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Growth and elemental composition (C, N, H) in larvae and early juveniles of a South American salt marsh crab, *Chasmagnathus granulata* (Decapoda: Grapsidae)

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Abstract

The semiterrestrial grapsid crab *Chasmagnathus granulata* Dana is one of the most predominant inhabitants of brackish salt marsh ecosystems in South America. Its early postembryonic stages were reared in the laboratory from hatching of the first larval stage through the first juvenile crab instar, and changes in the quantity and elemental composition of biomass (measured as dry weight, W; carbon, C; nitrogen, N; hydrogen, H) were investigated in short intervals of time (every 1 or 2 d). In a series of successive developmental stages, the accumulation of biomass per individual can be described as an exponential function of the number of moults. In contrast, the pattern of growth within individual moulting cycles is described with best fit of observed and predicted data as a quadratic function of development time elapsed since last ecdysis. Weight-specific instantaneous growth rates show decreasing trends within the moulting cycle. Cumulative biomass increments during larval development of *C. granulata* are among the highest on record for brachyuran crabs. The quantities and patterns of larval growth are in this species similar as in most marine brachyuran crabs, for which data are available, but different from those in some other semiterrestrial grapsid crab species, which live in similar brackish water habitats as *C. granulata*. Hence, the early postembryonic stages of *C. granulata* do not show special bioenergetic adaptations to the non-marine conditions, which prevail in the adult habitat of this species. This reflects a strategy of larval export to the sea, i.e. a reproductive dependence of this species on the marine environment.

Introduction

The true crabs (Brachyura) are considered marine by origin (Guinot, 1978). Among these, members of the family Grapsidae belong to the most typical and frequent inhabitants of salt marshes, mangroves, estuaries, and brackish coastal lagoons world-wide, many of them invading also marginal freshwater and terrestrial environments. However, only a minority of these species has completely adaptated to such non-marine habitats, spending here their entire life-cycle (Hartnoll, 1988; Anger, 1995). The majority seems to follow an "export strategy" (review of dispersal strategies: Strathmann, 1982; Morgan, 1995a, b): the adults may live in brackish, freshwater, or terrestrial environments, but their larvae must develop in sea water.

In species which retain their larvae in the adult habitat, physically extreme conditions and a highly variable, unpredictable plankton production select for physiological adaptations in the early life-history stages (review: Anger, 1995). A strategy of larval export, in contrast, may allow for a persistance of ancestral marine traits during the larval and early juvenile phase. As one of the most conspicuous adaptations to development in non-marine habitats, the larvae of some crab species show a high degree of nutritional independence, based upon enhanced initial lipid reserves; this endotrophic potential appears to be associated with unusually low larval growth rates (compared with marine species), even in the presence of sufficient food (Anger, 1995). However, only scarce data is available on development, physiology, and growth

in the larvae of decapod species that live in transitional zones between the sea, freshwater, and land.

The semiterrestrial grapsid crab *Chasmagnathus granulata* Dana is one of the most predominant inhabitants of the supratidal and intertidal zones of brackish salt marshes, estuaries, and coastal lagoons in southeastern South America (Boschi, 1964; Boschi et al., 1992). The adults survive for extended periods on dry land and in water with extremely low salinity (Santos et al., 1987; Spivak et al., 1994), where they also reproduce (Spivak et al., in press; Luppi et al., in press). Larval development of this species, in contrast, is presumed to take place in adjacent coastal marine waters (Anger et al., 1994). In the present study, patterns of growth and chemical compositon were investigated during the complete larval development and through the first juvenile stage of *C. granulata*, in order to detect possibly existing early bioenergetic adaptations to non-marine conditions in this species.

Materials and methods

Ovigerous *Chasmagnathus granulata* were caught in a salt marsh near the village of Mar Chiquita (Province of Buenos Aires, Argentina [37°44′ S, 57°25′ W]; for characterization of the habitat and local distribution of the adults: see Spivak et al. 1994). Crabs were transported to the Helgoland Marine Biological Station (Germany), where they were maintained in local seawater (32–33‰ S) at constant 18°C, with a 12:12 h daylight:darkness regime, until larvae hatched. These were mass-reared in gently aerated 10 L glass beakers, under the same conditions of temperature, salinity, and light. Every 24 h, food (freshly hatched *Artemia* spec. nauplii, San Francisco Bay Brand™) and seawater were changed, and the larvae were checked under a dissecting microscope. Dead larvae were discarded, while freshly moulted individuals were staged (according to size and morphological criteria; Boschi et al., 1967) and transferred with wide-bore pipettes to new rearing vessels. In this way, each beaker contained exclusively larvae which were not only in the same stage, but also had the same age within a given instar. Megalopae and juvenile crabs were reared, under otherwise identical conditions, in unaerated glass bowls (400 ml), with nylon gauze (300 μm mesh size) offered as an artificial substrate. In short intervals (every 1 or 2 days), samples of larvae or early juveniles, respectively, were taken for later determination of dry weight (W) and elemental composition (carbon, C; nitrogen, N; hydrogen, H; see Tables 1 and 2 for numbers of replicates, *n*, and total numbers of individuals, n', analysed). Until analysis, the samples were stored frozen at below –20°C in pre-weighed tin cartridges. W was measured to the nearest 0.1 μg on a Mettler UM3 microbalance. C, N, and H were measured with a model 1108 Carlo Erba CHN Analyser, applying standard techniques (Anger & Harms, 1990). The energy content of biomass (per individual or per mg W) was estimated from C (Salonen et al., 1976).

Statistical analysis of data followed standard methods (Sachs, 1984). Since goodness-of-fit G-tests showed that the data did not significantly deviate from a normal distribution, multiple comparisons of mean values were carried out employing parametric analysis of variance (ANOVA), pairwise comparisons with Student's t-test, after checking for equal or unequal variances (F-test). Three levels of statistical significance ($P < 0.05$, < 0.01, or < 0.001) are distinguished in comparisons of mean values and in regression analyses.

Results

Changes in dry weight (W) and elemental composition (C, N, H) measured during the course of larval and early juvenile development of *Chasmagnathus granulata* are fully documented in Tables 1 and 2. Typical patterns of growth are illustrated in Figures 1 and 2, with W as a measure of biomass, *B*. Changes in the relative composition (C, N, H in % of W) are shown in Figure 3. All parameters of *B* per individual (in μg or Joules, respectively), increased significantly during larval and early juvenile development both between subsequent stages and during the course of each moulting cycle (ANOVAs: in all parameters of *B* and in all developmental stages $P < 0.0001$).

When growth is described in a sequence of developmental stages, *B* increases exponentially with the number moults passed (stage number: S = 1 in Zoea I, = 2 in Zoea II, etc.):

$$B = c \cdot \mathrm{e}^{k \cdot S}, \qquad (1)$$

where *c* and *k* are fitted constants, and e is the base of the natural logarithm. Figure 1a shows, as an example, the increase in W from hatching to the first crab stage, for both the initial and final values in each stage. The gap between these two exponential curves represents the weight gain (ΔW) in each stage. Also this

Table 1. Chasmagnathus granulata. Changes in dry weight (W), carbon (C), nitrogen (N), hydrogen (H), and energy content (E), C:N, C:H weight ratios, during time (d) of zoeal development; $\bar{x} \pm$ SD, *n*: number of replicate analyses; n': total number of individuals analysed

Stage:	Zoea I					Zoea II					Zoea III						Zoea IV						
Time (d):	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	5	0	1	2	3	4	5	6
W (μg/ind)	8.45	11.58	13.18	14.52	16.03	21.69	24.35	26.97	29.12	30.15	33.21	42.69	48.86	50.40	56.65	63.95	76.57	92.97	108.68	123.55	127.50	135.48	140.35
±	0.34	0.15	0.53	1.24	0.54	1.00	0.59	0.71	2.42	1.54	1.15	2.05	4.05	5.34	3.07	1.53	2.80	2.87	7.24	6.20	4.61	5.76	3.43
C (%W)	35.46	34.61	36.08	38.43	38.89	36.22	36.24	37.75	39.30	39.12	38.61	35.43	36.29	37.61	42.49	43.58	37.43	40.41	42.14	42.45	43.89	43.86	44.79
±	0.54	0.27	0.74	0.50	1.09	0.50	0.24	0.57	0.88	1.57	1.76	0.39	0.76	0.69	1.08	0.88	0.37	0.22	0.64	0.43	0.29	0.62	0.47
C (μg/ind)	3.00	4.01	4.75	5.58	6.23	7.85	8.82	10.18	11.45	11.81	12.81	15.12	17.75	18.95	24.08	27.86	28.66	37.57	45.82	52.46	55.96	59.46	62.86
±	0.09	0.03	0.14	0.51	0.11	0.30	0.26	0.28	1.00	0.93	0.57	0.66	1.73	2.01	1.54	0.76	1.10	1.22	3.52	3.04	2.19	3.31	1.53
N (%W)	8.44	7.53	7.94	8.46	8.45	7.47	7.64	8.00	8.67	8.21	8.08	7.21	8.07	8.73	9.23	9.51	8.52	8.42	8.98	10.64	9.27	9.19	9.32
±	0.69	0.23	0.25	0.11	0.31	0.13	0.36	0.07	0.15	0.24	0.58	0.37	0.47	0.38	0.28	0.21	0.09	0.14	0.11	0.19	0.31	0.07	0.32
N (μg/ind)	0.71	0.87	1.05	1.23	1.35	1.62	1.86	2.16	2.52	2.47	2.68	3.08	3.94	4.41	5.23	6.08	6.52	7.82	9.76	13.15	11.82	12.45	13.08
±	0.04	0.03	0.07	0.10	0.03	0.06	0.10	0.07	0.23	0.11	0.21	0.12	0.35	0.58	0.32	0.20	0.21	0.26	0.66	0.78	0.53	0.56	0.57
H (%W)	5.48	5.22	5.62	5.60	5.51	5.94	5.92	5.43	5.44	5.34	5.53	5.82	5.88	5.90	6.19	6.51	5.30	6.19	5.17	6.41	6.88	6.59	6.91
±	0.48	0.54	0.33	0.28	0.17	0.46	0.19	0.29	0.33	0.43	0.84	0.15	0.44	0.19	0.13	0.52	0.09	0.20	0.10	0.34	0.14	0.16	0.15
H (μg/ind)	0.46	0.61	0.74	0.82	0.88	1.29	1.44	1.47	1.58	1.61	1.83	2.49	2.86	2.97	3.51	4.16	4.06	5.76	5.63	7.92	8.77	8.93	9.69
±	0.02	0.06	0.07	0.10	0.03	0.12	0.06	0.08	0.03	0.18	0.29	0.17	0.06	0.31	0.25	0.38	0.18	0.29	0.45	0.54	0.40	0.55	0.23
C:N	4.22	4.60	4.55	4.54	4.60	4.85	4.75	4.72	4.53	4.77	4.81	4.92	4.51	4.32	4.61	4.58	4.40	4.80	4.69	3.99	4.74	4.77	4.81
±	0.31	0.15	0.16	0.07	0.04	0.05	0.20	0.05	0.03	0.22	0.51	0.22	0.27	0.20	0.05	0.07	0.04	0.07	0.07	0.05	0.15	0.07	0.15
C:H	6.51	6.69	6.44	6.87	7.06	6.13	6.12	6.96	7.25	7.35	7.18	6.09	6.20	6.38	6.86	6.73	7.07	6.53	8.15	6.64	6.38	6.66	6.49
±	0.50	0.79	0.43	0.29	0.10	0.59	0.17	0.34	0.48	0.35	1.58	0.15	0.51	0.17	0.18	0.53	0.07	0.20	0.11	0.37	0.10	0.11	0.13
E (J/ind)	0.10	0.14	0.17	0.20	0.22	0.27	0.31	0.36	0.41	0.43	0.46	0.52	0.62	0.67	0.90	1.06	1.02	1.38	1.72	1.97	2.14	2.27	2.42
±	0.00	0.00	0.00	0.02	0.00	0.01	0.01	0.01	0.04	0.04	0.03	0.02	0.06	0.07	0.06	0.04	0.04	0.05	0.14	0.12	0.09	0.14	0.06
E (J/mg W)	12.28	11.86	12.59	13.79	14.03	12.66	12.67	13.43	14.24	14.15	13.89	12.26	12.69	13.36	15.97	16.58	13.27	14.83	15.77	15.94	16.75	16.74	17.26
±	0.27	0.13	0.37	0.26	0.57	0.05	0.12	0.29	0.46	0.81	0.91	0.19	0.38	0.35	0.59	0.49	0.19	0.12	0.35	0.23	0.16	0.35	0.27
n (analyses)	5	5	5	6	5	5	5	5	3	5	5	5	5	5	5	5	8	8	8	7	8	8	8
n′ (indiv.)	150	125	100	150	100	100	75	75	45	50	50	50	40	30	25	25	80	48	40	35	40	40	40

Table 2. *Chasmagnathus granulata*. Changes in dry weight (W), carbon (C), nitrogen (N), hydrogen (H), and energy content (E), C:N and C:H weight ratios, during time (d) of development in the Megalopa and Crab I stages; $\bar{x} \pm$ SD, *n*: number of replicate analyses; n': total number of individuals analysed

Stage:	Megalopa								Crab I					
Time (d):	0	1	2	4	6	8	10	12	0	1	2	4	6	7
W (μg/ind)	141.76	184.19	186.84	226.43	277.69	259.68	315.41	271.34	275.50	312.64	344.50	430.26	436.38	462.08
$\pm$	10.73	10.82	18.65	23.66	17.56	22.83	24.65	22.12	17.93	77.74	28.34	41.00	51.66	76.19
C (%W)	38.58	37.03	36.92	40.11	41.24	43.07	39.31	41.71	38.13	37.51	36.00	37.93	37.03	37.47
$\pm$	1.56	0.39	1.09	1.33	0.68	0.89	2.62	0.93	2.85	3.15	1.09	0.84	1.08	0.96
C (μg/ind)	54.60	68.19	69.11	91.02	114.56	111.98	123.54	113.25	104.84	115.80	124.07	163.09	161.82	173.17
$\pm$	3.20	3.78	8.46	11.02	8.17	11.52	5.88	10.64	7.11	24.39	11.58	14.47	22.27	29.25
N (%W)	8.52	7.81	8.08	8.34	8.27	8.65	7.75	8.51	8.33	8.04	7.85	8.00	8.14	8.07
$\pm$	0.36	0.25	0.16	0.21	0.20	0.21	0.58	0.21	0.43	1.53	0.30	0.31	0.30	0.33
N (μg/ind)	12.05	14.37	15.10	18.87	22.95	22.45	24.35	23.06	22.89	24.23	27.05	34.36	35.42	37.23
$\pm$	0.70	0.80	1.52	1.94	1.06	1.90	1.31	1.48	0.76	3.11	2.47	2.93	3.44	5.99
H (%W)	5.19	5.98	4.87	5.73	6.37	6.17	5.74	6.13	6.02	5.86	5.62	5.72	5.04	5.69
$\pm$	0.23	0.18	0.33	0.32	0.19	0.27	0.32	0.22	0.52	0.52	0.26	0.23	0.18	0.27
H (μg/ind)	7.35	11.02	9.13	13.02	17.68	16.07	18.03	16.65	16.55	18.24	19.33	24.58	22.05	26.33
$\pm$	0.61	0.85	1.36	1.87	1.26	1.94	0.91	1.80	1.20	4.54	1.20	2.36	3.18	4.64
C:N	4.53	4.75	4.57	4.81	4.99	4.98	5.08	4.91	4.59	4.75	4.59	4.75	4.56	4.65
$\pm$	0.11	0.13	0.12	0.14	0.14	0.16	0.13	0.19	0.38	0.65	0.19	0.17	0.26	0.16
C:H	7.44	6.20	7.60	7.01	6.48	6.98	6.85	6.81	6.34	6.41	6.41	6.64	7.35	6.59
$\pm$	0.21	0.20	0.32	0.24	0.16	0.20	0.10	0.14	0.12	0.40	0.26	0.14	0.06	0.18
E (J/ind)	1.96	2.41	2.44	3.33	4.25	4.24	4.48	4.22	3.75	4.10	4.33	5.82	5.71	6.14
$\pm$	0.11	0.13	0.32	0.46	0.32	0.47	0.27	0.43	0.34	0.83	0.43	0.51	0.84	1.06
E (J/mg W)	13.87	13.07	13.01	14.68	15.28	16.29	14.27	15.54	13.66	13.34	12.55	13.53	13.07	13.29
$\pm$	0.82	0.20	0.55	0.70	0.37	0.49	1.41	0.51	1.48	1.60	0.54	0.43	0.55	0.49
n (analyses)	8	8	8	8	8	8	8	8	5	5	5	5	5	5
n' (indiv.)	24	24	24	24	24	24	24	24	5	5	5	5	5	5

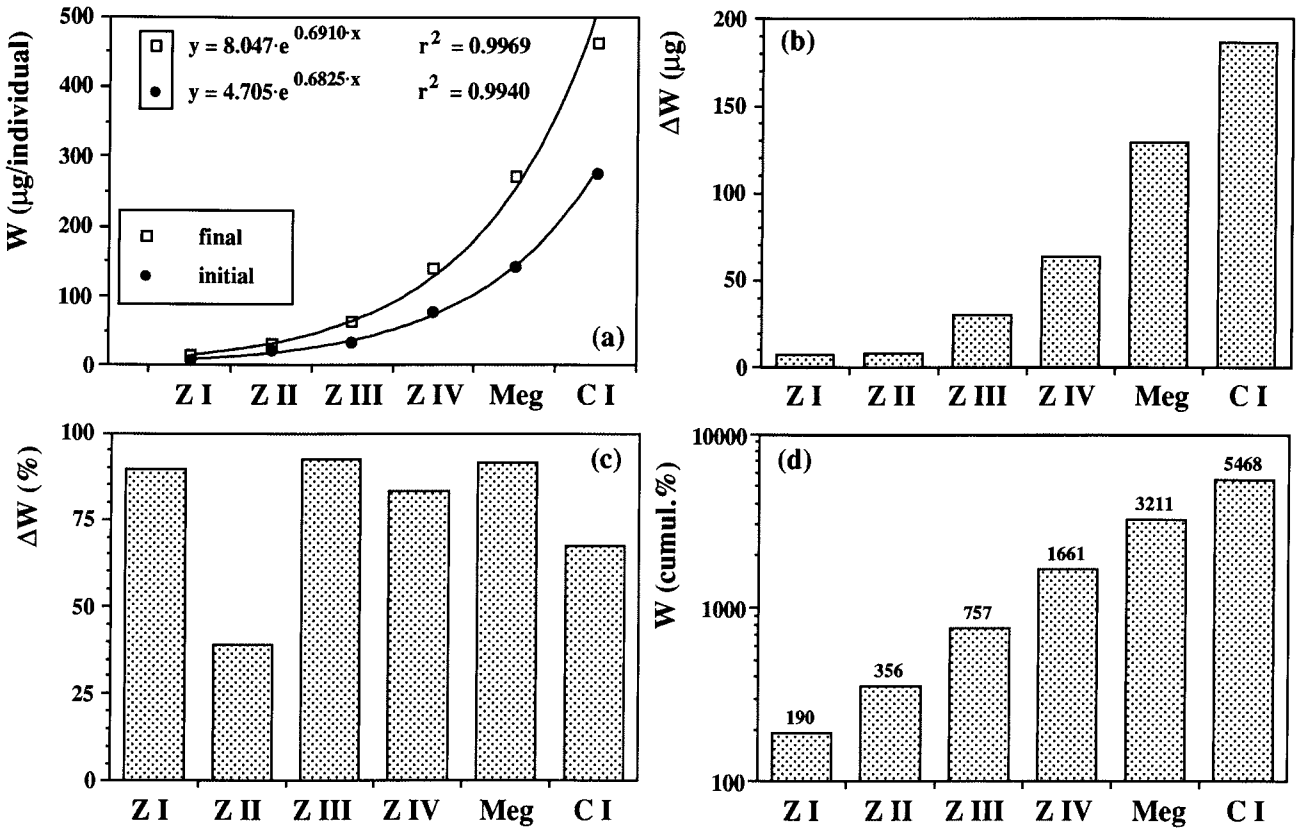

Figure 1. Chasmagnathus granulata. Growth (dry weight, W, per individual) in successive developmental stages (Zoea I–IV, Megalopa, Crab I). (a) Increase of initial and final W, respectively, as an exponential function of the number of stages; r^2: coefficient of determination for regression equations given; (b) growth increment (ΔW), in μg/individual; (c) ΔW as a percentage of intial (early postmoult) W in each stage; (d) cumulative growth, as a percentage of the initial W at hatching from the egg.

increment (ΔW in μg per individual) shows an exponential increase in a series of developmental stages (Figure 1b).

When ΔW is expressed as a relative increment (in % of early postmoult W in each stage), gains of 39–93% per moult cycle are obtained, with a minimum value measured in the Zoea II. The other larval stages gained 83–93% in W, and an increment of 68% was observed during the Crab I stage (Figure 1c).

Cumulative weight gain (ΔW expressed in % of the initial W of a freshly hatched Zoea I larva) showed an exponential increase, i.e. a linear increase on a logarithmic scale. Figure 1d shows that W increased from hatching to the end of the last zoeal stage by a factor of almost 16, or by a factor of 32 during complete larval development from hatching to metamorphosis. Similar growth patterns, but in most cases with larger percentage increments, were found also in the other parameters of *B* (not shown in graphs; cf. Tables 1, 2).

When the increment in each developmental stage is further analysed, growth during time (*t*, in days) of individual moulting cycles can be described with a simple 2nd-order polynomial (quadratic) equation:

$$B = B_o + a \cdot t - b \cdot t^2, \qquad (2)$$

where B_o, *a*, and *b* are fitted constants. B_o is an estimate of the initial *B* value for a given parameter (W, C, N, H, or E) within a given moulting cycle, and the constants *a* and *b* define the curvature of the model. The fitted constants for all developmental stages and parameters of *B* are given in Table 3. With the exception of H in the Crab I stage, all coefficients of determination (r^2) were ≥ 0.9 and significantly different from zero ($P < 0.001$; in Crab I: $r^2 = 0.839$, $P = 0.01$). In all developmental stages and all parameters of *B*, the biomass curves were parabola-shaped, with a tendency to flatten during the course of a moulting cycle (Figure 2: W shown as an example).

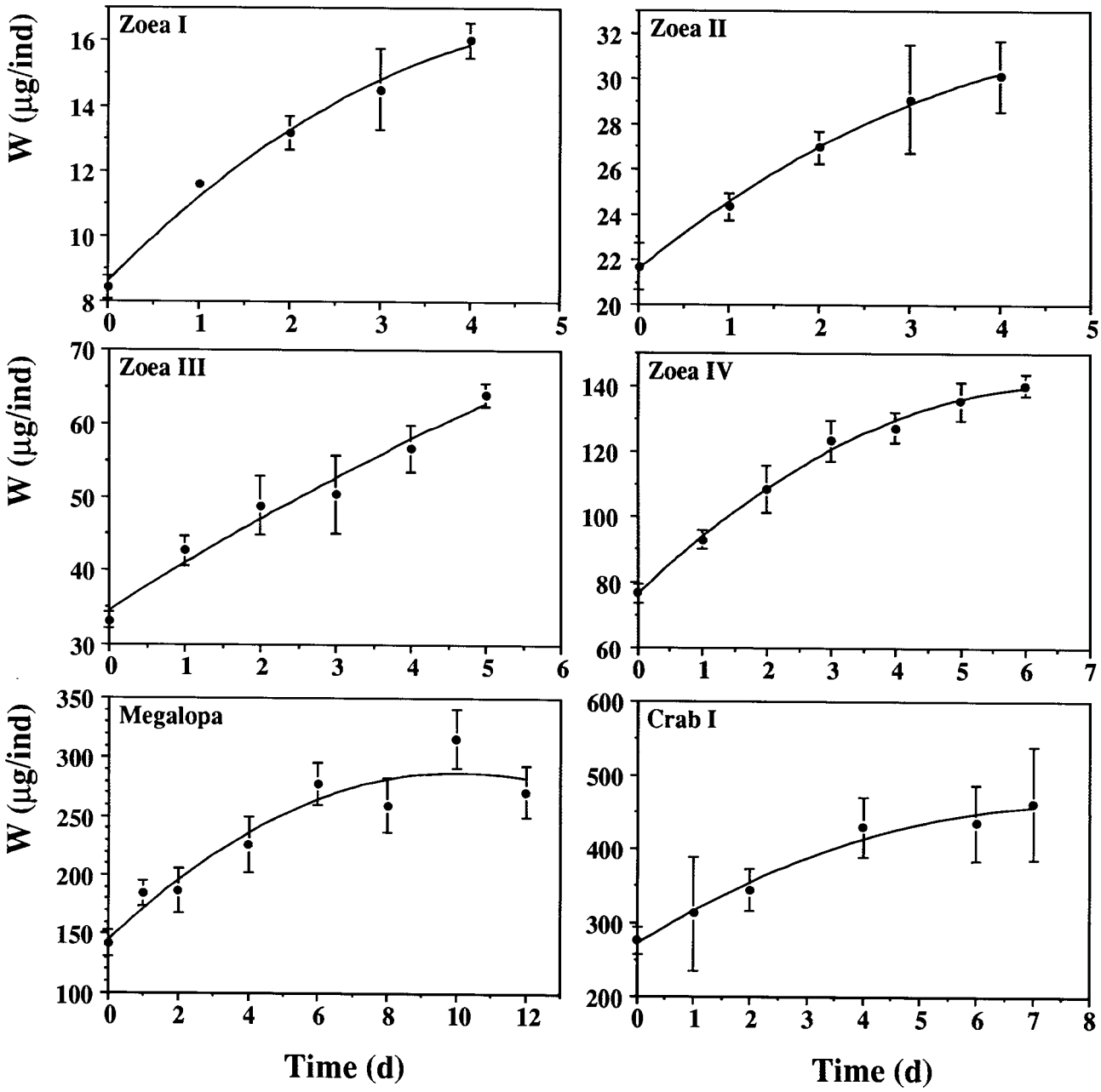

Figure 2. Chasmagnathus granulata. Growth (dry weight, W, in μg/individual; $\bar{x} \pm$ SD) during time (d) of development in successive moulting cycles. Parameters of regression curves: see Table 3.

These parabolic patterns indicate that the instantaneous (daily) rates of growth, *G*, decreased during time of development in each moulting cycle. Instantaneous growth rates (*G* in μg or J·individual^{-1}·d^{-1}) are obtained by derivation of Eq. 2:

$$G = \mathrm{d}B/\mathrm{d}t = a - 2 \cdot b \cdot t. \qquad (3)$$

Thus, our model predicts a linear decrease in *G* during the time (*t*) of the moulting cycle, and the fitted constant *a* becomes an estimate of the initial (maximum) daily growth rate. Only in the Zoea III, where negative

Table 3. Chasmagnathus granulata. Fitted constants (B_o, *a*, *b*; see text: Eq. 2) and coefficients of determination (r^2) of polynomial regression equations describing changes in biomass (dry weight, W; carbon, C; nitrogen, N; hydrogen, H; energy content, E; in μg or Joules per individual, respectively) during time (d) of development in subsequent stages (Zoea I–Crab I)

	Stage:	Zoea I	Zoea II	Zoea III	Zoea IV	Megalopa	Crab I
W	B_o	8.6	21.6	34.6	76.4	144.2	270.8
	a	2.81	3.24	6.58	18.98	28.50	48.02
	b	0.250	0.266	0.189	1.406	1.422	3.054
	r^2	0.9912	0.9976	0.9717	0.9953	0.9210	0.9801
C	B_o	3.0	7.7	13.1	28.8	52.3	101.6
	a	0.98	1.43	1.40	9.70	13.19	16.87
	b	0.045	0.094	–0.310	0.686	0.656	0.981
	r^2	0.9990	0.9851	0.9872	0.9978	0.9648	0.9531
N	B_o	0.70	1.58	2.65	6.18	11.74	21.97
	a	0.187	0.385	0.497	2.489	2.374	3.383
	b	0.0057	0.0371	–0.0373	0.2302	0.1172	0.1726
	r^2	0.9975	0.9580	0.9954	0.9097	0.9761	0.9701
H	B_o	0.46	1.30	1.95	4.06	7.42	16.42
	a	0.171	0.124	0.367	1.380	2.017	2.030
	b	0.0164	0.0114	–0.0113	0.0730	0.1018	0.1135
	r^2	0.9995	0.9689	0.9669	0.9520	0.8983	0.8394
E	B_o	0.10	0.27	0.47	1.03	1.83	3.61
	a	0.041	0.053	0.029	0.390	0.513	0.582
	b	0.0029	0.0029	–0.0182	0.0269	0.0256	0.0327
	r	0.9994	0.9908	0.9866	0.9982	0.9683	0.9367

b values were obtained (Table 4), slightly increasing daily rates of biomass accumulation are described by our model.

Since the absolute rates of *G* (in μg or J·individual^{-1}·d^{-1}) depend on the absolute amounts of *B* present in a larva or juvenile, *G* was consistently highest in W, followed by C (or E, estimated from C), N, and H. Likewise, it showed in all parameters of *B* a clear increase in subsequent developmental stages.

In order to make daily growth rates comparable for different measures of *B*, and among different stages and species, they must be normalized. Biomass-specific growth rates (*G/B*; dimension: fraction [or %] of *B*·d^{-1}) are calculated by division of Eq. 3 by the corresponding parameter of biomass:

$$G/B = \mathrm{d}B/(B \cdot \mathrm{d}t) = (a - 2 \cdot b \cdot \mathrm{t})/B. \quad (4)$$

In all developmental stages and all parameters of biomass considered (except for C in the Zoea III), maximum *G/B* values were observed in early postmoult, with initially ca. 15–30% growth per day, and decreasing increments during the later parts of the moulting cycle. In late larval stages (Zoea IV, Megalopa), growth reached zero values and eventually, became negative prior to ecdysis.

Changes in the relative composition of biomass (C, N, H in % of W; elemental ratios; W-specific energy content) are documented in Tables 1 and 2, and some typical patterns are illustrated in Figure 3. After hatching or moulting, respectively, W showed mostly a steep immediate increase, followed by only little changes thereafter. In contrast, the fractions of C, N and H, and the energy content (E) increased more steadily during each moulting cycle. As a consequence of these differential rates of increase, the percentage C, N and H as well as the W-specific energy values decreased during postmoult. Later during the moulting cycle (in intermoult and premoult), these values increased again. This typical sequence caused a cyclic pattern, which was particularly conspicuous in C (Figure 3).

The average level of these measures of organic constituents within total biomass (W) increased throughout zoeal development, then it decreased slightly in the Megalopa and in the first juvenile stage (Figure 3). The C:N weight ratio showed an increasing tendency

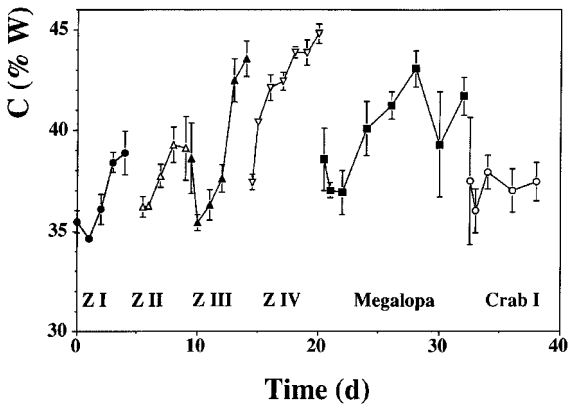

Figure 3. Chasmagnathus granulata. Changes in carbon (C, in % of dry weight, W; $\bar{x} \pm$ SD) during time (d) of development in successive moulting cycles. Z: Zoea stage.

throughout larval development (from ca. 4.2 to about 5.0, if one particularly low measurement in the Zoea III is ignored); after metamorphosis, this index remained at a level of ca. 4.5 to 4.7.

Discussion

The semiterrestrial crab *Chasmagnathus granulata* is typically found in habitats with extremely variable and often very low salinity conditions (Boschi, 1964; Boschi et al., 1992; Spivak et al., 1994). After hatching from the egg, this species passes through four (Boschi et al., 1967), or exceptionally through five zoeal stages (Pestana & Ostrensky, 1995; Anger, unpubl. obs.). Within the family Grapsidae, this type of larval development is quite typical of coastal marine species, whereas those living in brackish water habitats show frequently an abbreviation of the zoeal phase (review: Rabalais & Gore, 1985; Anger, 1995).

As in morphological development, also the patterns of growth and chemical composition of larval biomass resemble in *C. granulata* (Tables 1 and 2, Figures 1 to 3) closely those of marine decapod crustacean species (for review see Anger, 1991, Anger in press). In the early Zoea I, about 35% C and a C:N ratio of 4.2 were measured, which is quite similar to the average in marine decapod larvae (Anger & Harms, 1990). This is in contrast, however, to some other grapsid crab species which live in brackish Jamaican mangroves: their larvae hatch with great yolk reserves persisting from the egg (reflected by enhanced C contents and C:N ratios) and, probably as a consequence of partial degradation of those yolk reserves, show reduced zoeal growth rates even in the presence of sufficient food (Anger, 1995).

Also the order of magnitude and the patterns of change in instantaneous biomass-specific growth rates during individual moulting cycles of larval *C. granulata* were similar as in marine decapod species (cf. Anger, 1991): they were maximum (ca. 15 to 40% d^{-1}) in early postmoult, then they levelled off during intermoult and premoult. When cumulative zoeal growth from hatching to the end of the zoeal phase (here: to the premoult Zoea IV), is compared with that in other brachyuran larvae (cf. Anger, 1995), *C. granulata* does not show a reduced, but rather one of the highest rates of biomass accumulation so far recorded in larval decapods. Likewise, the patterns of larval respiration rate in relation to different temperatures suggest adaptations to development in marine rather than in the shallow waters of coastal lagoons and salt marshes (Ismael et al., in press). In summary, the brackish-water crab *C. granulata* shows in the bioenergetics of its larval and early juvenile stages the typical traits of a marine species, without apparent adaptations to the brackish and semiterrestrial conditions, under which the adults live and where the larvae are released. This indicates a strategy of larval export out of the adult habitat, i.e. rapid transport of early larvae towards the sea, corroborating the conclusions drawn by Anger et al. (1994) from patterns of larval occurrence in the lagoon plankton. Since a stable plankton production should be expected in coastal marine waters (in contrast to lagoons or mangrove swamps), there may be no selection for an enhanced maternal energy investment into egg production of this species. However, other physiological adaptations to non-marine conditions should be expected in *C. granulata* larvae, namely an enhanced salinity tolerance of the Zoea I and the Megalopa, because these stages leave and re-enter, respectively, salt marshes and brackish coastal lagoons.

More comparative data on larval growth, physiology, and ecology of decapod crustacean species that live in transitional zones between sea, freshwater, and land, should improve our understanding of early life-history adaptations, and eventually, of the evolutionary transition of crustaceans from marine to limnic or terrestrial environments.

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