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Patterns of larval and early juvenile growth in a semiterrestrial crab, *Armases angustipes* (Decapoda: Sesarmidae): comparison with a congener with abbreviated development

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Abstract In a semiterrestrial and estuarine tropical crab, *Armases angustipes* Dana (Grapsoidea: Sesarmidae), changes in biomass (measured as dry mass, W; carbon, C; nitrogen, N; and hydrogen, H; per individual) and relative elemental composition (C, N, H, in percent of W; C:N mass ratio) were studied during development from an early egg stage through hatching, the complete larval phase, metamorphosis and the first juvenile crab stage (CI). In the megalopa and CI, growth was measured also within the moulting cycle, and biomass and elemental composition were determined in cast exuviae. From an early egg stage to the freshly hatched larva, *A. angustipes* lost about 20% of W, 29% of C, 5% of N and 32% of H. Proportionally higher losses in C than in N were reflected also in a significantly decreasing C:N mass ratio (from 5.02 to 3.74). These results indicate that lipids mobilised from yolk reserves represented the principal metabolic substrate for embryonic energy production, while proteins were catabolised at a much lower rate. The present data of growth and exuviation are compared with previously published data from a congener, *A. miersii* Rathbun, which has an abbreviated and facultatively lecithotrophic mode of larval development (with three instead of four zoeal stages; stages I and II in principle independent of food). When growth is measured as an increase in the final (premoult) biomass of successive developmental stages, both species show an exponential pattern. Within the moulting cycles of the megalopa and the first juvenile, both species show parabola-shaped growth curves, with a rapid biomass increase in postmoult and intermoult stages, and losses in the premoult phase. Thus, the two *Armases* species show, in general, similar patterns of larval and early juvenile growth. However, the initial size of eggs and larvae is about four times larger in *A. miersii*, and its biomass remains higher throughout the period of larval and early juvenile development. *A. angustipes* is able to partially make up for this difference, as it has an additional zoeal stage, and its megalopa and CI stages show higher relative biomass increments (in percent of initial values). Due to this compensatory growth pattern, *A. angustipes* reaches in its CI stage about half the biomass of a juvenile *A. miersii*. When exuvial losses of megalopae and juveniles are compared between these two species, *A. miersii* shows higher biomass losses per individual (corresponding with its larger size), but lower relative losses (C, N, H, in percent of late premoult body mass or in percent of previously achieved growth increments). Differences in larval and early juvenile growth and in the exuvial losses of megalopae and juveniles of these two congeners are discussed in relation to their differential ecology, life history and reproductive strategy.

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Introduction

Patterns of larval and juvenile growth, as well as developmental and environmentally induced changes in the chemical composition of early life-history stages, have been studied in numerous decapod crustacean species (for recent reviews, see Anger 1998, 2001). Most of those studies, however, have been conducted on marine species, primarily those from temperate regions of Europe, North America and Australia. By contrast, much less is known about estuarine and semiterrestrial species, especially those from other geographic regions including South America and the Caribbean.

The present paper deals with the early life-history stages of a semiterrestrial, estuarine crab species, which lives in the brackish mangrove regions of the South

American Atlantic coast: *Armases angustipes* Dana (formerly *Sesarma angustipes*, family Grapsidae; for recent changes in the taxonomy of grapsoid crabs, see Abele 1992; Schubart et al. 2000, 2002). Like almost all *Armases* spp. for which larval development is known, *A. angustipes* passes through four planktonic zoeal stages and a megalopa prior to metamorphosis, followed by the first benthic juvenile stage (Anger et al. 1990; Cuesta and Anger 2001). In the present investigation, we studied developmental changes in the elemental composition (C, N, H) of eggs, larvae and early juveniles, as well as in patterns of larval and early juvenile growth observed under controlled rearing conditions in the laboratory. In the megalopa and first juvenile crab stage, exuvial losses were also quantified.

The present data are compared with previously published results from another estuarine and semiterrestrial, neotropical crab, the Caribbean congener *Armases miersii* Rathbun (Anger and Schultze 1995; Anger et al. 2000). This species has a similar adult ecology but, in contrast to *A. angustipes*, an abbreviated mode of larval development, with only three instead of four zoeal stages (Cuesta et al. 1999). This is associated with partial independence of the zoeal stages from planktonic food (facultative lecithotrophy; see Anger 2001, and earlier references cited therein). These peculiar reproductive traits of *A. miersii* are considered to be adaptations to larval development in an unusual, land-locked breeding habitat, supratidal rock pools, where food limitation has selected for the enhanced energy investment of females into the production of large, yolky eggs (Anger 1995, 2001). Based on a comparison of these closely related species, relationships between differential developmental traits and reproductive ecology are discussed.

Materials and methods

An ovigerous *Armases angustipes* (carapace width: 22.0 mm) carrying eggs in an early stage of development was collected on 20 February 1996, in the vicinity of the São Sebastião Marine Biological Station (CEBIMAR) of the University of São Paulo, Brazil. A sample of eggs was immediately removed for later determinations of biomass and elemental composition (see below). In ten eggs, size (largest diameter) was measured under a dissecting microscope (Wild M3B, with calibrated eyepiece micrometer) to the nearest 0.01 mm. The female was transferred live to the Helgoland Marine Biological Station (Germany) and kept at a constant temperature of 24°C, 25‰ salinity and in an artificial 12 h light:12 h dark cycle.

Three weeks later (12 March), about 22,500 larvae hatched (number estimated from three subsamples taken from the aquarium). They were mass-reared in gently aerated 1 l beakers (ca. 100 individuals per beaker) under the same conditions of temperature, salinity and light. Water and food (freshly hatched *Artemia* sp., ca. 10 nauplii ml^{-1}) were changed daily, and the larvae were checked for moulting and mortality. Freshly moulted larvae were removed from the cultures and placed in separate rearing containers, so that each beaker contained exclusively individuals that had reached the same larval stage on the same day, i.e. being approximately in the same stage of the moulting cycle. The rearing salinity was obtained by dilution of filtered natural seawater from the North Sea (32‰) with deionised water; this condition was chosen because a previous experimental study (Anger et al. 1990) had shown that a slightly reduced salt concentration was more favourable for the larval development of this species than full-strength seawater. The rearing methods for the semibenthic megalopae and benthic juvenile crabs differed from those applied for the planktonic zoeae in that nylon gauze (0.3 mm mesh size) was provided as an artificial substrate, no aeration was applied and culture bowls (400 ml capacity) instead of beakers were used (maximum 20 individuals per bowl).

Samples of larvae for measurements of growth and elemental composition were taken first on the day of hatching (zoea I, day 0) and thereafter from rearing containers where moulting had commenced; we sampled exclusively individuals that had not yet moulted, assuming that these were approaching the end of the moulting cycle and thus represented final (premoult) biomass. In each of the four successive zoeal stages, moulting began on day 4 (samples zoea I–IV). In the megalopa and crab I, the moulting cycles lasted for about 8 days each. This allowed for a higher temporal resolution of sampling, with five or six successive analyses of biomass, respectively (see Table 1).

Biomass of eggs, larvae, juvenile crabs and exuviae (the latter collected only from megalopae and juveniles) was measured as dry mass (W), carbon (C), nitrogen (N) and hydrogen (H) content; following common use in the literature, C, N, H are later collectively referred to as CHN. The following standard techniques were applied (Anger and Harms 1990): removal of samples from cultures with wide-bore pipettes; short rinsing in distilled water; blotting on fluff-free Kleenex paper for optical use; frozen storage at –20°C in preweighed tin cartridges; freeze-drying in a Lyovac GT-2E vacuum apparatus; weighing to the nearest 0.1 μg on a Mettler UM-3 microbalance; and CHN analyses in a Fisons (Carlo Erba) model EA 1108 elemental analyser, using acetanilid as a standard. Each analysis of W, C, N and H comprised five replicate determinations with 1 (juvenile crabs) to 50 individuals (eggs) each (depending on dry mass) to meet the requirements for optimal accuracy of the CHN analyser. Mean values and standard deviations ($\pm$SD) were calculated from the replicate analyses ($n = 5$).

All statistical analyses followed standard techniques (Sokal and Rohlf 1995). When data deviated significantly from a normal distribution (Kolmogorov–Smirnov test) or when variances deviated significantly from homogeneity (Levene's median test), the non-parametric Mann–Whitney rank sum test was used for comparisons of mean values; otherwise, a Student's *t*-test was used. Differences are referred to as significant when the probability of error for rejecting the null hypothesis was $P < 0.05$.

Results

Changes in biomass and elemental composition (CHN) observed in *Armases angustipes* during the time of development from an early egg stage to hatching, and further throughout complete larval development, metamorphosis and eventually through the first juvenile stage, are documented in Table 1. Patterns of growth are visualised in Figs. 1 and 2, the latter including a comparison with patterns previously found in *A. miersii*. Exuvial losses in the megalopa and first crab stage (CI) of these two congeneric species are shown in Table 2.

Embryonic development

Eggs removed from the ovigerous female immediately after capture were in an early stage of development, consisting of >90% undifferentiated yolk. Average egg

Table 1. *Armases angustipes*. Growth and elemental composition (*W* dry mass; *C* carbon; *N* nitrogen; *H* hydrogen) during embryonic, larval and early juvenile development. Data are means ± 1 SD from $n = 5$ replicate analyses (*day* time after reaching a given stage)

Stage	Day	W (µg ind.$^{-1}$)		C (µg ind.$^{-1}$)		N (µg ind.$^{-1}$)		H (µg ind.$^{-1}$)		C (%W)		N (%W)		H (%W)		C:N mass ratio	
		Mean	±SD	Mean	±SD	Mean	±SD	Mean	±SD	Mean	±SD	Mean	±SD	Mean	±SD	Mean	±SD
Early egg		13.3	0.2	6.57	0.03	1.31	0.01	0.95	0.01	49.4	0.7	9.8	0.1	7.1	0.1	5.02	0.01
Zoea I	0	10.7	0.1	4.64	0.02	1.24	0.01	0.65	0.02	43.4	0.4	11.6	0.1	6.0	0.2	3.74	0.01
	4	14.9	1.4	5.05	0.69	1.29	0.16	0.69	0.10	33.7	1.7	8.6	0.3	4.6	0.3	3.92	0.06
Zoea II	4	24.6	2.2	7.55	0.70	1.82	0.16	1.02	0.11	30.8	3.7	7.4	0.9	4.2	0.6	4.15	0.03
Zoea III	4	40.9	2.5	14.38	1.01	3.25	0.21	2.01	0.17	35.2	0.4	8.0	0.1	4.9	0.1	4.42	0.06
Zoea IV	4	69.3	4.3	26.72	2.59	6.19	0.64	3.97	0.43	38.5	1.4	8.9	0.4	5.7	0.3	4.32	0.08
Megalopa	0	77.6	9.0	28.72	3.18	6.96	0.57	4.31	0.51	37.0	0.9	9.0	0.5	5.6	0.1	4.12	0.14
	2	113.1	5.0	38.52	2.22	8.69	0.38	5.43	0.39	34.1	1.0	7.7	0.2	4.8	0.2	4.43	0.10
	4	142.6	6.7	54.27	3.48	11.11	0.43	8.08	1.16	38.1	0.7	7.8	0.3	5.7	0.6	4.89	0.23
	6	149.6	7.4	57.24	3.97	12.03	0.49	8.34	0.62	38.2	0.8	8.1	0.1	5.6	0.2	4.75	0.14
	8	128.5	16.1	47.43	7.21	10.48	1.78	6.87	1.11	36.8	1.3	8.1	0.4	5.3	0.2	4.54	0.14
Crab I	0.5	145.9	8.6	55.36	3.73	11.94	0.83	7.70	0.64	37.9	0.9	8.2	0.4	5.3	0.2	4.64	0.22
	1	172.5	10.2	59.78	3.47	12.80	0.76	7.81	0.48	34.7	0.4	7.4	0.1	4.5	0.1	4.67	0.13
	2	191.0	16.9	62.71	7.49	13.63	0.74	8.21	1.12	33.2	0.9	7.3	0.4	4.3	0.2	4.59	0.33
	4	207.1	26.1	77.78	9.15	15.32	1.53	10.90	1.46	37.6	0.8	7.4	0.3	5.3	0.1	5.07	0.19
	6	214.7	16.0	75.56	9.14	15.82	1.93	10.78	1.36	35.1	2.1	7.4	0.4	5.0	0.3	4.78	0.18
	8	204.0	21.0	70.30	9.78	15.45	1.98	9.64	1.76	34.4	1.5	7.6	0.3	4.7	0.4	4.55	0.16

size was 0.400 ± 0.007 mm ($n = 10$). Their dry mass, carbon, nitrogen and hydrogen contents are given in Table 1. Compared with these early embryos, freshly hatched zoea larvae showed significantly lower values of biomass per individual ($P < 0.001$). These losses reflect principally the metabolic utilisation of yolk materials during 3 weeks of embryogenesis (plus minor losses through the egg membrane discarded at hatching); they amounted to 20% in W, 29% in C, 5% in N and 32% in H.

Since the embryos catabolised much higher amounts of C and H compared with N, the C:N mass ratio also decreased significantly ($P < 0.001$) from the early egg (5.02) to the freshly hatched zoea (3.74). Congruent with this pattern, the mass-specific values of elemental composition (CHN in percent of W) changed significantly during embryonic development (all $P < 0.001$), decreasing from 49.4% to 43.4% and from 7.1% to 6.0% in C and H, respectively, while N increased from 9.8% to 11.6%. These patterns of change in CHN indicate that the lipid fraction of stored yolk (mostly comprised of C and H) represented the principal metabolic substrate for energy production during embryonic development, while only minor amounts of proteins (rich in N) were catabolised.

Zoeal stages

Development from hatching through the four successive zoeal stages was characterised by an exponential pattern of increase in W and CHN per individual (Table 1; Figs. 1, 2). When metamorphosis from the last zoeal stage to the megalopa was imminent, the final dry mass of a zoea IV was, on average, about 6.5 times higher than the initial W of a zoea I at hatching. The fractions of C, N and H increased concomitantly by factors of 5.8, 5.0 and 6.1, respectively (C increments are shown, as an example, in Fig. 2b).

Since the increment in total W was generally higher than those in the organically bound elements C, N and H, the percentage CHN values showed decreasing tendencies (Table 1). The C:N mass ratio, on the other hand, increased throughout the planktonic zoeal phase of development, from 3.74 to 4.32 ($P < 0.001$), indicating that during this period proportionally more lipids than proteins were accumulated.

Megalopa and first juvenile crab stage

After the zoeal phase, changes in late larval and early juvenile biomass were measured with a higher temporal resolution, allowing for an analysis of moult-cycle-related patterns. These were similar in the megalopa and crab I stages, consistently showing a fast initial increase in individual biomass, which was followed by a phase of decelerating growth and, eventually, by a period with slight or moderate biomass losses prior to ecdysis (Table 1; Fig. 1).

In spite of these premoult losses, each stage accumulated during its moulting cycle a considerable quantity of organic matter (CHN). In the megalopa alone, this increment was almost as high as that recorded during the entire preceding growth period, from hatching to the end of the zoeal phase; in the C fraction, for instance, the growth of the megalopa stage corresponded to about 85% of total zoeal growth (zoea I–IV) combined. Although the biomass accumulation during the first juvenile stage was not as high, a premoult crab I contained about 15 times more C per individual than a freshly hatched zoea I. Similar patterns of increase can be seen also in the H fraction, while generally lower accumulation rates occurred in N (Table 1). As in the zoeal stages, the megalopa and the crab I accumulated lower amounts of organically bound elements (CHN) compared with total dry mass. In consequence, the

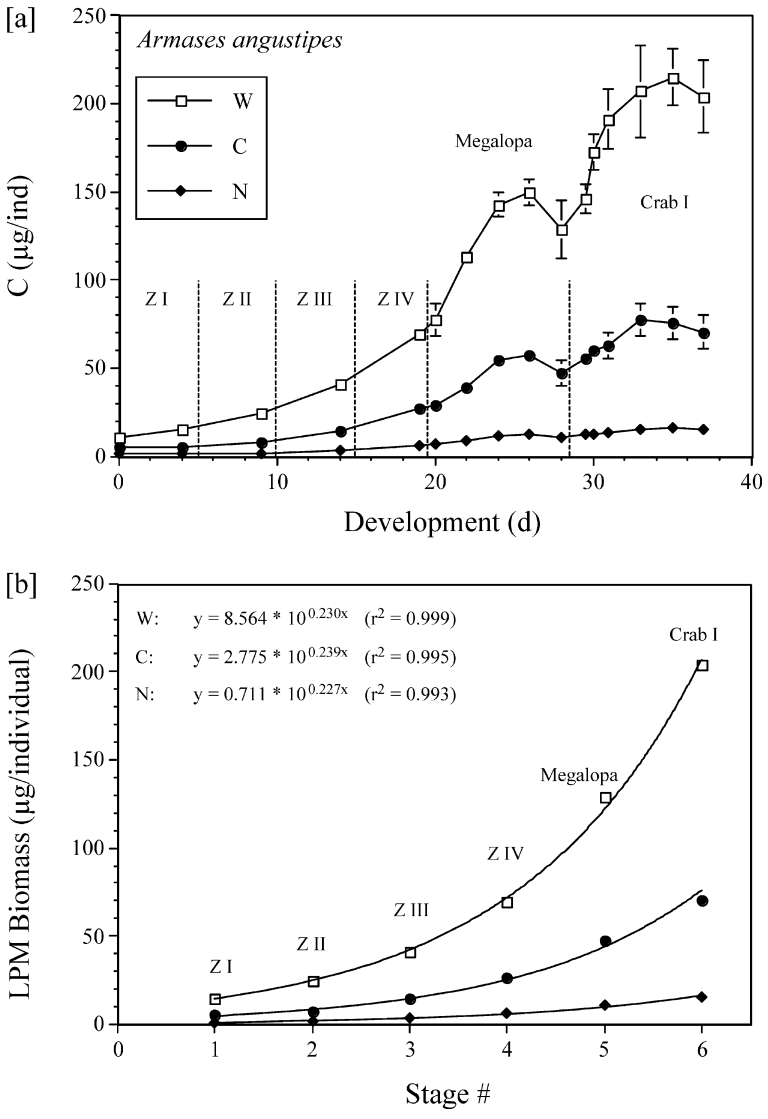

Fig. 1a, b. *Armases angustipes*. Patterns of biomass growth (arithmetic means ± 1 SD, from $n = 5$ replicate analyses; *error bars* apparently lacking where smaller than plot symbols): **a** during the time of development (days from hatching) through successive larval stages [zoeal stages I–IV (*ZI–ZIV*), megalopa] and in the first juvenile crab instar; **b** exponential increase in late premoult (*LPM*) biomass (mean values; for *error bars* see a; r^2 coefficient of determination for exponential regression equations) (*W* dry mass; *C* carbon; *N* nitrogen; all in µg ind.$^{-1}$)

percentage CHN values tended to decrease in these stages.

When changes in the mass-specific values of CHN (in percent of W) are considered within individual moulting cycles, a sinusoidal pattern can be seen both in the megalopa and the first juvenile crab stage. This pattern was characterised by a decrease during the postmoult phase, followed by higher values in the middle of the moulting cycle (i.e. in intermoult) and another decrease during premoult (Table 1). Significant moult-cycle-related changes occurred also in the C:N mass ratio of the megalopa and crab I, with an initial increase from low postmoult values to a maximum in intermoult, followed by a decreasing tendency in premoult.

Overall growth patterns: comparison with *A. miersii*

When the increase in biomass (in µg ind.$^{-1}$) during larval and early juvenile development is compared between *A. angustipes* and *A. miersii*, the patterns of accumulation appear to be similar, in spite of a far higher average level of individual biomass in the latter species (Fig. 2a). A freshly hatched zoea I of *A. miersii* had an almost fourfold higher C content than the same stage in *A. angustipes*, and the biomass of a premoult zoea III of *A. miersii* exceeded that of an *A. angustipes* megalopa shortly before metamorphosis to the first juvenile crab stage (cf. Anger et al. 2000; Table 1). This indicates that the additional zoea (stage IV) passed in the latter species cannot fully compensate the great species-specific biomass difference which already exists in eggs and freshly hatched zoea I larvae. However, this difference appeared to diminish during the course of larval development and growth, from about fourfold at hatching to a factor of only two in the crab I stage.

The explanation for this convergence in biomass is illustrated in Fig. 2b, where percentage C increments (in relation to initial C values at hatching) are shown. This comparison indicates that the relative growth rates of these two species are similar throughout the zoeal stages I–III, remaining equal or slightly higher in *A. miersii*.

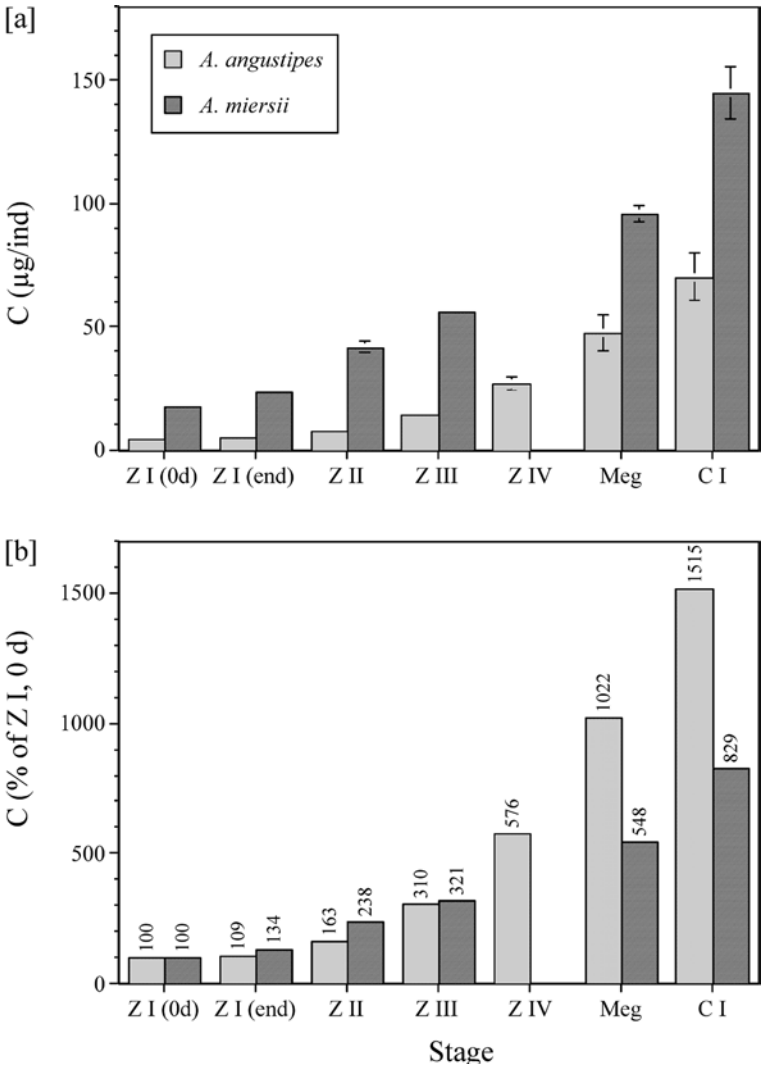

Fig. 2a, b. *Armases angustipes*, *A. miersii*. **a** Comparison of biomass (*C* carbon; in µg C ind.$^{-1}$) growth in successive larval stages [zoeal stages I–IV (*ZI–ZIV*), megalopa] and in the first juvenile crab instar (*CI*) and **b** percentage increase, with C in the freshly hatched zoea I (ZI, 0 days) defined as 100%

After passing through its additional zoeal stage (IV), however, *A. angustipes* had achieved in total a 5.8-fold biomass increase since hatching; approximately the same relative increase (5.5-fold) was reached in *A. miersii* only by the end of the megalopa stage. This partial compensation of initially lower biomass in *A. angustipes* was continued throughout the megalopa and crab I stage, where eventually a 15-fold C accumulation since hatching was achieved in *A. angustipes*, while a premoult crab I of *A. miersii* reached only an eightfold C value (Fig. 2b). In summary, *A. angustipes* is, compared with *A. miersii*, able to partially make up for its lower biomass of eggs and freshly hatched larvae, due to both an additional zoeal stage and higher relative biomass increments in the megalopa and first juvenile stage.

Exuvial losses in the megalopa and first crab stage of *A. angustipes* and *A. miersii*

Dry mass and elemental (CHN) composition of the exuviae of megalopae and first-stage juveniles of *A. angustipes* and *A. miersii* are compared in Table 2. These exuvial biomass values are expressed also as percentage exuvial losses in relation to late premoult (LPM) body mass measured in the same species and stages (for *A. angustipes*, see Table 1; for *A. miersii*, see Anger and Schultze 1995). Moreover, exuvial losses are given as a percentage of the respective growth increment previously achieved in a given stage (same data sources, in *A. miersii* complemented with crab I growth data from Anger et al. 2000).

In *A. angustipes*, W, C and H per exuvia doubled from the megalopa to the first crab stage, while N increased to a lesser extent (Table 2). Similar patterns were found in the exuvial biomass of *A. miersii* megalopae and juveniles. The elemental composition of the exuviae (in percent of W) differed in both species significantly from that of the complete larval or juvenile body, with consistently far lower percentage CHN levels and much higher C:N mass ratios in exuviae (Table 2; cf. Table 1). This reflects a substantially different chemical composition of the entire body versus the exuvia alone.

Table 2. *Armases angustipes*, *A. miersii*. Comparison of exuvial biomass and elemental composition in the megalopa and crab I stage (*W* dry mass; *C* carbon; *N* nitrogen; *H* hydrogen); exuvial losses expressed as a percentage of total late premoult (*LPM*) body mass and as a percentage of the growth increment (in μg ind.$^{-1}$) achieved in each stage; mean ± 1 SD from $n = 5$ replicate analyses; data for *A. miersii* from Anger and Schultze (1995; exuvial biomass) and Anger et al. (2000; LPM values)

	Species	Stage	W		C		N		H		C:N mass ratio	
			Mean	±SD	Mean	±SD	Mean	±SD	Mean	±SD	Mean	±SD
Biomass (μg ind.$^{-1}$)	*A . angustipes*	Megalopa	26.9	2.0	5.3	0.5	0.75	0.06	0.78	0.09	7.07	0.19
		Crab I	63.9	3.6	10.4	0.5	1.11	0.07	1.26	0.07	9.35	0.60
	A. miersii	Megalopa	52.8	10.1	8.4	1.6	1.08	0.17	1.08	0.17	7.72	0.36
		Crab I	83.3	24.6	12.7	2.2	1.52	0.26	1.57	0.72	8.40	1.48
Elemental composition (% of W)	*A. angustipes*	Megalopa			19.9	1.3	2.8	0.1	2.9	0.2		
		Crab I			16.2	0.7	1.7	0.1	2.0	0.1		
	A. miersii	Megalopa			15.9	0.3	2.1	0.1	2.1	0.1		
		Crab I			14.1	3.7	1.7	0.5	1.6	0.7		
Loss (% of LPM)	*A. angustipes*	Megalopa	20.9		11.2		7.2		11.4			
		Crab I	31.3		14.7		7.2		13.1			
	A. miersii	Megalopa	30.0		12.6		7.1		10.8			
		Crab I	20.5		8.8		5.2		7.3			
Loss (% of growth)	*A. angustipes*	Megalopa	45.4		25.7		17.5		26.9			
		Crab I	84.6		45.3		22.3		45.5			
	A. miersii	Megalopa	47.7		21.4		15.2		20.0			
		Crab I	49.0		25.9		15.0		20.9			

When exuvial losses are expressed as a percentage of total LPM body mass, mostly similar figures are obtained for the megalopae of the two species, except for a higher percentage W loss in *A. miersii* compared with *A. angustipes* (Table 2). Stronger differences occurred between the juvenile crabs of the two species, with *A. miersii* showing conspicuously lower relative biomass losses. In this species, the crab I stage also showed lower percentage biomass losses than the megalopa (expressed in percent of LPM biomass), while the opposite tendency may be seen in the exuvial losses of *A. angustipes*.

When exuvial losses are expressed as a percentage of previous biomass increments measured in a given stage, a clear increase from the megalopa to the first crab stage was recognised in *A. angustipes*, but not in *A. miersii*. In the megalopa and crab I, *A. angustipes* lost 45% and 85%, respectively, of the previously achieved W growth. Compared with the losses of total W, however, those in the CHN fractions were far lower (Table 2).

Discussion

The changes in individual biomass and elemental composition observed in *Armases angustipes* during the developmental period from an early egg stage to hatching, through all larval stages and eventually in the first juvenile crab instar are, in general, quite similar to the patterns previously reported for other decapod crustacean species with a planktotrophic mode of larval development (for recent reviews, see Anger 1998, 2001). This applies also to the losses in egg biomass during embryonic development, which are characterised by a particularly strong decrease in the C content and in the C:N mass ratio. These changes in the elemental composition of egg biomass indicate the preferential utilisation of lipids rather than proteins as a metabolic substrate for embryonic energy production. Similar patterns have been found in several other decapod species (e.g. Katre 1977; Clarke et al. 1990; Petersen and Anger 1997; Wehrtmann and Graeve 1998; Heras et al. 2000).

A strong decrease observed both in the individual CHN values and in the C:N ratio suggest that most of the lipid reserves stored in the egg yolk were metabolically degraded during embryogenesis. However, preliminary experiments (authors' unpublished data) revealed that the zoea I of *A. angustipes* may retain sufficient energy to survive for several days and, occasionally, to develop successfully to the zoea II stage in complete absence of food. This indicates an endotrophic potential which is stronger than that in most marine crab species, but clearly weaker than that in the congener *A. miersii*. The latter shows an abbreviated mode of development and facultative lecithotrophy through at least two zoeal stages (for comparison among neotropical sesarmid species, see Anger 2001, his Table 5.1). It is remarkable, however, that *A. angustipes*, which has an "extended" type of larval development (Gore 1985), also shows a tendency of initial independence from food. This developmental trait has been observed in several other crab and shrimp species, which, as adults, live and produce offspring in upper estuaries with low salinity and unpredictable planktonic food production, and the larval stages of which are typically transported downstream, out of the parental environment (export strategy; for references, see Anger 2001). Hence, an enhanced endotrophic potential in the earliest larval stage may be considered as an adaptation to initial food limitation at hatching. In *A. angustipes*, for instance, hatching may take place in unpredictable habitats such as brackish mangrove creeks, but this is soon followed by export of the early larvae to highly productive lower estuarine or

coastal waters, where the salinity conditions are more favourable (Anger et al. 1990). Short and often incomplete initial lecithotrophy is also a typical trait of palaemonid shrimps that live in freshwater, but export their larvae to estuarine or marine waters (for references, see Anger 2001).

An exponential increase in the final (premoult) biomass of successive stages (Fig. 1b), as well as parabola-shaped biomass curves during the course of individual moulting cycles (see Fig. 1a, megalopa and first juvenile instar) represent common patterns of larval and early juvenile growth in decapod crustaceans (Anger 1998, 2001). At metamorphosis from the megalopa to the first juvenile crab stage, *A. angustipes* showed a 10 times higher carbon content than at hatching and 15 times higher biomass values were measured at the end of the crab I stage (Fig. 1b).

When *A. angustipes* is compared with *A. miersii*, it becomes evident that the latter species starts with significantly larger eggs and freshly hatched larvae and, at each larval ecdysis, shows much higher biomass increments per individual (Fig. 2a). On the other hand, *A. angustipes* passes through an additional zoeal stage that partially compensates for this difference in larval biomass. Moreover, its megalopa and crab I stage accumulate, compared with those of *A. miersii*, higher relative quantities of biomass (expressed as a percentage of the initial biomass values; Fig. 2b). As a consequence of these compensatory patterns of growth, a premoult first juvenile of *A. miersii* showed only about twice the C content of the equivalent stage in *A. angustipes*, although the zoea I larvae of these species differed initially by a factor of almost four (Table 1; cf. Anger et al. 2000).

These differences in the growth patterns of two closely related species may reflect differential reproductive strategies: *A. miersii* shows lower fecundity, but a higher maternal energy investment per offspring, allowing for the reduced dependence of its early larvae on planktonic food. This strategy, which includes also an abbreviation of the larval phase, should be advantageous in environments where prolonged or repeated periods of food limitation are likely to occur. In the particular case of *A. miersii*, larval development takes place in ephemeral, land-locked, rock pools above the level of high tide (for references, see Anger 2001). Adult female *A. angustipes* with a similar body size as an adult *A. miersii* produce a higher number of larvae, but these are smaller. Although the larvae of *A. angustipes* may tolerate a short initial period of food limitation, they require in general a more stable availability of planktonic food sources. Under favourable nutritional conditions, they are capable of fast uptake and accumulation of organic matter, so that their body mass may increase, from hatching to metamorphosis, by a factor of ten. The strategy of larval development and growth in *A. angustipes* is similar to that of most marine decapods (Gore 1985), while that of *A. miersii* shows a tendency towards "freshwaterization" (cf. Rabalais and Gore 1985; Hines 1986; Jalihal et al. 1993; Anger 1995).

Species following an export strategy, e.g. *A. angustipes*, experience, during their ontogenetic migrations, strong ecological changes, not only in food availability, but also in salinity. As an adaptation to hatching in dilute media and later development in waters of gradually increasing salinity, the successive larval stages of the same species may differ in salinity tolerance, which is based on differential capabilities for osmoregulation (Charmantier 1998). This was recently shown in another estuarine grapsoid crab, *Chasmagnathus granulata* (Charmantier et al. 2002). The first larval stage of this species showed a weak, yet significantly stronger, hyperosmoregulatory capacity in brackish water as compared to the subsequent zoeal stages. The megalopa, on the other hand, showed again an increased potential for osmoregulation and, thus, for reinvading estuarine environments. Future studies may find a similar pattern of ontogenetic changes also in the osmoregulatory functions of *A. angustipes*.

In the biomass and elemental composition of exuviae of megalopae and juveniles, a few differences can be seen between *A. angustipes* and *A. miersii* (Table 2). Corresponding with its larger larval size, the latter species produces heavier exuviae, but the differences in the CHN contents per exuvia are smaller than would be expected from the differences in larval and early juvenile dry mass. This reflects lower percentage CHN values within exuvial W of *A. miersii*, suggesting that the megalopae and juveniles of this species have a more heavily mineralised exoskeleton than those of *A. angustipes*.

When the exuvial losses of organic matter (CHN) are considered in relation to late premoult biomass or previously achieved growth increments (Table 2), it appears that the megalopae of these two species are similar. The first juvenile crabs, on the other hand, differ greatly, with consistently higher losses in *A. angustipes* than in *A. miersii*. Comparably low percentage CHN values and reduced exuvial losses (as a percentage of premoult body mass or in relation to previously achieved growth) have also been observed in other species with partially endotrophic development (e.g. Anger and Schultze 1995). This trait may represent an energy-saving mechanism that might have evolved under the selective pressure of planktonic food limitation (Anger 1995, 2001). Further comparisons between closely related species differing in ecology and life-history traits should be worthwhile in identifying evolutionary adaptations.

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