

Somatic growth in juveniles of the estuarine crab *Chasmagnathus granulata* Dana 1851 (Brachyura, Grapsidae), under laboratory conditions

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ABSTRACT: Male and female juvenile crabs of the species *Chasmagnathus granulata* were collected in Samborombón Bay (Argentina), on October 1994 and February 1995; these dates correspond to the beginning and end of the reproductive period of the species, respectively. No differences in the initial size (measured as carapace width, CW) existed between both clutches. Each clutch of juveniles was observed during a 1-year period, recording the percentage of molted crabs, intermolt period and percentual increment of size after each molting. At the end of the observation period, males and females from the October clutch reached the size of sexual maturity, while crabs of the remaining clutch did not. This difference was due to the higher increment in size of the October crabs at the third and fourth molts, compared to the February ones. Such difference seems to be related to an increase in reproductive effort during the breeding season, once the sexual maturity was attained.

Key words: somatic growth, juveniles, crabs, laboratory conditions.

Crecimiento somático en juveniles del cangrejo de estuario *Chasmagnathus granulata* Dana 1851 (Brachyura, Grapsidae), bajo condiciones de laboratorio

RESUMEN: Se recolectaron en Bahía Samborombón (Argentina), ejemplares juveniles de ambos sexos de la especie *Chasmagnathus granulata*, durante octubre de 1994 y febrero de 1995; estos meses corresponden, respectivamente, al inicio y al final del período reproductivo de la especie. No se hallaron diferencias entre lotes para el ancho inicial de caparazón (CW). Cada lote de cangrejos juveniles fue observado durante un año en condiciones de laboratorio, registrándose el porcentaje de cangrejos mudados, período de intermuda e incremento porcentual de talla luego de cada muda. Al finalizar el período de observación, machos y hembras del lote de octubre alcanzaron la talla de madurez sexual mientras que los del lote de febrero no consiguieron alcanzar esa talla. Esta diferencia se debió al mayor incremento de talla de los cangrejos del lote de octubre en su tercera y cuarta muda, comparados con los cangrejo del otro lote. Tal diferencia parece estar relacionada con un incremento del esfuerzo reproductivo durante el período reproductivo, una vez alcanzada la madurez sexual.

Palabras claves: crecimiento somático, juveniles, cangrejos, condiciones de laboratorio.

INTRODUCTION

Tissue growth is essentially a continuous process in Crustacea, although the increase in body size is a discontinuous one, which involves a series of integument molts allowing a rapid increase in body size before the new cuticle hardens and becomes rigid (Hartnoll, 1982 ; 1983). Growth can be

estimated by several methods, such as: molt increment (increase in size at molting) together with frequency of molting (Hyatt, 1948 ; Spivak, 1988), observations of age and size (Oliva *et al.*, 1997), mark-recapture observations (Arana, 1992 ; Lovrich and Vinuesa, 1995) and statistical analysis of size

frequency data (D'Incao *et al.*, 1993 ; Roa and Bahamonde, 1993 ; Oliva *et al.*, 1997). These studies are also important tools for understanding population dynamic of marine species and for recommending alternative strategies for exploitation and management of marine resources (Arana, 1992 ; Roa and Bahamonde, 1993 ; Lovrich and Vinuesa, 1995 ; Oliva *et al.*, 1997).

Different patterns of growth in juvenile stages have been extensively studied in relation with the acquisition of sexual maturity (Hartnoll, 1974; 1978). Larvae, juveniles or adults of a particular species may exhibit different growth patterns (Hartnoll, 1965, 1982, 1983 ; Felder *et al.*, 1985 ; Fukui, 1988). Growth, survival and feeding rate of larvae and juveniles can be modulated by temperature (Klein Breteler, 1975 ; Kondzela and Shirley, 1993 ; Wainwright and Armstrong, 1993). This could explain why the age at sexual maturity of some crustaceans, or their incorporation to the commercial fishery, may vary with location (Hines, 1989 ; Kondzela and Shirley, 1993 ; Stevens, 1990).

Chasmagnathus granulata (Decapoda, Brachyura, Grapsidae) is an intertidal estuarine crabs from salt marsh environments along the Atlantic coast of Argentina, Uruguay and southern Brazil. In Samborombón Bay (36°18'S, 56°48'W, Argentina), the reproductive season of this species comprises the spring and summer months, i.e., September to March (Rodríguez, 1991), and even extent to April (unpublished observations). Each female can spawn up three or four times during the reproductive period, with an egg incubation period of nearly a month (López, 1997). By this way, females can produce more than one cohorts during the same reproductive period. After four zoea instars (Boschi *et al.*, 1967), the megalopa stage reaches the coastline for molting to the first juvenile instar. Juveniles successively molt to reach the size of sexual maturity (López *et al.*, 1997) and thus the beginning of the adult condition.

The growth rate of *C. granulata* (Bertalanffy growth rate curves) has been studied from crabs sampled at Lagoa dos Patos, Brazil (D' Incao *et al.*, 1993). The present work was aimed at evaluating the somatic growth of *C. granulata* juvenile crabs from Samborombón Bay, during 1 year and under controlled conditions. We have also tried to evaluate if juvenile crabs of the same size, but sampled at the beginning or end of the reproductive season, are equally able to reach the mature size in the next reproductive period.

MATERIALS AND METHODS

Males and females juvenile crabs were collected at Faro San Antonio beach, southern edge of Samborombón Bay on two dates: October 1994 and February 1995. Number of collected crabs, together with the mean carapace width at the beginning of experiments, are listed in Table 1. Carapace width (CW) was always measured behind the third cephalothoracic spine (maximum CW). Because of their sizes, selected crabs necessarily hatched as larvae in the previous reproductive period they were sampled (Boschi *et al.*, 1967). The size of employed crabs were also below the size at sexual maturity reported previously, according to changes in allometric growth of secondary reproductive characters (López *et al.*, 1997).

Once in the laboratory, a two week acclimation period took place, under the same environmental conditions to be used later during the experiments. These experiments comprised a 1 year observation period. Each crab was isolated in a plastic container of 200 ml capacity, filled with 30 ml of artificial saline water at 12 ‰ salinity (HW Germany salts added to dechlorinated tap water) renewed twice a week after feeding . Temperature was always maintained at $20 \pm 1^\circ\text{C}$, while photoperiod was kept at 14:10 L:D from September to March (the reproductive months) or 12:12 L:D during the rest of the year. Crabs were fed *ad libitum* twice a week on pellets of rabbit food with the following composition (in relation to wet weight): protein 17%, fat 3%, fiber 15%, digestible energy 2700 kcal/kg. All crabs were daily examined, recording the following events: occurrence of molt, date of molting and size (CW) after molting.

The observation period began on October 10th and February 20th, for crabs sampled on October 1994 (clutch 1) and February 1995 (clutch 2) respectively. The initial size of crabs, for males and females, was compared between clutches by Student t - test.

Percentage of molted crabs, intermolt period and percentual increment of size after each molting were estimated from recorded data. Pre-molt size was measured in the exuvia, while the post-molt size was measured in hardened, 20-d post-molted crabs, by means of a vernier caliper (precision 0.02mm). The percentual increment of size (%inc) was calculated as follows :

$$\% \text{ Inc} = \frac{\text{Post-molt size (CW)} - \text{Pre-molt size (CW)}}{\text{Pre-molt size (CW)}} \times 100$$

while the annual size increment (% Ann-Inc) was calculated as:

$$\% \text{ Ann-Inc} = \frac{\text{FCW} - \text{ICW}}{\text{ICW}} \times 100$$

where FCW: final carapace width (one year after the beginning of the experiment) and ICW: initial carapace width (at the beginning of the experiment)

No determination of crab weight was made. Fisher exact test was used to compare proportions of molted crabs between sexes or clutches. Chi-square test was applied for contingency tables greater than 2x2. A two-way ANOVA was applied to analyze time between molts, taking as factors clutch and sex, while the increment of size after molting was analyzed by a two-way ANCOVA test, considering the same factors above mentioned and taking the initial size as the covariables (Sokal and Rohlf, 1979). A significance level of 0.05 was employed for all tests.

RESULTS

Table 1 shows the final carapace width of crabs, together with the annual increment in CW, i.e. the

increment in the size of crabs that were alive at the end of the observation period, regardless of the number of molts they had. Results of the statistical comparisons between sexes and clutches by ANCOVA (Table 1), showed no differences ($p > 0.05$) between sexes but significant ones ($p < 0.05$) between clutches, the higher increment corresponding to the October clutch.

No significant differences ($p > 0.05$) existed between clutches, as for the initial mean carapace width, neither for males nor for females. As for % of molted crabs (Table 2), a significant difference ($p < 0.05$) was only found between clutches at the second molt, a higher percentage corresponding to the February clutch. No significant differences ($p > 0.05$) were in the intermolt period, in neither case. Concerning the increment in CW, no differences existed between sexes, but a significant difference was detected between clutches at the third ($p < 0.001$) and fourth ($p < 0.05$) molts, the higher increments corresponding to the October clutch (Table 2).

Results of statistical comparisons by Chi-square of the percentages of molt occurrence in regard to season and lunar phase (Table 3), recorded for each clutch during the complete 1-year observation period, indicated that no significant differences between clutches were evident neither for seasons

Table 1. Mean carapace width and number of *Chasmagnathus granulata* (initial values). SE: standard error of mean; ICW: initial carapace width; Ni: initial number of crabs; FCW: final carapace width; Na and %Annual-Inc: number of alive crabs and annual size (CW) increment at the end of the 1-year observation period, respectively. ANCOVA results of comparing FCW (taking ICW as covariable) between clutches and sexes are also indicated.

Tabla 1. Ancho de caparazón promedio y número de ejemplares de *Chasmagnathus granulata* (valores iniciales). SE: error estándar de la media ; ICW: ancho inicial de caparazón; FCW: ancho final de caparazón; Na and %Ann-Inc: número de cangrejos vivos e incremento anual de talla (CW) al final del período de observación de 1 año, respectivamente. se indican los resultados de la comparación por ANCOVA de FCW (tomando ICW como covariable) entre lotes y sexos.

Clutch	Sex	ICW±SE	Ni	FCW±SE	Na	%Ann-Inc ±SE	p value
1 (October)	males	12.45±0.31	13	18.83±0.76	7	52.83±6.54	between clutches ($p < 0.001$)
	females	12.74±0.54	11	19.95±0.65	6	56.84±7.73	
2 (February)	males	11.71±0.33	40	15.59±0.40	26	38.18±3.46	between sexes ($p > 0.05$)
	females	12.31±0.23	60	15.73±0.34	35	34.06±3.21	

Table 2. Percentages of molted crabs, time between molts (days) and percentages of size increment for both juvenile clutches of *C. granulata*; % molted.: percentage of molted crabs, always on the initial crab number (see Table 1); $T_{i.m.} \pm SE$: mean time of intermolt (since the previous one) \pm standard error of mean; %Inc. $\pm SE$: mean percentage of CW increment \pm standard error of mean. N.D.: not determined; p values are indicated for the statistical comparisons between sexes and clutches.

Tabla 2. Porcentaje de cangrejos mudados, tiempo entre mudas (días), porcentajes de incremento de talla y resultado de las comparaciones estadísticas entre sexos y lotes para cangrejos juveniles de *C. granulata*: % molted: porcentaje de cangrejos mudados (referidos al número inicial, ver tabla 1); $T_{i.m.} \pm SE$: valor medio de intermuda (desde el evento previo) \pm error estandar de la media ; %Inc. $\pm SE$: incremento porcentual medio en el ancho de caparazón \pm error estandar de la media; N.D.: no determinado; se indican los valores de p de las comparaciones estadísticas entre sexos y lotes.

Molt event	Variable	Clutch 1		Clutch 2		between sexes	between clutches
		males	females	males	females		
First	% molted	100	90.90	100	100	>0.990	0.19
	$T_{i.m.} \pm SE$	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.
	% Inc. $\pm SE$	10.85 \pm 0.93	9.97 \pm 0.82	10.71 \pm 0.66	10.84 \pm 0.61	0.87	0.79
Second	% molted	92.30	72.70	100	96.70	0.24	0.01
	$T_{i.m.} \pm SE$	91.10 \pm 7.50	112 \pm 5.30	108.70 \pm 8.60	101.90 \pm 5.70	0.53	0.74
	% Inc. $\pm SE$	13.13 \pm 1.04	17.75 \pm 1.98	12.94 \pm 1.02	14.44 \pm 0.79	0.06	0.05
Third	% molted	92.30	72.70	57.50	68.30	0.85	0.09
	$T_{i.m.} \pm SE$	105.90 \pm 9.30	104.80 \pm 8.60	113.40 \pm 10.0	107.20 \pm 5.30	0.71	0.62
	% Inc. $\pm SE$	14.78 \pm 1.26	15.82 \pm 0.62	9.42 \pm 0.91	10.81 \pm 0.65	0.17	<0.001
Fourth	% molted	30.80	9.10	22.50	15	0.17	0.77
	$T_{i.m.} \pm SE$	103.50 \pm 8.14	93.00 \pm 0.00	104.10 \pm 9.20	91.60 \pm 11.00	0.66	0.46
	% Inc. $\pm SE$	12.67 \pm 1.66	14.50 \pm 0.00	9.67 \pm 1.41	12.29 \pm 1.27	0.60	0.04

Table 3. Percentages of molting by season and lunar phase, for each clutch of *Chasmagnathus granulata*. Nm: number of molts. LQM: last quarter moon, NM: new moon, FQM: first quarter moon, FM: full moon.

Tabla 3. Porcentajes de mudas por estación y fase lunar, para cada lote de *chasmagnathus granulata*. Nm: número de mudas. LQM: luna cuarto menguante, NM: luna nueva, FQM: luna cuarto creciente, FM: luna llena.

Clutch	Nm	Season				Lunar phase			
		Spring	Summer	Autumn	Winter	LQM	NM	FQM	FM
October	69	33.30	18.80	27.50	20.30	29.00	30.40	23.20	17.40
February	278	22.70	11.90	37.80	27.70	32.70	31.30	20.50	15.50

($p=0.062$) nor for lunar phases ($p=0.902$). Most of molting events occurred at night.

DISCUSSION

Juvenile crabs usually grow at a higher rate than adults, i.e. the percentage increment in body size

declines as the size of crabs increases (Hartnoll, 1982; 1983). This relative rapid growth of juveniles would be relevant for their efficient recruitment to the reproductive stock of the species, the growth rate depending on the availability of food among other factors (Sastry, 1983). In general terms, the significance of environmental signals to the

neuroendocrine mechanisms that regulate growth and maturation of juvenile crabs is far to be well established.

We have observed up to four consecutive molts of the juvenile crabs assayed, being more frequently three molts as maximum, at least under the laboratory conditions maintained during the 1-year observation period. Nevertheless, extrapolation of these results to a field situation should be done carefully. In this regard, we have no information about the annual number of molts, neither about the temporal distribution of molting throughout the year, for crabs in their natural environment. It is well known that low temperatures may inhibit the molting process in crabs (Hyatt, 1948; Boschi *et al.*, 1967; Tsuchida and Watanabe, 1997). Ambient temperature in Samborombón Bay annually ranges from 8.2 to 23.3°C (Piccolo and Perillo, 1997), the mean being significantly lower than the constant we maintained in the laboratory during the entire observation period. According to Boschi *et al.*, (1967) a laboratory temperature ranging 12-17°C could be responsible of the "slow growth" of small *C. granulata* juvenile crabs. Nevertheless, juvenile and early adults of the grapsid crab *Cyrtograpsus angulatus*, who lives in the same environments that *C. granulata*, molted throughout the year, both in field and laboratory conditions (Spivak, 1988).

Besides temperature, other factors can affect the process and the timing of molting in the field and in the laboratory. Nutrition often appears to be the dominant factor in postlarval growth (Felder *et al.*, 1985). Food is the main growth determinant in the field for juvenile and adult crabs of *Aratus pisonii* (Conde and Díaz, 1989) and for *Carcinus maenas* juveniles, to whom the interaction between food and temperature, under laboratory conditions, seemed to affect the size increment with molting and the intermolt period (Klein Breteler, 1975).

The seasonal ecdysis pattern of *C. granulata* juvenile crabs has shown to be quite different from the adult pattern, since the former molted throughout the year while the latter mainly during April and May, at the same experimental conditions as the juveniles (López, 1997). Since somatic growth and reproduction have been recognized as antagonistic events in adult crabs (Adiyodi, 1988), they molt once the reproductive period has ended, while juveniles molt during the entire year. In the case of *Paralomis granulosa*, while adult crabs only molted during spring and summer, juveniles also molted during

winter (Lovrich and Vinuesa, 1995).

There have been described diary and seasonal patterns of ecdysis in crustaceans. As observed in our experiments, molting at night could minimize the effect of cannibalism and has been also reported for the grapsid crabs *Pachygrapsus crassipes* (Hyatt, 1948) and *Cyclograpsus punctatus* (Broekhuysen, 1941), and for other decapod crustaceans (Broekhuysen, 1941; Skewes *et al.*, 1994; Dworschak, 1988; Mac Diarmid, 1989). We have also observed a close correlation between the timing of molting and the lunar cycle. Juvenile crabs mainly molted during the less shining phases, likely to minimize the risk of predation or cannibalism. Interestingly, this molting rhythm was maintained under constant laboratory conditions (as for temperature and photoperiod). The crab *Carcinus maenas* showed both a circadian and circatidal rhythm of ecdysis, related to the minimization of cannibalism and to the juvenile recruitment (Zeng *et al.*, 1997).

The size increment after molting we have recorded in *C. granulata* (9,67 to 17,75 % of the premolt carapace width) was similar to that of other juvenile grapsid, semiterrestrial crabs (Table 4). Size increment of those species, was always lower than that showed by crabs from strictly aquatic environments (specially Majidae, Cancridae and Portunidae) and greater than that of terrestrial crabs (Hartnoll, 1965). Comparing the intermolt periods recorded for the *C. granulata* juvenile crabs with those of other juvenile grapsid crabs showed a high degree of variability, as reported in Table 5.

In accordance with the reported for other grapsid crabs like *P. crassipes*, *A. pisonii*, *Sesarma ricordi*, *Pachygrapsus transversus*, *Pachygrapsus gracilis* y *Cyclograpsus integer* (Hartnoll, 1965; Fukui, 1988; Warner, 1967) no difference between sexes were noted in the size increment of *C. granulata* juveniles. Once the sexual maturity is achieved, the mentioned species showed differential somatic growth between sexes (females growing lesser than males).

The reproductive size of the *C. granulata* was previously determined, for both sexes (López *et al.*, 1997). For males, the body size associated with a change in the relative growth of reproductive characters was 16.50 mm CW, this size seems to be the functional maturity one, since mating was observed just above it. As for females, mature ovaries were observed at 19.00 mm CW, the smallest

Table 4. Size increment after molting in juvenile grapsid crabs.**Tabla 4. Incrementos de talla después de la muda en juveniles del cangrejo de estuario.**

Species	Size increment (%)	Reference
<i>Chasmagnathus granulata</i>	9.7-17.8 %	This study
<i>Pachygrapsus crassipes</i>	14-29 both sexes	Hyatt, 1948
<i>Pachygrapsus marmoratus</i>	15% both sexes	Vernet and Charmantier-Daures, 1994
<i>Cyclograpsus punctatus</i>	9-20 both sexes	Broekhuysen, 1941
<i>Cyrtograpsus angulatus</i>	16- 24 males 17- 22 females	Spivak, 1988
<i>Eriocheir sinensis</i>	nearly 6 both sexes	Vernet and Charmantier-Daures, 1994
<i>Sesarma jarvisi</i>	11.2 both sexes	Diesel and Horst, 1995
<i>Hemigrapsus sanguineus</i>	17.4-30	Fukui, 1988
<i>Hemigrapsus penicillatus</i>		Fukui, 1988
<i>Gaetice depressus</i>		Fukui, 1988
<i>Acmaeopleura parvula</i>		Fukui, 1988
<i>Nanosesarma gordonii</i>		Fukui, 1988

Table 5. Intermolt period of juvenile grapsid crabs.**Tabla 5. Período de intermuda en juveniles del cangrejo de estuario.**

Species	Intermolt period (days)	reference
<i>Gaetice depressus</i>	4-117 *	Fukui, 1988
<i>Acmaeopleura parvula</i>	86-211 *	Fukui, 1988
<i>Nanosesarma gordonii</i>	22-53 *	Fukui, 1988
<i>Hemigrapsus sanguinolentus</i>	> 200 *	Fukui, 1988
<i>Cyclograpsus punctatus</i>	82-130	Broekhuysen, 1941
<i>Cyrtograpsus angulatus</i>	36-50	Spivak, 1988
<i>Pachygrapsus crassipes</i>	18-30	Hyatt, 1948

* Adults also included

size for ovigerous females being 20.28 mm CW (López *et al.*, 1997). Although we have not dissected the gonads of juveniles used in the current experiments, it becomes clear in this context that juveniles captured at the beginning of the reproductive season have reached the sexual maturity 1 year later, while juveniles of the same

initial size than the former ones, but captured at the end of the reproductive period, did not.

As stated in the Introduction, sampled juveniles from both clutches had necessarily hatched in the previous reproductive season, probably from early and late spawns of females, according to Boschi *et al.* (1967) and López (1997). Therefore, from our

results we conclude that a minimum of two and a maximum of three years are needed to reach the sexual maturity from the larval stages. This estimation is similar to that reported for other grapsid crabs (Diesel and Horst, 1995; Fukui, 1988; Tsuchida and Watanabe, 1997). For instance, larvae of *Plagusia dentipes* (Grapsidae), hatched at the beginning of the reproductive period, acquire the sexual maturity nearly one year before than those larvae hatched at the end of the same reproductive period. As a result, both cohorts differ in size at the onset of sexual maturity. As size is a major determinant of crab fecundity (Hines, 1982, 1988), the fecundity of both cohort differs (Tsuchida and Watanabe, 1997).

Adult females of *C. granulata* are able to have up to four spawning during a reproductive period (López, 1997). Juveniles sampled in October would have the opportunity to reproduce more than once during the next reproductive season if they reached the sexual maturity in one year, as it was the case according to our experimental results. Even presenting a similar growth rate, juveniles collected in February would have reached the sexual maturity only by the end of the next reproductive period, thus having the chance for only one reproductive event. In fact, they grew at a lower rate than the October juveniles. Therefore, we believe that an extra energy investment for growth takes place in juveniles that can reach the sexual maturity at the beginning of a reproductive period, perhaps as part of a strategy to maximize the efficiency of juvenile recruitment to the reproductive stock and thus, as a way of optimizing the reproductive investment of the species.

The difference encountered between clutches was related to the size increment at molting, instead of percentual of molted crabs or intermolt period. Such difference did not seem to be related to fluctuations in physical or abiotic factors, since temperature, salinity, quantity and quality of food were maintained at a same constant level during the entire year comprised by each one of the clutches. Some environmental cues received by juvenile crabs during their recent history, i.e. previously to their sampling at the beginning or end of the reproductive period of the species, seems to be crucial for determining the subsequent molting pattern.

Besides, the "advantage" taken by the October clutch in size increment took place at the third molt (eventually the fourth as well). The higher

photoperiod maintained in the laboratory during spring and summer (14L:10D), than during autumn and winter (12L:12D), did not seem to act as an environmental cue to trigger the observed difference in size increment, since the third molt of October juveniles occurred in the winter while the third molt of the other clutch took place during spring. Perhaps, the natural photoperiod or other stimulus were relevant as triggers at sampling dates. Even an endogenous component might be acting, since juveniles hatched as larvae, but the nature of these mechanisms should be subject of further research.

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