zar 1984).

For morphometric analyses, quotients between body dimensions (CW, CL, CHH, CHL, PW) were calculated as relative growth indices (RGI) in each instar. Sexual differences between RGI values of successive instars were statistically tested using a non-parametric Mann-Whitney rank test, because the data did not always fulfill the assumptions of normality and homogeneity (Zar 1984). Additionally, larger juveniles and adults were collected by hand in Mar Chiquita and sorted according to size (CW) and sex. From these samples, 20 males and 20 females belonging to each of the following size-classes were selected: 10±1, 15±1, 20±2, 30±2 mm (*Ch. granulata*); 15±1.5, 20±2, 30±2, 40±3 mm (*Cy. angulatus*). CW, CL, CHH, CHL and PW were measured and used for the calculation of RGI values.

Effects of temperature on growth

In January 1996, megalopae of both species were collected in Mar Chiquita, transported to the laboratory, and placed in 3 l containers with water of 23‰ salinity. Immediately after molting, 15 crabs of each species were placed individually in 100 ml plastic bowls and reared at 21°C and 12°C, 23‰ S, and a 16:8 h light:dark photoperiod. Crabs were fed with *Artemia* sp. nauplii every 48 h, after each water change. The presence of exuviae was recorded daily. CW was measured after 30 days, and mean size values were compared using a Mann-Whitney *U* test.

Field sampling

In total, 104 samples of recently metamorphosed crabs (54 *Cy. angulatus*, 48 *Ch. granulata*) were taken from October 1992 to December 1995. The frequency of collection was two or three times a month in summer and less frequently in winter. *Cy. angulatus* recruits were collected from ten core samples (300 ml) extracted from *Ficopomatus enigmaticus* "reefs". *Ch. granulata* were obtained by hand in an area with a high density of adult burrows and a variable number of sample units (0.25 cm²), selected at random along a transect. In all individuals, CW was measured.

A size frequency distribution (SFD) was constructed for each sample, with the following size intervals (CW): size class 1–4 mm: intervals of 0.25 mm; 4.01–8 mm: 0.5 mm; 8.01–11 mm: 1 mm. For species with a short but intense recruitment period and with low intracohort variability in growth, several graphical and statistical methods have been developed to estimate growth rates from the displacement of modal SFD classes (Hartnoll 1978, 1982, 1983; Klein Breteler 1975; Orensanz and Gallucci 1988).

The two species studied here, however, show a long recruitment period with several pulses of reproductive activity, as well as intracohort variability in growth, due to small-scale and short-term heterogeneity in the environmental conditions (Luppi 1999). Consequently, the available analytical methods could not be used in this study. The displacement of modal classes was thus determined visually, and linear least-square regressions of modal values and time elapsed from the first appearance of the putative cohorts were calculated. The slopes of regression lines obtained in the field and laboratory were compared using an ANCOVA (Zar 1984).

Field experiments

Megalopae of *Cy. angulatus* and *Ch. granulata* were collected in Mar Chiquita in February 1997 and 1998, transported to the laboratory and reared through metamorphosis as previously described. Groups of 20 *Cy. angulatus* in the C1 instar were placed in 3 l plastic containers with perforated walls and lids, covered with a plastic screen (500 µm mesh size). A piece of polychaete "reef" (approximately 500 ml, without crabs) was placed as refuge. Five replicates were suspended from a rope and submerged in the lagoon (30 cm above the bottom). After 30 days, the survivors were collected, counted, and measured (CW).

Groups of 20 *Ch. granulata* in the C1 instar were placed in each of four 10 l tubes with perforated walls and top, covered with a plastic screen (500 µm mesh size). These tubes were buried 15 cm deep in the substrate near adult burrows, after the removal of naturally occurring juvenile crabs. The numbers and CW of the survivors were recorded after 21 days. Differences in mean size among replicates were evaluated with a one-way ANOVA followed by Student-Neuman-Keuls test or with a Kruskal-Wallis test for median comparison in case of deviations from normality or homoscedasticity.

Results

Laboratory growth and morphometric changes

Cyrtograpsus angulatus

Survival was high, with 93.5% of all individuals still alive after 105 days of rearing (Table 1). The crabs reached instar C9 and 13±0.6 mm CW after 92 days (Fig. 2a). The intermolt period (IP) increased during juvenile growth, more rapidly after the C4 instar, from 5.8±1.4 days (C1–C2) to 34.3±6.2 days (C8–C9; Fig. 2b). The percentage size increment (PSI) did not show a clear pattern, varying between 24% and 37% (Fig. 2c). All regressions of body size on instar number were significant. The slopes of the relationships between

Table 1 Survival (individual number and percentage) in successive crab instars of *Cyrtograpsus angulatus* and *Chasmagnathus granulata*. *n* Number of individuals at the beginning of experiment

Species	Instar								
	<i>n</i>	1	2	3	4	5	6	7	8
<i>Cyrtograpsus angulatus</i>	30	30	30	30	28	28	28	28	28
(%)	100	100	100	100	93	93	93	93	93
<i>Chasmagnathus granulata</i>	30	29	28	28	26	26	25	25	–
(%)	97	93	93	87	87	83	83	–	–

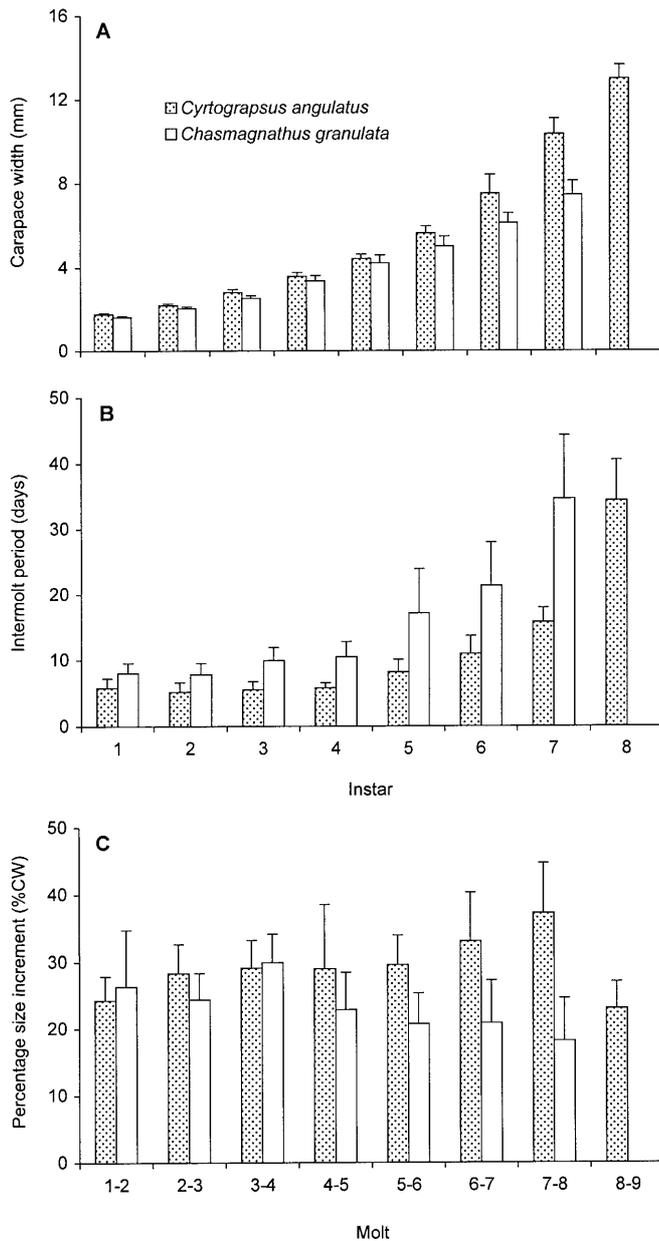


Fig. 2A–C Growth of *Cyrtograpsus angulatus* and *Chasmagnathus granulata* through successive juvenile instars. **A** Carapace width *CW*, **B** intermolt period *IP*, **C** percentage size increment *PSI*, in successive molts (mean values \pm SD)

CHH, CHL and PW regressed on the instar number differed significantly between sexes (Fig. 3a–e).

The RGI allowed for the examination of morphometric changes during the course of juvenile development, and hence, was able to detect those instars where sex-specific differences appeared. In the C1 instar, the carapace was longer than wide ($CW < CL$), but this relationship reversed in the C2 so that *CW* was larger than *CL* in all later instars. The *CL/CW* quotient, however, did not show a statistically significant difference between sexes in any instar (Fig. 4a). From the C4 instar stage, the chelae tended to become proportionally higher and longer

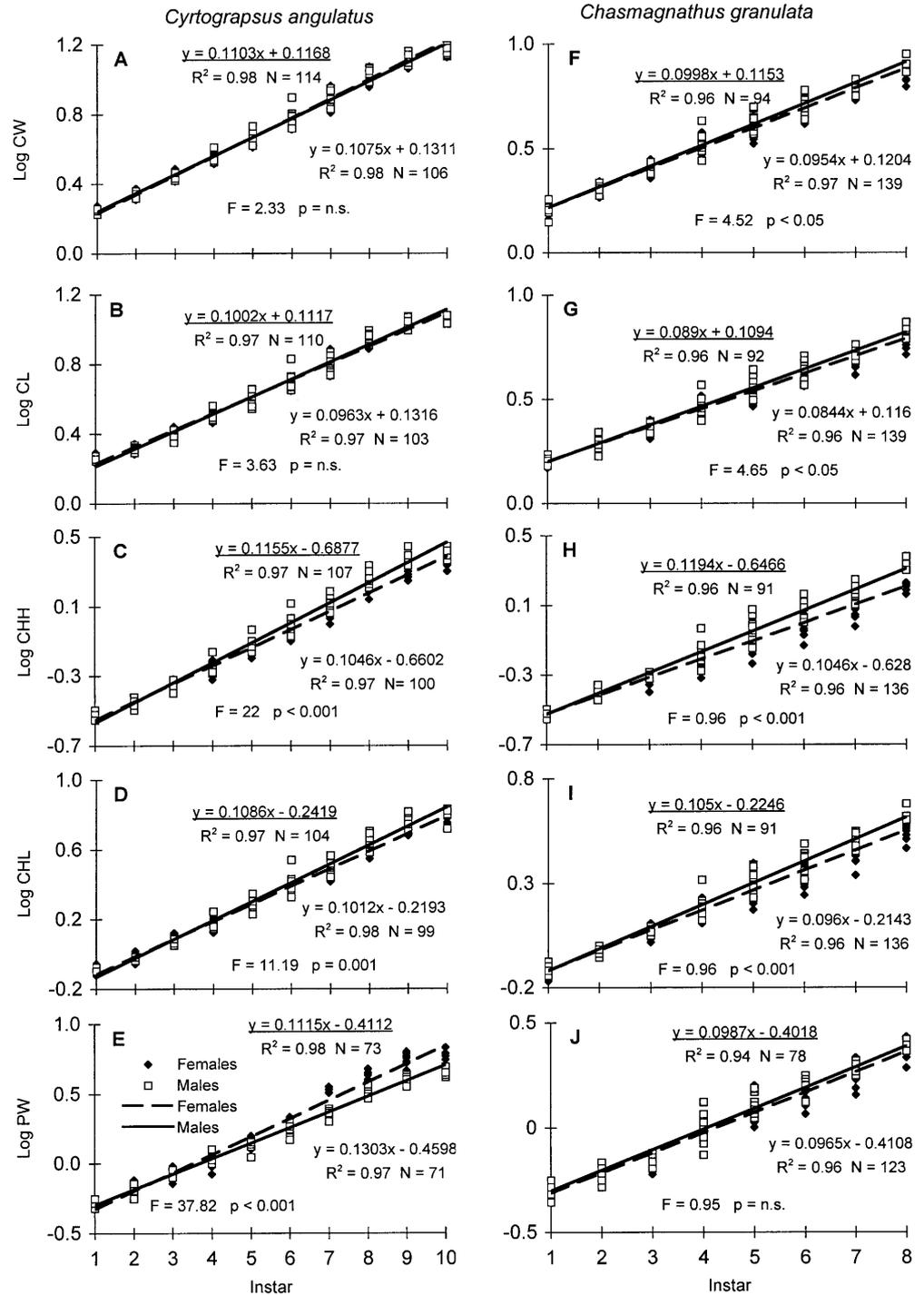
in males than in females, and these sex-specific morphometric differences increased throughout juvenile development (Fig. 4b, c). From the C5 onward, the pleon was significantly wider in females than in males; this typical sex-specific character became increasingly conspicuous in the subsequent juvenile instars, with a stabilizing *PW/CW* relation reached by instar C9 (Fig. 4d).

Chasmagnathus granulata

After 120 days, 25 individuals (83%) were still alive (Table 1). During this period, the crabs reached the C8 instar and an average *CW* of 7.4 ± 0.6 mm (Fig. 2a). The *IP* increased from 8 ± 1.5 days (instars C1–C2) to 34.6 ± 9.6 days (C7–C8; Fig. 2b). The *PSI* showed no clear tendency, varying between 18% and 30% (Fig. 2c). All regressions of the various measurements of body size and the instar number were statistically highly significant (Fig. 3). Significant sex-specific differences between the slopes of these regression lines were observed in *CW*, *CL*, *CHH* and *CHL* (Fig. 3f–j). In the C1 instar, carapace length and width were almost identical ($CL/CW = 1$), but as *CW* grew proportionally faster in the subsequent instars, the *CL/CW* index decreased thereafter, stabilizing from C5; it did not differ significantly between males and females in any instar (Fig. 4e). From the C3 or C4 instar, respectively, the chela was significantly higher and wider in males than in females; these sex-specific morphometric differences increased in later juvenile instars (Fig. 4f, g). The pleon width in relation to *CW* did not differ significantly between sexes; thus, this sex-specific character develops in *Ch. granulata* only after the C8 instar (Fig. 4h).

Data from field-collected crabs allowed us also to study the relative growth patterns in later juvenile instars (5). In *Cy. angulatus*, the *CL/CW* quotient had a virtually constant value in the size range between 15 and 40 mm *CW*. It was 7.7% higher than the value observed in the largest laboratory-reared crabs (C9 instar, 13 mm *CW*). On the other hand, *Ch. granulata* had already reached the same *CL/CW* value as in larger field-collected crabs by the C8 instar stage (Fig. 4a, e). The sex-specific differences in relative chela width and height continued to increase in larger crabs, although these morphometric changes also differed between the two species. In large female *Cy. angulatus*, the size proportions of the chelae were similar to those observed in laboratory-reared C9 crabs, while the relative chela size of the males continued to increase throughout later growth (Fig. 4b, c). In *Ch. granulata*, chela size in relation to *CW* continued to increase in both sexes, but this proportional increase was greater in males, so that the sex-specific differences tended to increase from juvenile to adult crabs (Fig. 4f, g). In both species, the pleon shape did not change after the C9 instar in males, while the *PW/CW* relation of female crabs increased until a *CW* of about 20 mm was reached, remaining constant only thereafter (Fig. 4d, h).

Fig. 3 *Cyrtograpsus angulatus* (A–E), *Chasmagnathus granulata* (F–J): least-square regression lines and equations describing changes in various body dimensions (measured in mm; logarithmic scale) as functions of the juvenile instar number; underlined equations males, not underlined equations females, R^2 coefficient of determination, N number of individuals, F statistic for slope comparisons, P level of significance for differences between slopes, CW carapace width, CL carapace length, CHH chela height, CHL chela length, PW pleon width



Instar duration was significantly affected by rearing temperatures in both species. In the C1 instar of *Cy. angulatus*, the IP was four times shorter at 21°C than at 12°C. During the time of the experiment, juveniles reached the C4 instar at 21°C, but at 12°C only the C2 was reached. On the other hand, C1 reared at 12°C were significantly larger than those reared at 21°C ($T=210$, $P<0.05$, Table 2) and also larger than those collected in the field ($T=4,713$, $P<0.0001$, Fig. 6a). *Ch. granulata* juveniles generally grew more slowly than *Cy. angulatus*

in the laboratory; at 21°C, they reached the C3 instar after 30 days, whereas no molts occurred at 12°C.

Growth in the field

Size frequency distributions

Only juvenile *Cy. angulatus* with $CW < 7$ mm were found in *F. enigmaticus* "reefs". Their size frequency

Fig. 4 *Cyrtograpsus angulatus* (A–D), *Chasmagnathus granulata* (E–H): changes in relative growth indices *RGI* (quotients of various body dimensions and carapace width *CW*, mean values \pm SD) during juvenile growth through successive instars in laboratory cultures; *** $P < 0.01$, ** $P < 0.05$ (comparisons between males and females; Mann-Whitney median tests); *CL* carapace length, *CHH* chela height, *CHL* chela length, *PW* pleon width

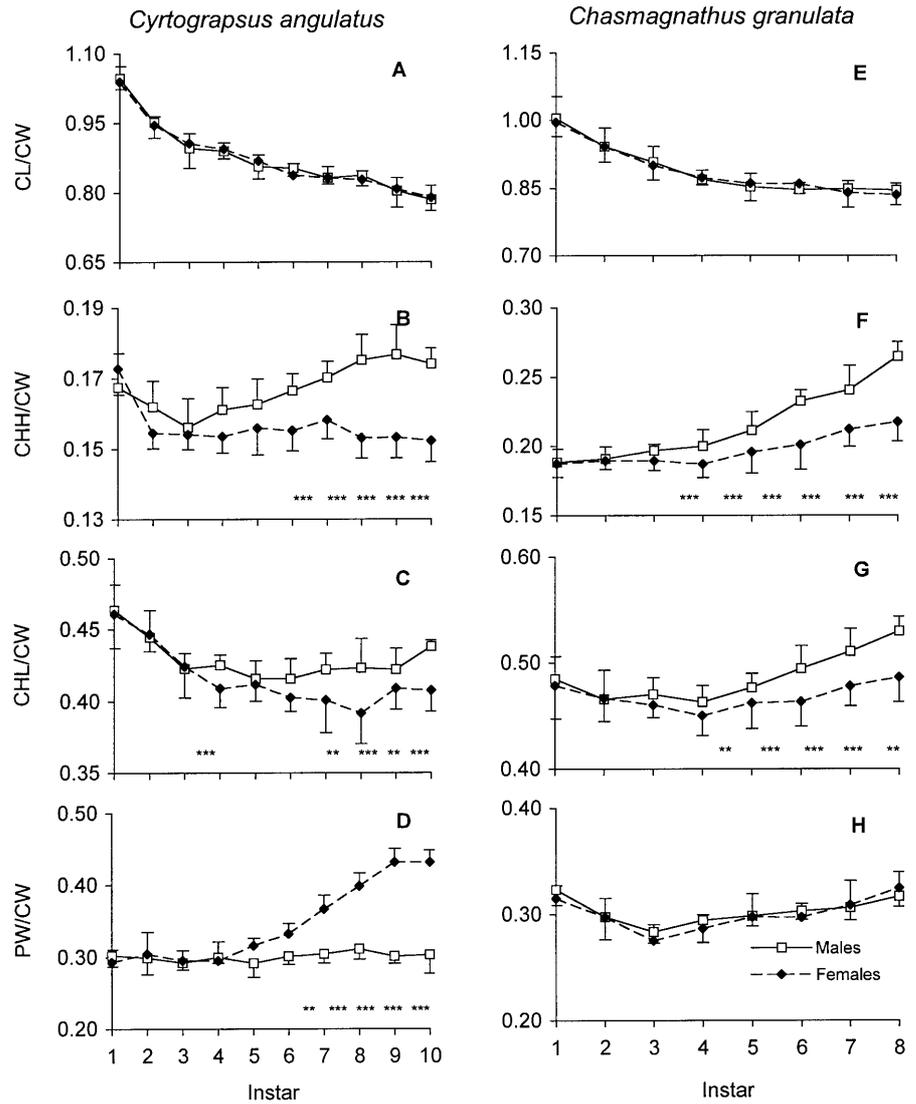


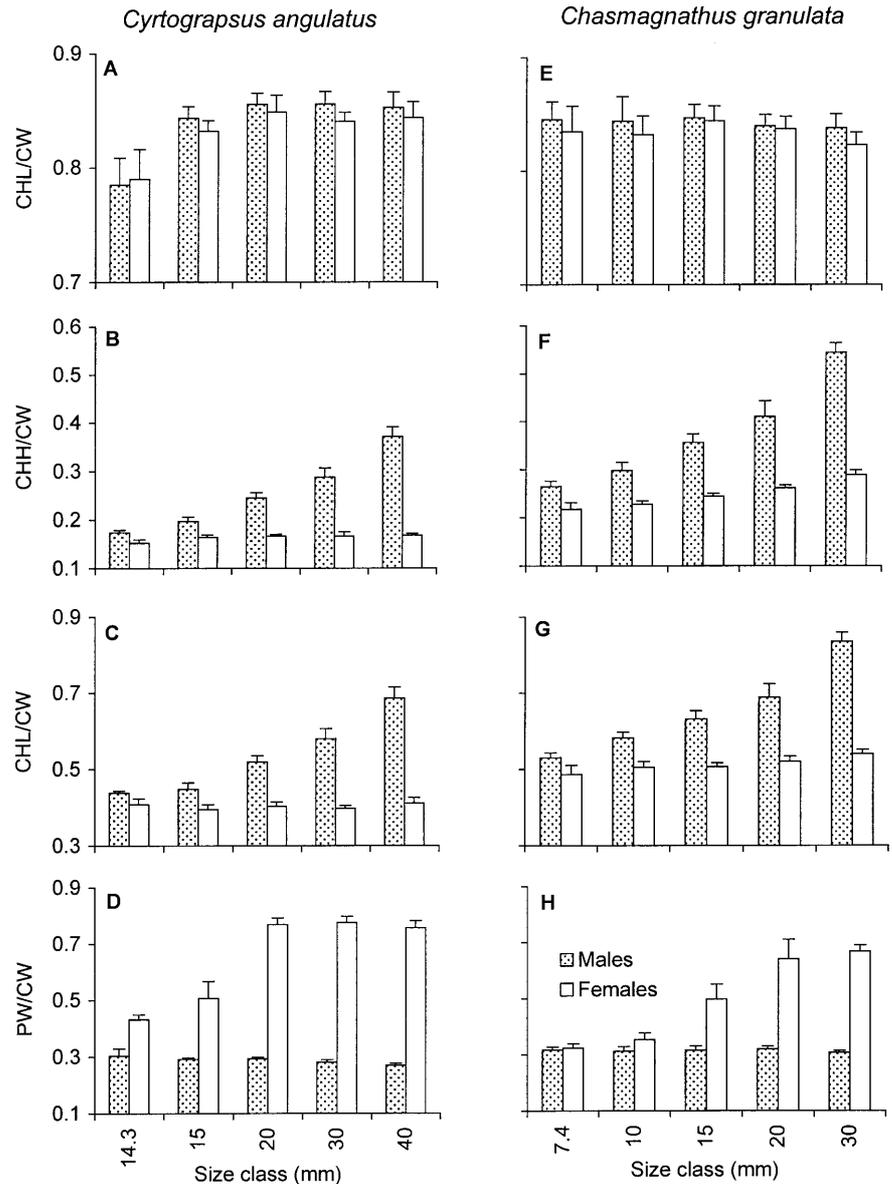
Table 2 Instar reached, duration, and size of the C1 instar of *Cyrtograpsus angulatus* and *Chasmagnathus granulata* reared in the laboratory at 21°C and 12°C (mean \pm SD)

Temperature (°C)	Instar	Duration of C1 (days)	Size (mm) of C1
<i>Cyrtograpsus angulatus</i>			
21	4	7.1 \pm 0.9	1.64 \pm 0.05
12	2	28 \pm 4.4	1.71 \pm 0.08
<i>Chasmagnathus granulata</i>			
21	3	10.9 \pm 2	1.51 \pm 0.05
12	1	–	–

distributions (SFDs) indicated a continuous recruitment throughout the summer and most of autumn, generally with the highest intensity in early summer and several smaller peaks thereafter (Fig. 6a). No conspicuous changes occurred during winter. In the spring, the SFDs were generally displaced towards larger size classes, indicating resumed growth, while a decreasing number of individuals indicated emigration or mortality. No single cohorts could safely be identified in this species and, consequently, the growth of *Cy. angulatus* in the field could not be estimated from SFDs.

In *Ch. granulata*, the analysis of SFDs permitted the identification of several summer recruitment periods throughout a 39 month sampling period: two in 1993, four in 1994 and three in 1995 (Fig. 6b). In January 1995, two successive recruitment periods were observed. Five cohorts could be identified, from which growth was estimated according to the displacement of modal size classes (Fig. 7). Daily growth rates varied between 0.043 and 0.067 mm/day (recruitment detected on 29 December 1992 and 15 January 1995, respectively), yielding an average value of 0.056 mm/day for the pooled data

Fig. 5 *Cyrtograpsus angulatus* (A–D), *Chasmagnathus granulata* (E–H): changes in relative growth indices (RGI) measured in the field (quotients of various body dimensions and carapace width, *CW* mean values \pm SD) in successive juvenile size classes (class means given in the X-axis; field-data); the first pair of columns is, for comparison, the RGI measured in the last crab instar reared in the laboratory; *CL* carapace length, *CHH* chela height, *CHL* chela length, *PW* pleon width



from all cohorts (Fig. 7). Crabs reared at 24°C in the laboratory grew 0.063 mm/day, which did not differ significantly from data estimated in the field (ANCOVA, $F=3.83$, $P>0.05$).

Field experiments

C1 instar *Cy. angulatus* collected from the field measured 1.63 ± 0.06 mm CW (mean \pm SD). The average air temperature during the field experiments was 18.8°C. After 30 days, the number of survivors varied from 7 to 18 individuals among the replicates, and their size varied from 5.6 to 8.2 mm CW (Table 3), differing significantly among replicates (ANOVA, $F=10.5$, $P<0.01$). Largest size and highest survival were observed in the same replicate experiment; smallest size and lowest survival coincided with the accidental presence of an adult *Cyrtog-*

rapsus altimanus. In this experiment, the growth rate of *Cy. angulatus* varied from 0.13 to 0.22 mm/day; the size reached in the field was significantly larger than that observed during an equally long period in the laboratory ($T=57, 55, 98, 55, 55$, respectively, for different replicates; $P<0.001$).

The size of the C1 instar of *Ch. granulata* was 1.5 ± 0.04 mm CW in the field. The mean air temperature during the experiments with this species was 18.2°C. The number of survivors after 30 days varied among replicates from eight to 26 individuals, and their size varied from 2.5 to 2.7 mm CW (Table 3). In this species, size did not differ significantly among replicates ($H=2.98$, $P>0.1$). In a few replicates, the number of crabs was higher at the end of the experiment, due to the immigration of megalopae; the lowest number of crabs was observed in one replicate that had been invaded by larger juveniles. The average growth rate was 0.051 mm/day;

Fig. 6 *Cyrtograpsus angulatus* (A), *Chasmagnathus granulata* (B): size-frequency distribution in Mar Chiquita lagoon; sampling date and number of individuals measured (in brackets)

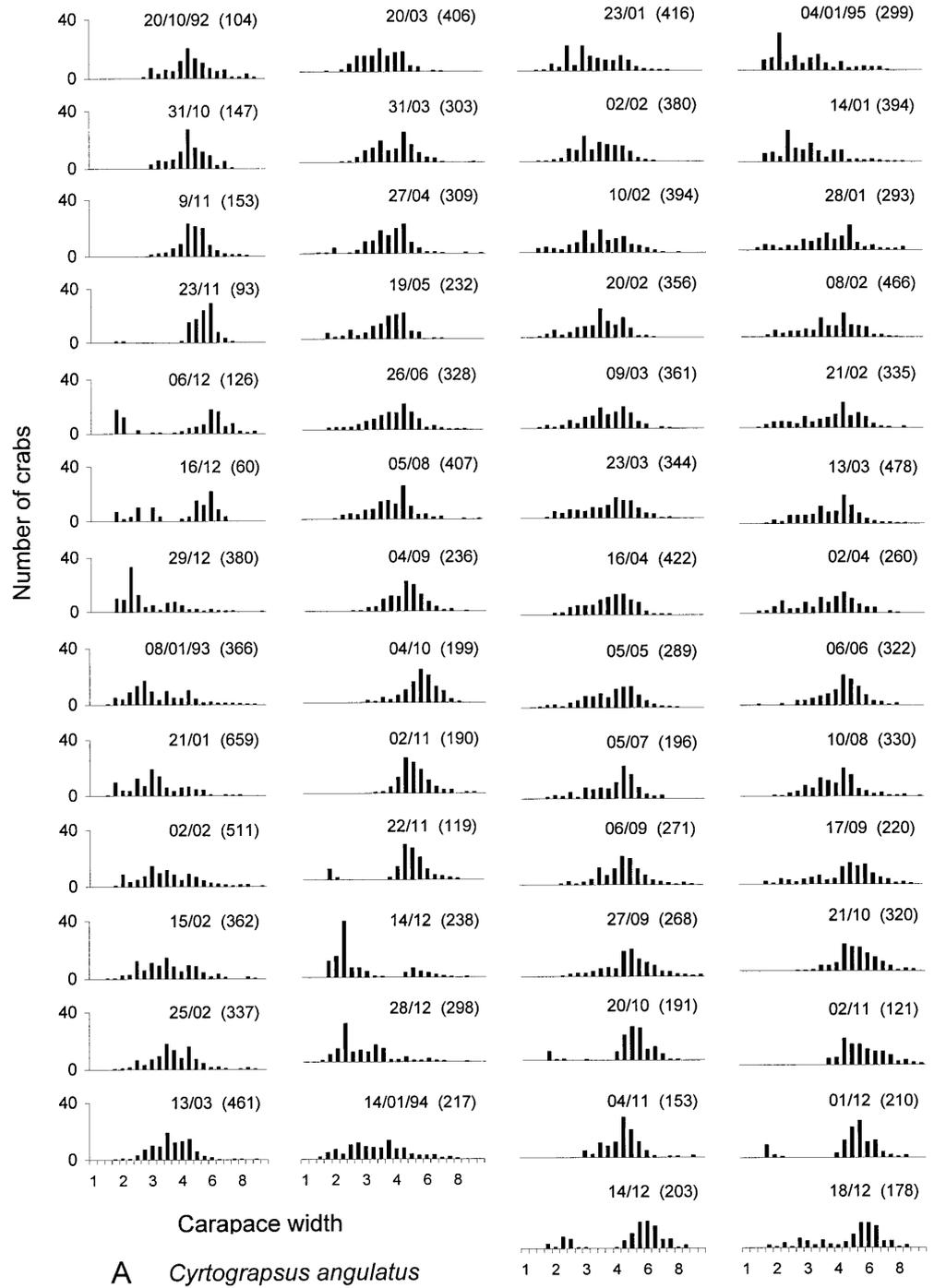
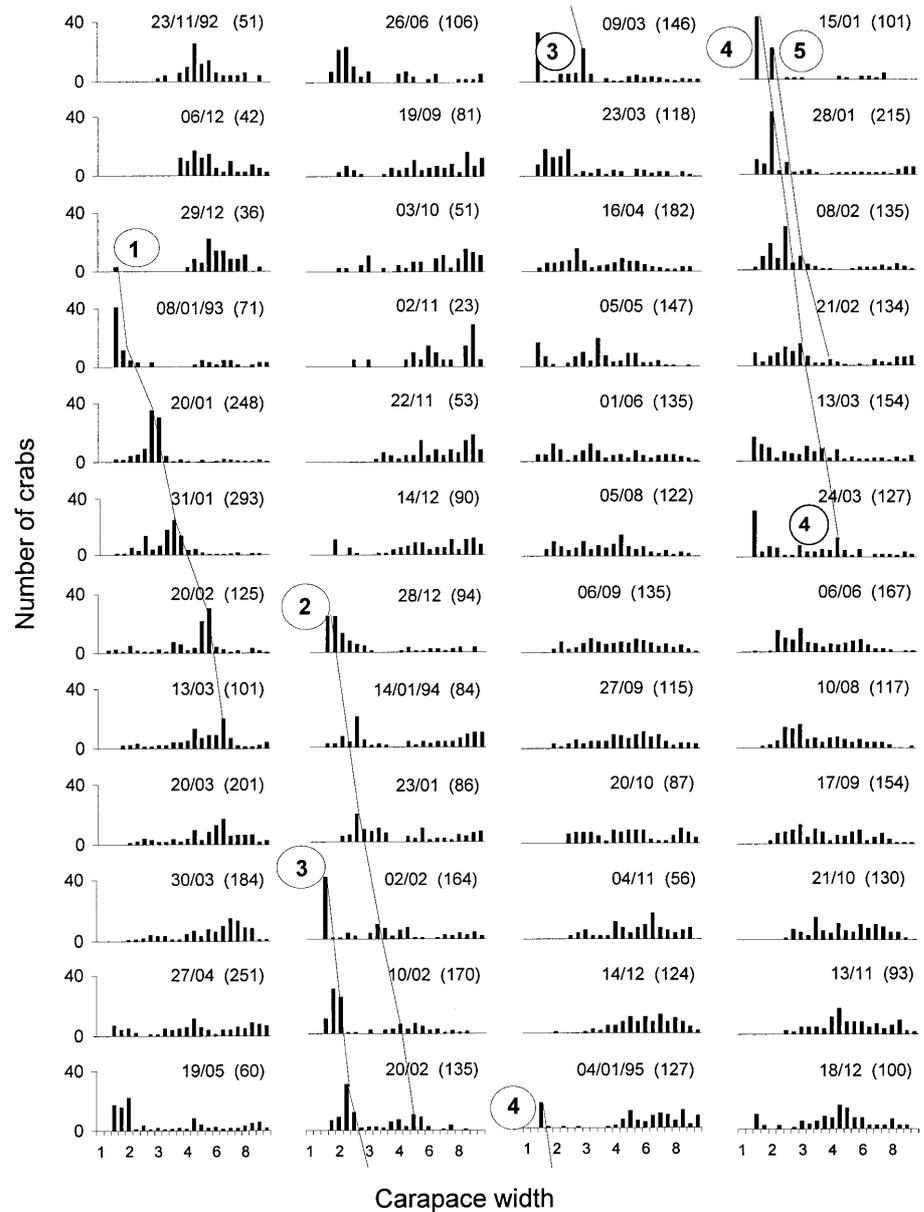


Table 3 Carapace width (mean ± standard deviation) and number of survivors (in brackets) in the field and laboratory, measured at the end of the field experiment (after 30 days in *Cyrtograpsus angulatus* and after 21 days in *Chasmagnathus granulata*); different letters indicate significant differences among replicates (*replicate experiment with invasion of adults or juveniles)

Species	Size (mm) and number of survivors in replicate field experiments					Size (mm) in the laboratory
	1	2	3	4	5	
<i>Cyrtograpsus angulatus</i>	6.7±1 (12) a	6.7±1.2 (18) a	5.6±1.1 (7)* b	7.8 ±1 (15) c	8.2±1 (18) c	4.4±0.2
<i>Chasmagnathus granulata</i>	2.5±0.3 (26) a	2.5±0.1 (17) a	2.6±0.3 (26) a	2.7±0.3 (8)* a	— —	2.5±0.1

Fig. 6 B

B *Chasmagnathus granulata*

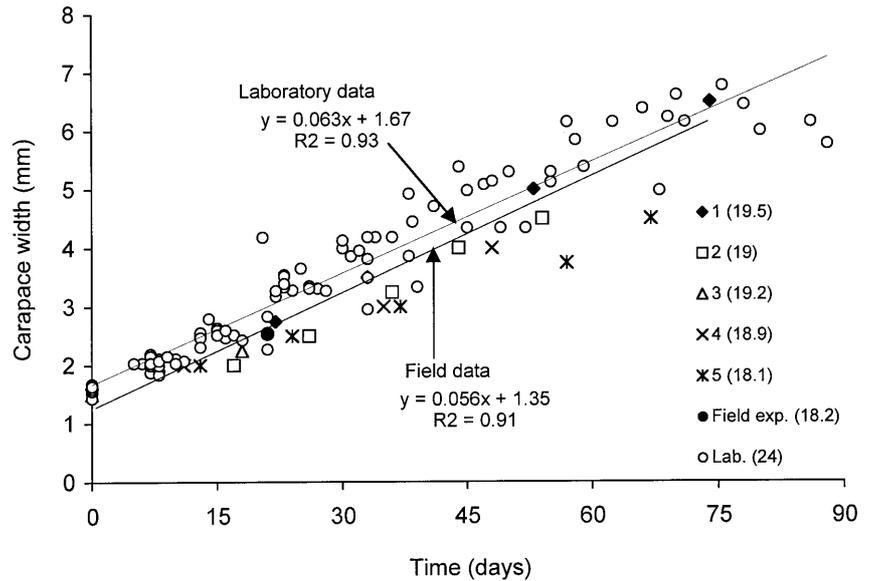
the size reached in the field did not differ significantly from that in the laboratory ($T=1,469$, $P>0.1$).

Discussion

During the juvenile development of *Cy. angulatus* and *Ch. granulata*, the intermolt period (IP) increased, especially after instar 4, while the percentage size increment (PSI) tended to decrease. These patterns have commonly been observed in various crustaceans (e.g. Kurata 1962; Mauchline 1977; Hartnoll 1982; Mohamedeen and Hartnoll 1989; Tweedale et al. 1993). Compared with a previous study by Spivak (1988) on a marine population of *Cy. angulatus*, the PSI measured in this study, in the

same species, was generally higher, while the IP was shorter. In individuals with 5 mm CW, for instance, the PSI observed in this study was 27% and the IP was 8 days, whereas Spivak estimated 22.4% and 17 days, respectively. The rearing conditions differed in these studies mainly in the type of food, while the temperatures were similar. Longer IP and lower PSI values were also reported for juvenile *Ch. granulata* from Lagoa dos Patos (Brazil) reared at 20°C (Rieger and Nakagawa 1995). In this case, the lower temperature explains differences in the IP. However, strong differences were observed also in size: the first crab instar was 28% larger in Mar Chiquita (CW=1.61 mm in Mar Chiquita vs 1.26 mm in Lagoa dos Patos); this difference increased in later instars, in spite of similar rearing conditions, reaching 57% in the C8 instar.

Fig. 7 *Chasmagnathus granulata*): growth of *Chasmagnathus granulata* according to field samples (sampling dates: 29 December 1992, 28 December 1993, 2 February 1994, 4 January 1995, 15 January 1995; corresponding to presumable cohorts 1–5 as identified from Fig. 6b), in field experiments (field exp), and in laboratory experiments (lab)



The carapace shape changes in both species during the development through the first juvenile instars; in the megalopae, it is notably longer than wide, especially in *Cy. angulatus*, while the opposite relation is typical of the adults. Rieger and Nakagawa (1995) and Gebauer et al. (1999) reported similar relationships between LC and CW for *Ch. granulata*.

The morphological traits of the chelae and of the pleon are considered as secondary sexual characters in the Brachyura (Hartnoll 1982; Yatsuzuka and Meruane 1987; Abelló et al. 1990; Minagawa 1993). Variations in the relative growth of these body parts are associated with different functions in reproduction. The larger male chelipeds are used in courtship, combat and carrying the female during copula; they show a higher proportional growth in relation to total body size (Hartnoll 1982; Minagawa 1993). The reverse was found in the pleon, which shows a faster relative growth in females, where it forms the incubatory chamber for developing eggs, while the male pleon protects and supports the intromittent organs (Hartnoll 1982; Minagawa 1993).

In both species, the chelae begin to show differences between the sexes early in development. This process of sexual differentiation starts earlier and is more intense in *Ch. granulata* than in *Cy. angulatus*. Chela dimorphism in Decapoda is frequently associated with sexual selection and mating systems (Orensanz and Gallucci 1988). It was suggested that the mating system is characterized by resource (burrow) defense in *Ch. granulata* and by female defense or male dominance in *Cy. angulatus* (Gavio and Spivak 1994). An early acquisition of chelar dimorphism in *Ch. granulata* could thus be associated with the building and defense of burrows, where mating usually takes place (T.A. Luppi, personal observation). The suggested mating system of *Cy. angulatus* is characterized by a less well developed sexual dimorphism of the chelae (Orensanz and Gallucci 1994).

The pleon differentiates early in *Cy. angulatus* females; in *Ch. granulata*, in contrast, it is impossible to recognize the sex before the C9 instar. The growth increment per molt is lower in *Ch. granulata* than in *Cy. angulatus* (Figs. 2 and 5). Since the females of both species mature at similar sizes (T.A. Luppi, unpublished data), there should be differences in the number of molts needed to reach maturity.

Sexual maturity in crabs occurs after a “puberty” molt, when morphological changes can be recognized by changes in the slopes of regressions describing relative growth. The immature phase of the crab life cycle includes an “undifferentiated period”, which is characterized by the lack of variation in allometric growth of those organs that both sexes have in common, followed by a “juvenile period” with sexual differences in relative growth, and these periods may be separated by a particular molt (Hartnoll 1982). In the species studied here, however, sexual differences in various structures became evident in different instars (Fig. 4).

Low temperature increases the IP in *Cy. angulatus*, as has been reported for many species of crustaceans (e.g. Tagatz 1968; Leffler 1972; Chittleborough 1975; Hartnoll 1982; Cadman and Weinstein 1988; Tunberg and Creswell 1991), and it appears to cause the attainment of a larger body size, as also observed in other crabs (Leffler 1972; Chittleborough 1975; Hartnoll 1982). Daily changes in water temperature (ranging in summer between 15 and 34°C) may thus explain also the larger range of variability in the size of the C1 instar in the field (25% of the mean) as compared with that observed under constant laboratory conditions (10%). Effects of physical factors (temperature, salinity), interacting with those of diet, were also suggested as an explanation for size variability in C1 *Cancer magister* (DeBrosse et al. 1990; Dinnel et al. 1993). On the other hand, a 5th zoea appeared in *Ch. granulata* under extreme environmental conditions (starvation, low salinity;

see Pestana and Ostrensky 1995), and C1 juveniles originating from this alternative developmental pattern tended to be larger (Gimenez 2000).

The SFDs of both species were characterized by a period of evident modal size displacement from October to May and a period without changes in winter. The latter should be a consequence of a reduced growth due to low temperatures (Fig. 1). Moreover, a marked decrease in juvenile activity occurs in the field during winter (T.A. Luppi, personal observation). Likewise, growth decreased or ceased in *Callinectes sapidus* and *Cancer magister* below critical temperatures in winter (Tagatz 1968; Leffler 1972; Orensanz and Gallucci 1988; McMillan et al. 1995).

The growth rates of *Ch. granulata* in the field, as estimated from the displacement of modal size classes, and those in laboratory cultures were similar, in spite of marked differences in the thermal regime. Among several cohorts, however, the size reached after a similar time span differed by up to 33%, which may be explained by combined effects of temperature and salinity variations. These environmental factors were also shown to affect juvenile growth in *Menippe mercenaria* (Brown et al. 1992).

In our study, *Cy. angulatus* generally grew faster in field enclosures than in laboratory cultures, as found also in *Ca. magister* (Collier 1983). On the other hand, the crabs in different parallel experiments (replicates) exhibited different sizes (Table 3), probably as a consequence of microscale differences in temperature which may reach about 4°C in Mar Chiquita lagoon (see Anger et al. 1994). Similarly, growth differs between early and late cohorts, due to marked seasonal temperature differences. A megalopa settling in early summer (December) should live for about 30 days within the polychete "reef", where it is prone to intra- and interspecific predation by larger crabs (Luppi 1999). After this initial period, the juveniles leave this nursery habitat and migrate to open sediment areas. The surviving recruits may become sexually mature before the end of recruitment period. However, ovigerous females were seldom observed in late summer or autumn, suggesting that *Cy. angulatus* normally produces its first offspring at the beginning of the following spring season (Spivak et al. 1996). Megalopae that settle only in late summer (March), by contrast, should remain in the "reef" habitat, until they resume their growth the next spring. Crabs from the latest cohort may not reach maturity until the end of the following summer.

In one of the field experiments, high mortality occurred in *Cy. angulatus* (but not in *Ch. granulata*), presumably caused by cannibalism or predation by invading juvenile or adult crabs, and coinciding with a particularly small recruit size in this species. In recruits of *Carcinus maenas*, reduced growth and feeding activity were also observed when larger conspecific crabs were present (Adelung 1971; Klein Breteler 1975). In *Ch. granulata*, in contrast, recruits and adults were observed to coexist in the natural habitat, showing apparently low pressure of cannibalism (Luppi 1999).

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