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Larval growth in the estuarine crab *Chasmagnathus granulata*: the importance of salinity experienced during embryonic development, and the initial larval biomass

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Abstract The importance of salinity experienced during embryonic development and initial larval biomass on larval growth was studied in the South American estuarine crab *Chasmagnathus granulata*. Ovigerous females were maintained at three salinities (15, 20, and 32‰) from egg laying to hatching of zoea 1. Larvae from all treatments were reared under constant conditions of photoperiod (12:12), temperature (18°C), and salinity (first instar at 20‰, subsequent instars at 32‰). Biomass was measured as dry weight, carbon, and nitrogen content per individual at egg laying, hatching of zoea 1, premoult zoea 1, and zoea 4, and in 8-day-old megalopa. From hatching to premoult zoea 4, biomass was higher for larvae from prehatching salinities of 15 and 32‰. There was a significant positive correlation between biomass at hatching and at premoult zoea 1 and zoea 4. Accumulated biomass during zoeal stages tended to be higher for larvae from broods with higher biomass at hatching, although this trend was not always significant. Zoea 4 either directly metamorphosed to megalopa or moulted to zoea 5, following, respectively, a short or long developmental pathway. The proportion of zoea 4 that followed the long pathway was negatively correlated with biomass of zoeal stages. Biomass at hatching was correlated with biomass of megalopae developed through the short pathway, although it was not correlated with the accumulated biomass at this stage. Megalopae developed through the long pathway (i.e. metamorphosed from zoeae 5) had higher biomass than those from the short pathway. The present results suggest that prehatching salinity and initial egg and larval biomass can be very important for larval growth.

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Introduction

Larval development of marine organisms is characterised by important changes in organic and inorganic constituents during growth and morphogenesis. Patterns of growth and morphogenesis depend on phylogeny and are affected by environmental factors (Pechenik 1987; Anger 1990, 1991, 1998; George 1996, 1999). In decapod crustaceans with conspicuous metamorphic changes (e.g. brachyuran crabs) growth is species and stage dependent (Anger 1990, 1998). Food availability and quality (Anger and Dawirs 1982; Dawirs 1986, 1987; Harms et al. 1991, 1994), temperature (Dawirs and Dietrich 1986; Anger 1987), and salinity (Anger et al. 1998, 2000) stress can have detrimental effects on growth, decreasing the rate of accumulation of biomass.

In coastal waters, osmotic stress due to low and variable salinities may reduce growth rates and then fitness of larvae. Low salinities lead to a decrement in growth rates or even loss of weight in larval instars of several marine and estuarine crustaceans (Johns 1982; Pfaff 1997; Anger et al. 1998, 2000); instars with osmoregulatory abilities seem to be less sensitive to low salinity (G. Torres et al., in press). Effects of salinity on larval growth may also depend on initial larval reserves or acclimation history, especially in estuarine crabs. For example, zoeae 1 of the South American estuarine crab *Chasmagnathus granulata* survive and successfully moult to the second zoea at low salinities (5–10‰) if previous embryos developed at 15 or 20‰ instead of 32‰ (Giménez 2000). This acclimation process also favours larval tolerance to short starvation periods at 20‰, through an increment in the rate of accumulation in carbon (C) and nitrogen (N; Giménez 2002). In this estuarine species, embryos are expected to develop under

the variable conditions of salinity. Additionally, as populations occupy different types of estuarine habitats of south Brazil, Uruguay, and Argentina (Boschi 1964) it should be expected that larvae from different populations hatch from embryos developed under different salinities. *C. granulata* exhibits an export strategy (Anger et al. 1994): zoeae 1 hatch in the estuarine water and are transported to the open sea where they develop through four or five zoeal stages and a megalopa (Boschi et al. 1967; Pestana and Ostrensky 1995). Biomass of freshly hatched zoea 1 depends on initial egg biomass and salinity experienced during embryogenesis (Giménez and Anger 2001). Besides, biomass affects larval survival and duration of development (Giménez 2000).

The previously described patterns of larval survival and development may be due to changes in the osmoregulatory capacity and effects of individual biomass at hatching on the amount of reserves existing at subsequent larval instars. Changes in osmoregulatory capacity during larval development of *C. granulata* have been recently studied (Charmantier et al. 2002). In the present article, we explored in laboratory experiments the effect of prehatching salinity and initial egg and larval biomass on the amount of reserves at all larval instars of *C. granulata*. In particular, we evaluated the effect of (1) prehatching salinity (i.e. the salinity experienced during embryonic development), and (2) initial individual larval biomass [i.e. individual dry weight (DW), C, and N content at hatching] on larval growth of *C. granulata* from the first instar to the megalopa.

Materials and methods

All experiments were conducted under controlled conditions of temperature (18°C) and photoperiod (12:12). Seawater (32‰) for experiments was filtered (Orion, mesh size: 1 μm); water of lower salinities was obtained by diluting appropriate quantities of seawater with artificially desalinated water. Three groups of ovigerous females (ten females/broods per group) were maintained, isolated from egg laying to hatching of larvae, in individual aquaria at three prehatching salinities (15, 20, and 32‰), respectively; that is, there were ten aquaria per prehatching salinity. Embryonic development takes about 30 days and it is not significantly influenced by salinity (Giménez and Anger 2001). Ovigerous females maintained at 15‰ during embryogenesis laid eggs at 15‰, other females at 32‰ (see Giménez and Anger 2001 for details). Females were fed isopods; water and food were changed every day. Freshly hatched larvae were mass reared at 20‰ during the first zoea, and at 32‰ from zoea 2 to premoult megalopa, simulating presumed natural conditions of export strategy. Individual larval biomass was measured as DW, C, and N content at egg laying (initial egg biomass), hatching of zoea 1 (initial larval biomass), premoult zoeae 1 and 4, and at about 70% of total development duration of the megalopa (i.e. on day 8 from metamorphosis of the last zoeal instar, when C and N reach their maximum levels: Anger and Ismael 1997). Three to five samples per brood were rinsed in distilled water for a few seconds, dried on filter paper, transferred to tin cartridges and dried for 48 h in a vacuum drier (Finn-Aqua Lyovac GT2E), weighed on a microbalance (Mettler UMT2, precision: 0.1 μg), and analysed in a Carlo Erba Elemental Analyser (EA 1108). The number of individuals per sample depended on larval stage: 40 for egg and zoea 1 at hatching, 35 for premoult zoea 1, 5 for premoult zoea 4, and 2 for megalopa.

Rearing of zoeal instars 1–4 was done in bottles (10 l), with gentle aeration. Freshly moulted zoea 4, zoea 5, or metamorphosed megalopa were sorted after the day of moulting to obtain homogeneous groups (i.e. individuals with the same age counting from the last moulting or metamorphosis). Zoeae 4 were reared in beakers (0.5–5 l) at a density of one individual per 10 ml. Megalopae were reared in aquaria, at a density of one individual per 30 ml, with a nylon gauze on the bottom as artificial substrate. Larvae were fed with *Artemia* sp.; water and food was changed every day.

Statistical analyses were run following Day and Quinn (1989), Zar (1996), and Underwood (1997). The effect of prehatching salinity on larval biomass was evaluated with one-factor analyses of variance (ANOVAs). The effect of initial larval biomass was added as a covariate to the ANOVAs (e.g. initial DW of zoea 1 as a covariate of DW at premoult zoea 1) and evaluated with Pearson correlation. The significance of correlations was adjusted by the sequential Bonferroni method (Rice 1989) for DW, C, and N content separately. The number of broods (=replicates) was 30 ($n=10$ for each prehatching salinity 15, 20, and 32‰) for eggs and zoea 1; 26 for zoea 4 ($n=7$, 9, and 10 for 15, 20, and 32‰, respectively); and 24 for the megalopae ($n=9$, 6, 9). This occurred because for some broods there was an insufficient number of zoea 4 for analyses, or because a considerable proportion of zoea 4 moulted to zoea 5 (see Results). The effect of prehatching salinity and initial larval biomass on biomass of megalopae was evaluated only for those larvae that followed the short larval pathway (i.e. those originated directly from the metamorphosis of a zoea 4). We also investigated possible correlations between the proportion of larvae that followed the long pathway (i.e. those originated from the metamorphosis of a zoea 5), and individual biomass at previous instars. Individual biomasses of larvae that followed the short and long pathways were compared with Student's *t*-test for paired samples. Before analyses, normality was checked with normal plots of residuals and heterogeneity of variance with Cochran's test; data were normally distributed and the variances were always homogeneous.

Results

Changes in biomass from egg laying to premoult zoea 4

Initial egg biomass was maximum for those laid at 15‰ (Fig. 1); eggs from broods incubated at 20 and 32‰ had similar biomass. After hatching, the highest C and N content were observed for larvae from prehatching salinities 15 and 32‰, although significant differences were found only between 15 and 20‰ (Fig. 1, Table 1). At premoult zoea 1 differences in biomass were significant only for DW, although for C and N content they were marginally significant ($0.05 < P < 0.10$). At premoult zoea 4 significant differences were found for C and N: larvae from 15 and 32‰ showed a significantly higher biomass than those from 20‰. For this stage, differences in DW were marginally significant (Table 1). The introduction of the initial larval biomass as a covariate gave the same results as described above.

Accumulated biomass, measured as DW, from hatching to premoult zoea 1 was higher for larvae from the prehatching salinity 15‰ (Fig. 2; Table 2); there were, however, no significant differences for C and N content. This pattern did not change when the initial larval biomass was used as a covariate. The highest accumulated biomass from hatching to premoult zoea 4 was for larvae from the prehatching salinities 15 and 32‰ (Fig. 2). However, significant differences were

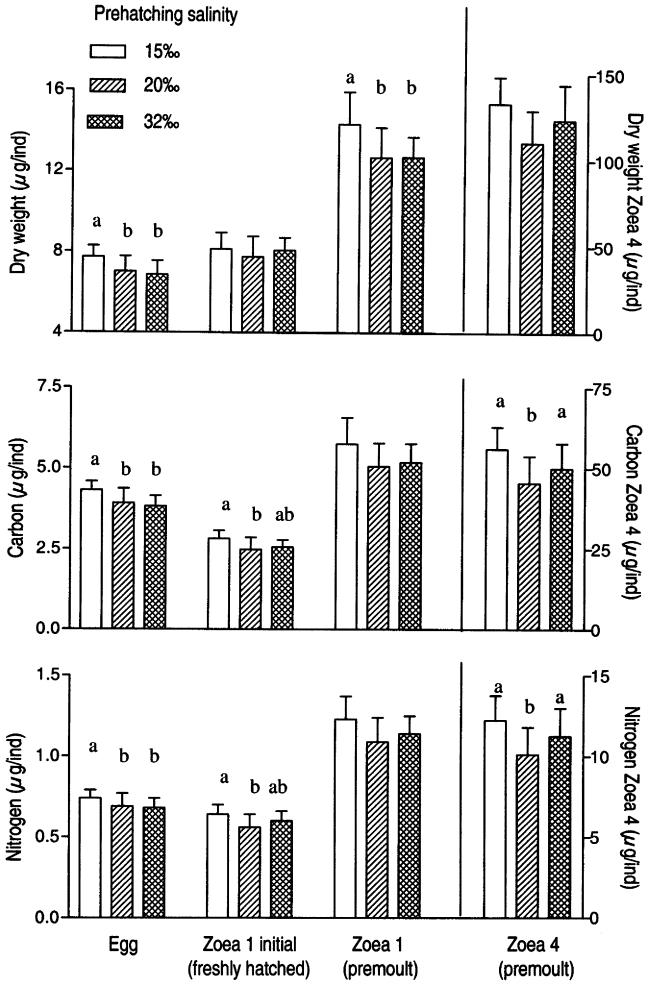

Fig. 1 *Chasmagnathus granulata*. Changes in biomass from egg laying to premoult zoea 4 in larvae from different prehatching salinities. *Error bars* Standard deviation. *Different letters* indicate significant differences ($P < 0.05$) among prehatching salinities

Table 1 *Chasmagnathus granulata*. One-factor ANOVA to evaluate the effect of prehatching salinity on individual biomass [as dry weight (DW), carbon (C), and nitrogen (N) content] at various stages of zoeal development. *MSF* and *MSE* Mean squares of factors and error, respectively; *dfe* degrees of freedom of error; degrees of freedom of factors = 2 in all cases. Significant effects ($P < 0.05$) are in *bold*

	MSF	dfe	MSE	*F*	*P*
Zoea 1 (initial)					
DW	0.42	27	0.70	0.60	0.55
C	0.36	27	0.08	4.18	**< 0.05**
N	0.02	27	0.004	3.97	**< 0.05**
Zoea 1 (premoult)					
DW	8.99	28	1.96	4.59	**< 0.05**
C	1.36	28	0.50	2.69	0.08
N	0.05	28	0.02	2.93	0.07
Zoea 4 (premoult)					
DW	1109.1	24	347.0	3.19	0.06
C	227.24	24	60.11	3.78	**< 0.05**
N	9.50	24	2.79	3.40	**< 0.05**

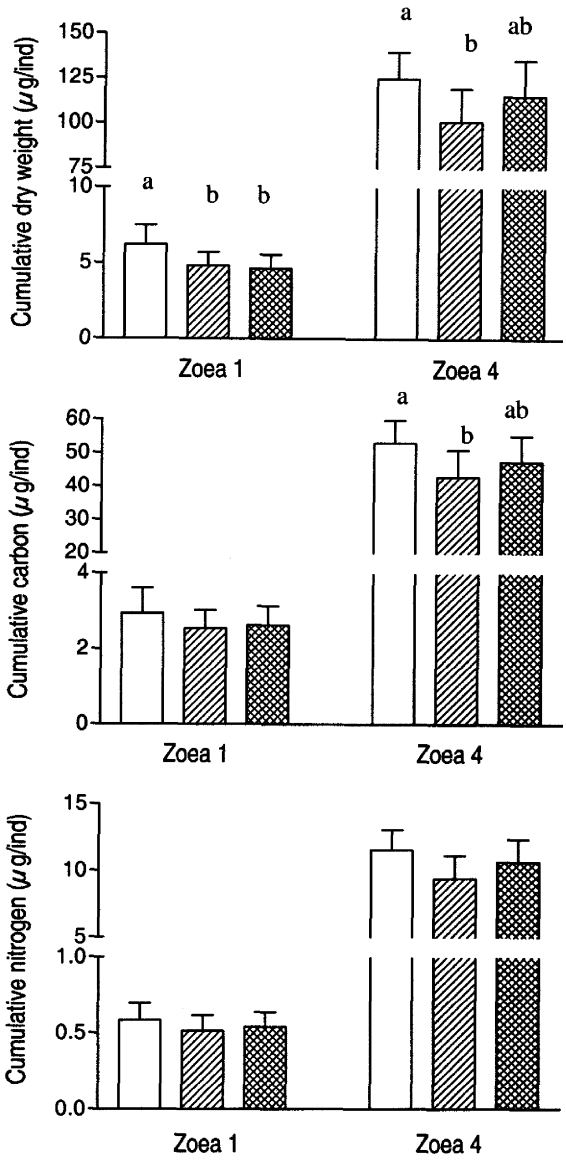

Fig. 2 *C. granulata*. Cumulative biomass from hatching to premoult zoeae 1 and 4 of larvae from different prehatching salinities. *Error bars* Standard deviation. *Different letters* indicate significant differences ($P < 0.05$) among prehatching salinities

Table 2 *C. granulata*. One-factor ANOVAs to evaluate the effect of prehatching salinity on growth, measured as accumulation of DW, C, and N during the first zoea (Z1i–Z1f) and fourth zoeal instars (Z1i–Z4f). Symbols and other details as in Table 1

	MSF	dfe	MSE	*F*	*P*
Z1i–Z1f					
DW	7.34	27	1.09	6.70	**< 0.01**
C	0.41	27	0.31	1.32	0.28
N	0.01	27	0.01	1.14	0.33
Z1i–Z4f					
DW	1154.6	23	335.14	3.44	**< 0.05**
C	210.54	24	57.66	3.65	**< 0.05**
N	9.25	23	2.73	3.39	0.05

found only between 15 and 20‰ for DW and C; for N they were marginally significant (Table 2). When biomass of freshly hatched zoea 1 was used as a covariate all significant differences disappeared ($P > 0.05$).

In general, biomasses of premoult zoeae 1 and 4 were correlated with those of freshly hatched zoea 1 ($r > 0.60$, $P < 10^{-3}$) and freshly laid eggs (Table 3): larger premoult zoeae 1 and 4 developed from broods with larger eggs and hatched zoea 1. The highest correlation coefficients were found when the independent variable was the biomass of freshly hatched larvae. There was no significant correlation between DW of eggs and that of premoult zoea 4 (Table 3). Correlations between biomass of eggs and that accumulated during zoeal development were positive, although not always significant (Table 4). C content at hatching correlated significantly with that accumulated during the zoea 1 ($r = 0.43$ $P < 0.05$) and all zoeal stages ($r = 0.61$, $P < 10^{-3}$), showing that larger larvae accumulated more carbon. N content at hatching correlated significantly with that accumulated during all zoeal stages ($r = 0.64$, $P < 10^{-3}$) but not with that accumulated during the zoea 1 ($r = 0.31$, $P = 0.09$); the same pattern occurred for DW ($r = 0.58$, $P < 0.01$ for all stages; $r = 0.14$, $P = 0.47$ for zoea 1). Accumulated biomass, expressed as a proportion of initial larval biomass, was independent of initial larval biomass ($P > 0.05$ for all correlations).

Table 3 *C. granulata*. Correlation coefficients between initial egg biomass and those of zoeae 1 and 4. Significant correlations (P adjusted by sequential Bonferroni method at $k = 2$) are in *bold*

	r	P
DW		
Zoea 1	0.64	**$< 10^{-4}$**
Zoea 4	0.32	0.11
C		
Zoea 1	0.52	**< 0.01**
Zoea 4	0.54	**< 0.01**
N		
Zoea 1	0.56	**< 0.01**
Zoea 4	0.44	**< 0.05**

Table 4 *C. granulata*. Correlation coefficients between initial egg DW, C and N, and that accumulated during zoea 1 (Z1i–Z1f) and fourth zoeal (Z1i–Z4f) instars. Significant correlations (P adjusted by sequential Bonferroni method at $k = 2$) are in *bold*

	r	P
DW		
Z1i–Z1f	0.44	**< 0.025**
Z1i–Z4f	0.31	0.14
C		
Z1i–Z1f	0.26	0.17
Z1i–Z4f	0.53	**< 0.01**
N		
Z1i–Z1f	0.25	0.19
Z1i–Z4f	0.42	0.03

Growth after zoea 4

A variable proportion (0–70%) of zoea 4 followed the long pathway (i.e. they moulted to zoea 5 instead of metamorphosing to megalopa). This proportion was negatively correlated with DW, C, and N of zoeae 1 and 4. The highest correlations were found in C content (Fig. 3) followed by those in N content ($r = -0.47$ or lower, always $P < 0.01$) and DW ($r = -0.42$, $P < 0.05$ for the DW of freshly hatched zoea 1; $r = -0.52$ or lower, $P < 0.01$ for DW of premoult zoeae 1 and 4).

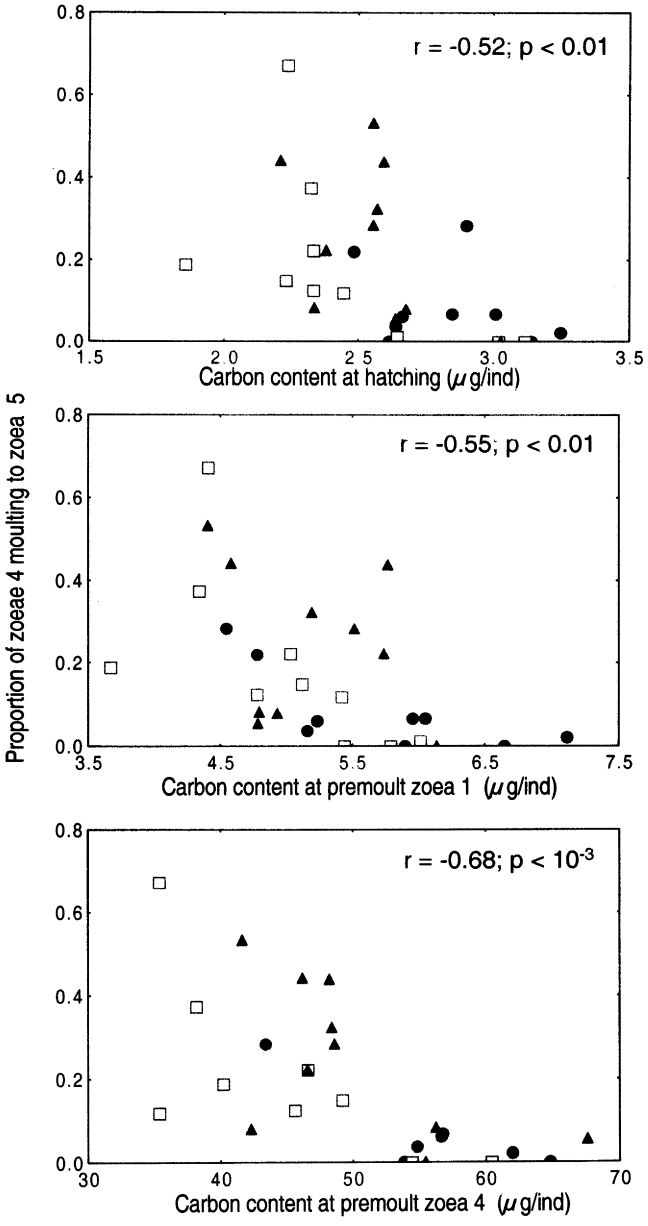

Fig. 3 *C. granulata*. Relationships between proportion of zoea 4 that moulted to zoea 5 and carbon content at hatching, premoult zoea 1, and premoult zoea 4. *Circles* 15‰; *squares* 20‰; *triangles* 32‰. Significance levels were corrected by sequential Bonferroni method at $k = 3$

The effect of prehatching salinity on biomass of the megalopae was only evaluated for those from the short pathway, since not all broods had larvae that followed the long pathway. The highest biomass and accumulated biomass were found for the megalopae from 15‰ prehatching salinity, followed by those from 20‰ (Table 5), although the differences were not significant (always $P \gg 0.05$).

Biomass of megalopa and that accumulated from hatching were higher for broods with higher initial larval biomass at hatching, especially when measured as C ($r = 0.61$, $P < 0.01$) and N ($r = 0.60$, $P < 0.01$). Lower but significant correlations were found for DW ($r = 0.55$, $P < 0.01$). The biomass of the megalopa was additionally correlated with that of the egg (DW: $r = 0.52$, $P < 0.05$; C: $r = 0.68$, $P < 10^{-3}$; N: $r = 0.61$, $P < 0.01$). The accumulated biomass at the megalopa from premoult zoea 4 was not significantly correlated with the biomass at hatching ($P \gg 0.05$).

Biomass of megalopae from the long and short pathways was measured for 12 broods. Those from the long pathway had higher levels of DW, C, and N (paired Student's t-test: DW: $t = 8.01$, $P < 10^{-5}$; C: $t = 7.01$, $P < 10^{-4}$; N: $t = 9.23$, $P < 10^{-5}$; Fig. 4).

Discussion

Biomass and growth of *C. granulata*, measured in terms of DW, C, and N, has been previously studied by Anger and Ismael (1997) using similar methodology to that used in this study. The values of DW, C, and N found by these authors are comparable to those reported in our study. For example, mean DWs estimated in their study (freshly hatched zoea 1 = 8.45 μg/individual; premoult zoea 1 = 16.0 μg/individual; premoult zoea 4 = 16.0 μg/individual; 8-day-old megalopa = 260 μg/individual) were in the range reported here (Fig. 1, Table 5). Additionally, we show a certain degree of interspecific variability and discuss possible causes.

Table 5 *C. granulata*. Biomass at the megalopal stage (age = 8 days) and growth (as accumulated DW, C, and N from premoult zoea 4) for larvae from different prehatching salinities

	Biomass (μg)		Growth (μg)	
	Mean	SD	Mean	SD
DW				
15‰	237.04	31.12	103.05	15.16
20‰	231.51	52.15	104.81	40.21
32‰	221.28	25.14	96.76	30.26
C				
15‰	99.48	15.33	43.21	7.29
20‰	95.17	22.11	42.78	17.37
32‰	90.77	13.43	39.79	11.76
N				
15‰	19.84	2.79	7.75	1.53
20‰	19.57	4.59	8.32	4.04
32‰	19.02	2.45	7.54	2.21

Our results showed that for the estuarine crab *C. granulata*, biomass at various stages of the larval development can be affected by factors operating before hatching (i.e. prehatching factors). Variability in larval biomass among broods took place as a consequence of a series of processes affected by variability in (1) egg biomass and (2) prehatching salinity (Fig. 5). Possible causes of variability in initial egg biomass were discussed by Giménez and Anger (2001). Significant correlations between egg and larval biomass evidence the influence of parental investment per offspring: this influence was noted even at the megalopa. Prehatching salinity must have acted on the rate of C and N loss during embryogenesis, as previously established (Giménez and Anger 2001): embryos maintained at 15 and 20‰ lost more C

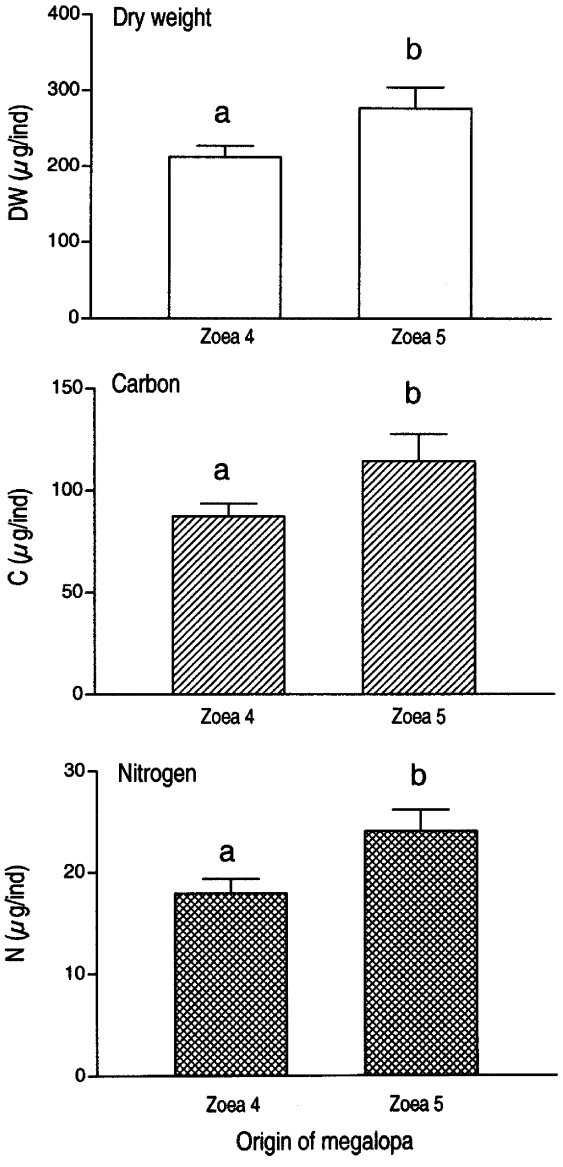

Fig. 4 *C. granulata*. Mean biomass (dry weight, carbon, and nitrogen) of 8-day-old megalopae that moulted directly from zoeae 4 or zoeae 5. *Error bars* Standard deviation. *Different letters* indicate significant differences ($P < 0.05$)

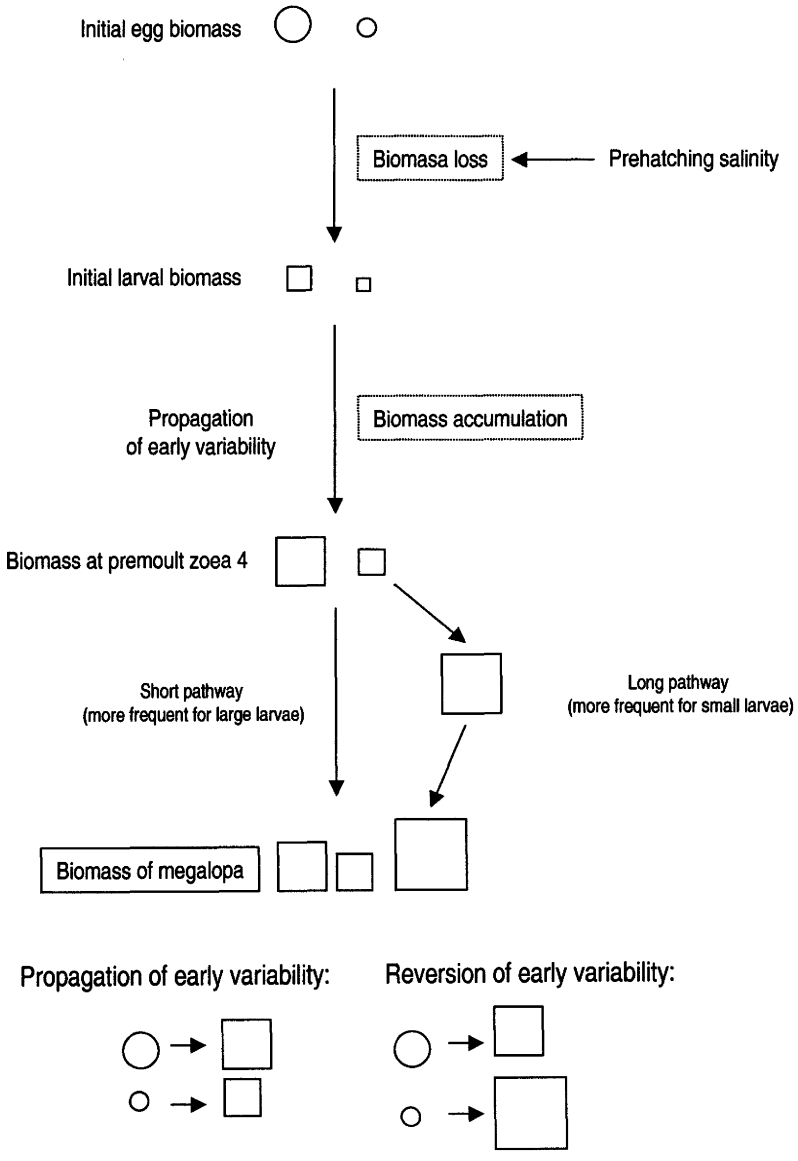

Fig. 5 *C. granulata*. Model of effect of variability in the initial egg biomass (*circles of different size*) and prehatching salinity on variability among broods in biomass at hatching, and subsequent propagation or reversion of early variability to other larval stages (*squares of different size*). Among-brood differences in initial egg biomass and exposure to different prehatching salinities set the early variability in larval biomass among broods. This early variability is propagated to the subsequent stages. After zoea 4, larvae either follow the long or short pathway. Considering only the short pathway, early variability is further propagated to the megalopa. Considering both pathways, there is a reversion of early variability, as larger megalopa are more frequently originated from broods with larvae of lower biomass

and N than those at 32‰. Thus, while at egg laying the highest levels of biomass were found at 15‰ and the lowest at 32‰, the lowest C and N at hatching occurred for individuals from the prehatching salinity 20‰, and those from 15 and 32‰ had the highest levels. The fact that DW depends partly on the inorganic fraction explains why it increased from eggs to freshly hatched zoea 1. Accumulation of biomass depended partly on the initial larval biomass, although correlations were not always significant. The best correlations were found when biomass was measured as C content, followed by N. Since in decapod crustacean larvae C content reflects total lipid and N content reflects the protein fraction (Anger 2001), the lipid rather than protein fraction of advanced stages may depend on the fraction existing in early stages.

The fact that correlations were always positive contributed to significant differences among treatments even at premoult zoea 4, especially in C content. Differences initially set at hatching "propagated" to subsequent stages (i.e. there was a propagation of early variability: see Fig. 5). The fact that the percentage of biomass accumulated by larvae from different broods was independent of initial larval biomass suggests that larger and smaller larvae tended to accumulate the same proportion of reserves. Differences in biomass of larvae may reflect differences in size and, thus, ability to move and capture prey or other abilities that allow them a differential accumulation of reserves. Increased abilities must have enhanced differences among treatments, contributing to significant correlations between biomass at hatching and at premoult zoea 1 or zoea 4, and to partial conservation of differences among broods.

Differences in initial larval biomass, especially in C content, were responsible for variability of biomass among broods before larvae followed either the long or the short developmental pathway. The significant negative correlation between the proportion of zoea 4 that

followed the long pathway and DW, C, and N content at previous larval instars suggests that biomass levels affect the switching to a given pathway. Thus, switching in *C. granulata* must take place as hypothesised by Knowlton (1974) for other decapods: under certain threshold of reserves, larvae should follow an alternative, longer developmental pathway, to prioritize maintenance and growth over morphogenesis (L. Giménez and K. Anger, in preparation). A high correlation between developmental pathway and biomass of premoult zoea 4 could partly be a consequence of sampling a differential proportion of zoea 4b in respect to zoea 4a. The zoea 4b is smaller than zoea 4a and moults to zoea 5; zoea 4a metamorphoses to the megalopa (Pestana and Ostrensky 1995). Zoeae 4a and 4b could not be morphologically distinguished without being killed, so we had to distinguish them following their subsequent development. However, in most cases moulting of zoea 4b to zoea 5 occurred earlier than the metamorphosis of zoea 4a to megalopa. For determination of biomass we waited for the first zoea 4a to metamorphose, to take samples from the remaining zoeae. Thus, differences among broods in biomass of premoult zoea 4 must reflect differences in average biomass of each substage (zoeae 4a and 4b) rather than a different proportion of substages in our samples. Therefore, significant correlations between developmental pathway and biomass at hatching suggest that the development to a zoea 4a or 4b is related to larval reserves in earlier stages.

In addition, we show some consequences of larvae following different pathways on the megalopa: those from larvae developed through the long pathway had significantly the highest DW, C, and N contents. As larger megalopae tended to originate from smaller zoeae, early variability in biomass existing previously was reversed. Therefore, the variability in biomass at hatching was reflected in the megalopae through either propagation or reversion of early variability. The propagation of early variability was as for zoeal stages and led to a significant correlation between biomass at hatching and that of the megalopae that followed the short pathway. The reversion of early variability was a consequence of having smaller larvae developing more frequently through an additional instar, the zoea 5, that accumulated biomass and led to larger megalopae.

There is scarce information on variability in larval growth for decapod crustaceans or other taxa. Variability in crustacean larval development (i.e. the existence of alternative developmental pathways) is common in non-brachyuran decapods but also occurs in grapsid and portunid crabs (Costlow 1965; Criales and Anger 1986; Montú et al. 1990) and has been related to environmental stress and genetic and maternal factors (Anger 2001). Concerning environmental factors, only those operating during larval stages have been studied. For instance, in *C. granulata*, larvae follow the long pathway if zoeae 1–3 are under food or osmotic stress (Ostrensky et al. 1997; Giménez 2000). The present study additionally shows that the probability of a zoea following the long pathway is partially determined before hatching. In *C. granulata* salinity experienced by embryos in combination with the initial reserves may be a key factor determining the subsequent developmental pathway. Initial egg reserves may be determined by salinity (Giménez and Anger 2001), but also by maternal factors. Effects of egg biomass (DW, C, and N, proteins and lipids) on larval developmental pathways have been found also in the shrimp *Crangon crangon*, where larvae that hatched from the larger winter eggs had higher biomass levels and developed through a shorter pathway than those from smaller summer eggs (Linck 1995; Paschke 1998). In this species, prehatching temperature affects initial larval biomass (Paschke 1998), so it may also affect the larval developmental pathway. On the other hand, to our knowledge no studies are available on consequences of alternative developmental pathways for advanced larval instars. The fact that larger advanced stages are the outcome of smaller initial stages is interesting if fitness depends on larval biomass. Biomass of the megalopa could indeed have important consequences for fitness, as it would affect the ability to find food or available substrate for settlement and to escape predators. Interspecific comparisons showed a positive correlation between swimming velocity and size of megalopae (Valero et al. 1999), and this could also occur intraspecifically. This hypothesis as well as other possible relationships between biomass and survival of the megalopae under food or salinity stress remain to be tested in future experiments.

Considering other taxa, intraspecific variability in egg quality and consequences for larval development have been studied in echinoderms. Females under food stress lay eggs with lower biomass (George 1996, 1999; Bertram and Strathmann 1998). To a certain degree, differences in egg quality are maintained during the larval development (George 1996; Bertram and Strathmann 1998; Meidel et al. 1999), so that early variability is propagated. Food stress during early larval development of some echinoderms and bivalves leads to a higher allocation of growth to feeding structures at the expense of the development of postlarval structures (Strathmann et al. 1993; George 1994, 1999). This type of plasticity may have the same effect on size of late stages as an additional larval stage of some decapod crustaceans: they may (1) prioritize maintenance and growth at a cost of morphogenic changes, and (2) buffer environmental effects on size at the expense of a lengthening of the larval phase. Thus, regardless of different body plans, some general patterns may emerge in different taxa of marine invertebrates.

In summary, our study shows that for *C. granulata* life history characters of different life phases and stages are correlated. Variability in biomass during larval development of *C. granulata* occurred through a combined effect of prehatching salinity and initial egg and larval biomass. Prehatching salinity regulated the amount of reserves invested per egg and lost during embryogenesis (Giménez and Anger 2001) and affected the osmoregu-

latory capacity and starvation tolerance of the first zoea (Charmantier et al. 2002; Giménez 2002). Differences in salinity experienced as embryos and initial larval biomass acted on a set of physiological and developmental processes taking part in the propagation or reversion of initial variability in biomass. Variability in larval biomass may have consequences for survival and growth at advanced larval or early juvenile stages. Future studies should address these topics in *C. granulata*, as well as in other species.

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