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Influence of limited food supply on growth and elemental composition (C, N, H) of *Carcinus maenas* (Decapoda) larvae, reared in the laboratory[1]

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ABSTRACT: Zoea 1 larvae of *Carcinus maenas* L. (Decapoda, Brachyura, Portunidae) were reared in the laboratory through ecdysis at 18 °C. Dry weight (DW) and elemental contents of carbon (C), nitrogen (N), and hydrogen (H) were analyzed in newly hatched Zoea 1, after different initial feeding periods, and in newly moulted Zoea 2. If food was continuously available, Zoea 1 larvae revealed considerable growth through the moult cycle, and biomass slightly declined shortly before ecdysis. Changing biomass and energy show best fits to quadratic equations with time. Gain at times of maximum biomass has been defined as maximum growth (MG; Dawirs et al. 1986), which was attained with 60 % DW, 71 % C, 52 % N, 89 % H, and 73 % energy. Zoea 1 larvae lost considerable amounts of biomass and energy whenever food supply was interrupted. Biomass of newly moulted Zoea 2 is linearly correlated with feeding periods in Zoea 1, showing higher values the longer initial feeding lasted. The point-of-reserve-saturation (PRS) was reached at the transition of intermoult to premoult, when about 80 % of MG was attained. If food supply ceased after this point, newly moulted Zoea 2 exhibited, at the most, 33 % DW, 40 % C, 31 % N, and 41 % J ind^{-1} less than their continuously fed siblings. Growing Zoea 1 gained C at higher rates than N. During periods of subsequent starvation C decreased at higher rates than N. Lipid is assumed to be the main source of energy, which controls the maintenance of the moult cycle and further development through periods of occasional starvation.

INTRODUCTION

Carcinus maenas, the common shore crab, has become a standard object in laboratory research on brachyuran crab larval ecology during the past 8 yr. The larvae hatch from eggs into non-feeding prezoeae, which moult to free-swimming zoeae within a few minutes. Altogether, 4 successive zoea and 1 terminal megalopa stage remain in the plankton for about 36 to 55 d until metamorphosis (Dawirs 1985). If sufficient food is available, larvae feed and grow at various rates during all instars (Dawirs & Dietrich 1986, Dawirs et al. 1986). *C. maenas* larvae are not, however, dependent on continuous feeding, but were found to be well adapted to natural prey shortages (Dawirs 1984). Besides temperature variations, acute changes in natural food availability seem to be a very important influence on planktotrophic organisms (for recent review see Dawirs 1984). The occurrence of suitable prey organisms fluctuates considerably in boreal seas (Ikeda 1974).

Little information is available on the effects of limited food supply and starvation on the physiology of brachyuran crab larvae. The influence of food limitations on mortality and development durations at different stages of a crab larval moult cycle have been reported by Kurata (1959), Kon (1979), Anger & Dawirs (1981), Anger et al. (1981), and Dawirs (1984), and on crab larval morphogenesis by McConaugha (1982) and Anger (1984). Storch & Anger (1983) and Anger et al. (1985) investigated changing ultrastructures in hepatopancreas cells of crab larvae which were exposed to different nutritional conditions.

Three main questions were posed here. (1) What minimum amount of biomass and energy must *Car-*

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cinus maenas Zoea 1 accumulate to develop successfully and moult to the Zoea 2 instar? (2) What are the natural limits for growth and necessary food intake? (3) Are reserve proteins or lipids mostly metabolized during times of starvation? To answer these questions, Zoea 1 larvae of *Carcinus maenas* were reared in the laboratory and fed during different parts of the moult cycle. Dry weight (DW) and elemental composition (C, N, H) were measured shortly after hatching, at the end of each initial feeding period, and in newly moulted Zoea 2.

MATERIAL AND METHODS

Obtaining and handling of larvae. Gravid *Carcinus maenas* females were collected from the rocky intertidal region of northern Helgoland in March 1984 and taken to the laboratory. Maintenance of ovigerous crabs, and larval collecting and handling procedures follow the methods in Dawirs (1982).

Groups of 15 Zoea 1 were kept in glass crystallizing dishes (9.5 cm diameter), containing 200 ml of filtered (1 µm) natural sea water from Helgoland (31 to 33 ‰ S), at constant 18 °C. Larvae were fed newly hatched brine shrimp nauplii *Artemia* spp. (San Francisco Bay Brand, Inc., Newark, California 94560), and sea water was changed at least every other day.

The present experiments are of the type STEX-A, as distinguished by Dawirs (1984) where Zoea 1 larvae were starved after initial feeding periods. Larvae were then transfered to clean sea water, and starved until death or moulting to the Zoea 2 stage. A total of 4500 Zoea 1 larvae were starved after 1, 1.5, 2, 2.5, 3 and 4 d of initial feeding. An additional 1500 larvae were continually fed from hatching until moulting to Zoea 2. A total of about 6000 laevae were thus available for larval biomass analyses.

If initial feeding periods were long enough to ensure successful development of Zoea 1, they exceeded the individual 'point-of-reserve-saturation' (PRS). Since 100 % survival rates are rare in the laboratory, 50 % survival (PRS_{50}), was used for describing the minimum necessary food supply Maximum initial feeding periods which were insufficient for any larval moulting are defined as PRS_0 (see Anger & Dawirs 1981, Dawirs 1984).

Dry weight and elemental analyses. Biomass (DW, C, N, H) of continually fed *Carcinus maenas* Zoea 1 larvae was measured shortly after hatching (Day 0), and after 1, 1.5, 2, 2.5, 3, and 4 d of development. Newly moulted Zoea 2 from each of the described subexperiments were immediately analyzed. Ten replicates of 20 Zoea 1 larvae per analysis, or 13 to 23 replicates of 7 to 23 newly moulted Zoea 2, were carried out. A total of 3475 larvae were measured in 205 analytical samples. The larvae were pipetted into a clean dish containing ion exchange water to remove adherent salts. After about 3 s, they were pipetted onto clean filter paper to remove excess water. The larvae were then carefully transferred into pre-weighed Sn-cartridges using a small needle-shaped applicator, deep frozen and dried at $<10^{-2}$ mbar in a GT2 (Leybold-Heraeus) for a minimum of 3 h. After drying the cartridges were immediately closed and stored in a desiccator over silica gel until analysed. DW was determined on a UM 3 (Mettler) to the nearest 0.1 µg. Elemental analyses (C, N, H) were carried out with an Elemental Analyzer Model 1106 (Carlo Erba Science) using cyclohexane-2,4-dinitrophenyl-hydrazone as a standard. Energy equivalents were calculated by the N-corrected formula given by Salonen et al. (1976) and expressed in Joule units (1 J = 0.239 cal).

Mean values were computed as arithmetic means ± 95 % confidence intervals, and time-dependent trends described by means of least square regressions, with correlation coefficiencies tested for significant differences from zero (Sachs 1974).

RESULTS

Biomass results are presented in Table 1. Empirical and predicted data for individual DW, C, N, H, and energy of Zoea 1 are best fit to quadratic equations (Fig. 1, Table 2). When food was offered continuously through the moult cycle, individual Zoea 1 larvae of *Carcinus maenas* gained energy and weight steadily, reaching a maximum shortly before ecdysis at about 18.6 µg DW, 6.5 µg C, 1.4 µg N, and 0.222 J ind^{-1}. Thus, maximum growth (MG), relative to newly hatched Zoea 1, was 60 % DW (7.0 µg), 71 % C (2.7 µg), 52 % N (0.5 µg), and 73 % energy (0.094 J ind^{-1}) (Fig. 2A).

DW, C, N, H, and energy values of newly moulted Zoea 2 were highest when larvae were fed during the entire Zoea 1 moult cycle (Table 1). When feeding was limited to reduced initial periods of the Zoea 1 moult cycle, less biomass and energy were attained at ecdysis. Significant linear correlations were found between individual biomass of newly moulted Zoea 2 and duration of initial feeding periods in Zoea 1 (Fig. 1, Table 2). Larvae may moult successfully after only 1 d of feeding, but did so with about 57 % (DW), 50 % (C), 60 % (N), and 48 % (Joule) of that of their continuously feeding siblings. These percentages increase linearly with extension of the initial feeding periods (Fig. 2B).

Individual biomass and energy decreased whenever starvation occurred, but with less absolute and relative losses the later this happens in the Zoea 1 moult cycle. Maximum losses measured about 25 % DW, 33 % C,

Table 1. *Carcinus maenas*. Starvation experiment of type STEX-A (Dawirs 1984), where Zoea 1 larvae are starved after initial feeding periods; changing Zoea 1 biomass and energy equivalents during the moult cycle (Day 0 to 4) at 18°C; newly moulted Zoea 2 develop from continuously fed Zoea 1 (F) and from those with feeding limited to 1 to 4 d. DW: individual dry weight; C: carbon; N: nitrogen; H: hydrogen; J ind^{-1}: individual energy content (Joule); J $mgDW^{-1}$ DW-related energy content (Joule); percentages are DW-related; mean ± 95% confidence interval; number of reference analyses, with individuals per analysis in brackets

Zoea 1 Parameter	0	1 d	1.5 d	2 d	2.5 d	3 d	4 d
DW (µg)	11.64 ± 0.38	16.36 ± 0.19	17.39 ± 0.58	16.77 ± 0.35	19.16 ± 0.29	18.04 ± 0.57	18.13 ± 0.44
C (µg)	3.79 ± 0.07	5.21 ± 0.06	5.63 ± 0.20	5.54 ± 0.13	6.73 ± 0.13	6.56 ± 0.16	6.25 ± 0.14
N (µg)	0.94 ± 0.03	1.15 ± 0.03	1.22 ± 0.05	1.23 ± 0.04	1.44 ± 0.02	1.41 ± 0.02	1.42 ± 0.04
H (µg)	0.46 ± 0.02	0.69 ± 0.03	0.73 ± 0.05	0.69 ± 0.03	0.91 ± 0.07	0.91 ± 0.10	0.77 ± 0.06
C (%)	32.87 ± 0.85	31.84 ± 0.31	32.42 ± 1.05	33.03 ± 0.25	35.09 ± 0.54	36.38 ± 1.00	34.55 ± 0.38
N (%)	8.12 ± 0.37	7.04 ± 0.17	7.00 ± 0.19	7.32 ± 0.19	7.52 ± 0.11	7.84 ± 0.28	7.85 ± 0.19
H (%)	3.97 ± 0.17	4.21 ± 0.18	4.18 ± 0.20	4.13 ± 0.19	4.73 ± 0.31	5.01 ± 0.50	4.24 ± 0.37
C:N	3.97 ± 0.18	4.52 ± 0.10	4.64 ± 0.15	4.52 ± 0.13	4.67 ± 0.06	4.64 ± 0.07	4.39 ± 0.07
J ind^{-1}	0.128 ± 0.003	0.172 ± 0.003	0.189 ± 0.009	0.187 ± 0.005	0.232 ± 0.006	0.229 ± 0.008	0.213 ± 0.006
J $mgDW^{-1}$	10.89 ± 0.44	10.54 ± 0.15	10.82 ± 0.49	11.10 ± 0.12	12.10 ± 0.26	12.75 ± 0.50	11.78 ± 0.22
Analyses	10 (20)	10 (20)	10 (20)	10 (20)	10 (20)	9 (20)	10 (20)
Newly moulted Zoea 2	(F)	(1 d)	(1.5 d)	(2 d)	(2.5 d)	(3 d)	(4 d)
DW (µg)	20.59 ± 0.54	11.16 ± 0.29	12.20 ± 0.28	14.41 ± 0.52	16.90 ± 1.13	17.55 ± 1.04	19.24 ± 0.67
C (µg)	7.00 ± 0.08	3.54 ± 0.11	3.83 ± 0.11	4.08 ± 0.25	5.24 ± 0.38	5.56 ± 0.38	6.22 ± 0.35
N (µg)	1.59 ± 0.03	0.97 ± 0.04	1.01 ± 0.02	1.04 ± 0.04	1.33 ± 0.07	1.35 ± 0.09	1.50 ± 0.06
H (µg)	0.76 ± 0.05	0.48 ± 0.03	0.51 ± 0.03	0.49 ± 0.05	0.49 ± 0.08	0.50 ± 0.07	0.57 ± 0.07
C (%)	34.06 ± 0.85	31.75 ± 0.50	31.44 ± 0.49	33.00 ± 1.41	31.00 ± 0.67	31.63 ± 0.61	32.46 ± 0.84
N (%)	7.76 ± 0.18	8.72 ± 0.29	8.33 ± 0.18	8.45 ± 0.37	7.95 ± 0.29	7.71 ± 0.37	7.85 ± 0.21
H (%)	3.67 ± 0.22	4.32 ± 0.30	4.16 ± 0.27	3.88 ± 0.30	2.93 ± 0.48	2.92 ± 0.44	2.96 ± 0.29
C:N	4.39 ± 0.08	3.66 ± 0.10	3.79 ± 0.09	3.39 ± 0.23	3.94 ± 0.15	4.14 ± 0.19	4.14 ± 0.13
J ind^{-1}	0.239 ± 0.004	0.117 ± 0.004	0.126 ± 0.005	0.139 ± 0.010	0.174 ± 0.013	0.183 ± 0.014	0.209 ± 0.015
J $mgDW^{-1}$	11.60 ± 0.41	10.51 ± 0.23	10.36 ± 0.23	11.11 ± 0.68	10.39 ± 0.53	10.45 ± 0.28	10.84 ± 0.39
Analyses	13 (15)	29 (15–20)	32 (11–23)	15 (11–18)	18 (7–22)	15 (9–19)	14 (12–16)

17 % N, and 35 % individual energy when the initial feeding period was limited to the first day of the Zoea 1 moult cycle (Fig. 3).

C accumulates at higher rates than N in growing Zoea 1 (Fig. 2A). On the other hand, C is metabolized at higher rates than N during starvation at any state of the moult cycle (Fig. 3).

DW-related percentages of both C and N have similar patterns in growing Zoea 1, showing an overall increase (Fig. 4). DW-related N-content increased during starvation of Zoea 1 larvae when fed initially for less than 3 d. Highest values were for newly moulted Zoea 2 larvae which were starved after 1 d of initial feeding in Zoea 1. On the other hand, DW-related C-content generally decreased during starvation. Differences between Zoea 1 and newly moulted Zoea 2 larvae reached a maximum when food deprivation of the Zoea 1 occurred after 3 d of initial feeding.

Under optimum feeding conditions, the C:N ratios increased at the beginning of the moult cycle and slightly decreased towards ecdysis, with values between about 4.0 and 4.7 (Fig. 4). C:N ratios generally decreased during starvation following previous feeding. The shorter the initial feeding period lasts in the Zoea 1 stage, the lower are the C:N ratios obtained by newly moulted Zoea 2 larvae. Values increase from about 3.7 to 4.4, for 1 d fed to continuously fed Zoea 1 larvae (Fig. 4).

DISCUSSION

It has been reported that, in decapod crustaceans, growth during larval moult cycles differs significantly from growth between successive larval instars. Biomass at comparable states of successive larval instars follows exponential sequences with time, and within single moult cycles parabolic or power functions (for recent discussion see Dawirs et al. 1986). Individual DW, C, N, H, and energy contents increase generally during moult cycles of *Carcinus maenas* lar-

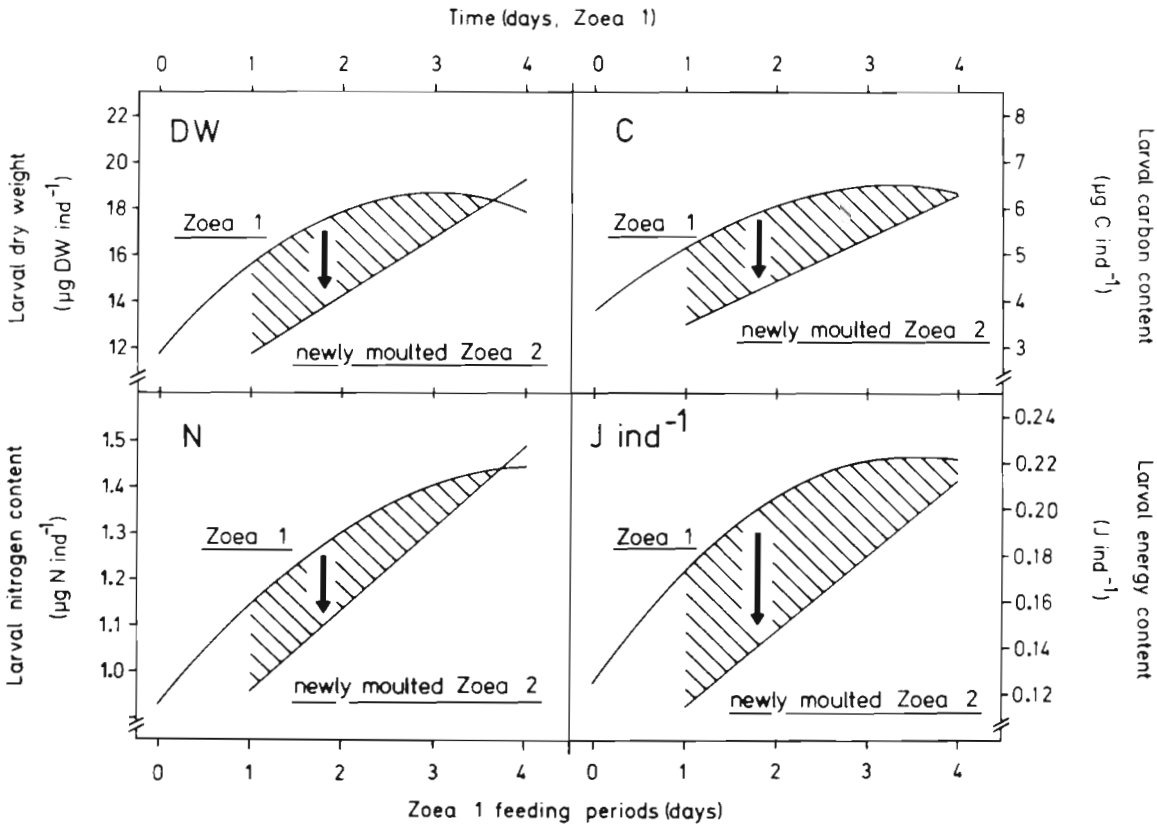

Fig. 1. *Carcinus maenas*. Individual dry weight (µg DW ind^{-1}), carbon (µg C ind^{-1}), nitrogen (µg N ind^{-1}), and energy (J ind^{-1}) follow quadratic equations with time during the moult cycle of Zoea 1; linear lines represent individual biomass (DW, C, N) and energy (J) of newly moulted Zoea 2, correlated with initial Zoea 1 feeding periods (formulae in Table 2); striped areas denote range of biomass or energy losses after food supply has ceased, and arrows mark the point-of-reserve-saturation (PRS_{50} = 1.8 d; Dawirs 1984)

Table 2. *Carcinus maenas*. Time dependent (t, d) changes in individual larval biomass and energy (B) of Zoea 1 (Z 1) at 18°C, described by quadratic equations; individual biomass and energy of newly moulted Zoea 2 ($B_{Z2\,(0)}$) are correlated linearly with initial Zoea 1 feeding periods (t, d). DW: dry weight (µg); C: carbon (µg); N: nitrogen (µg); H: hydrogen (µg); J ind^{-1}: individual energy content (Joule); a_0: initial biomass or energy at hatching; a, a_1, a_2, b: constants; r: correlation coefficient; levels of significance: $^{\bullet}$ $p < 0.05$, $^{\bullet\bullet}$ $p < 0.01$, $^{\bullet\bullet\bullet}$ $p < 0.001$, $^{\bullet\bullet\bullet\bullet}$ $p < 0.0001$

Zoea 1		$B_{Z1} = a_0 + a_1 t + a_2 t^2$			
Parameter	a_0	a_1	a_2	r	p
DW	11.971	4.445	− 0.741	0.958	$^{\bullet\bullet\bullet}$
C	3.755	1.639	− 0.247	0.961	$^{\bullet\bullet\bullet}$
N	0.930	0.246	− 0.030	0.968	$^{\bullet\bullet\bullet}$
H	0.450	0.265	− 0.044	0.911	$^{\bullet\bullet}$
J ind^{-1}	0.125	0.057	− 0.008	0.952	$^{\bullet\bullet\bullet}$
Zoea 2		$B_{Z2(0)} = a + bt$			
Parameter		a	b	r	p
DW		9.192	2.538	0.973	$^{\bullet\bullet\bullet}$
C		2.529	0.945	0.985	$^{\bullet\bullet\bullet\bullet}$
N		0.778	0.178	0.966	$^{\bullet\bullet\bullet\bullet}$
H		0.379	0.061	0.823	$^{\bullet}$
J ind^{-1}		0.081	0.033	0.991	$^{\bullet\bullet\bullet\bullet}$

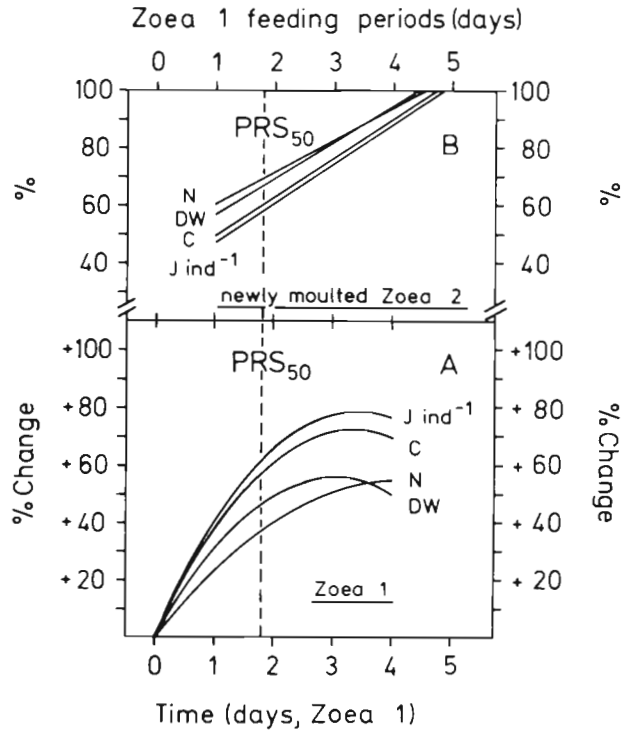

Fig. 2. *Carcinus maenas*. (A) Changes in individual dry weight (DW), carbon (C), nitrogen (N), and energy (J ind^{-1}) during Zoea 1 moult cycle as percentages of newly hatched larvae. (B) Individual biomass (DW, C, N) and energy (J ind^{-1}) of newly moulted Zoea 2 relative to length of initial feeding periods of Zoea 1; 100 % represents values of newly moulted Zoea 2 fed continuously during Zoea 1 moult cycle. PRS_{50}: point-of-reserve-saturation

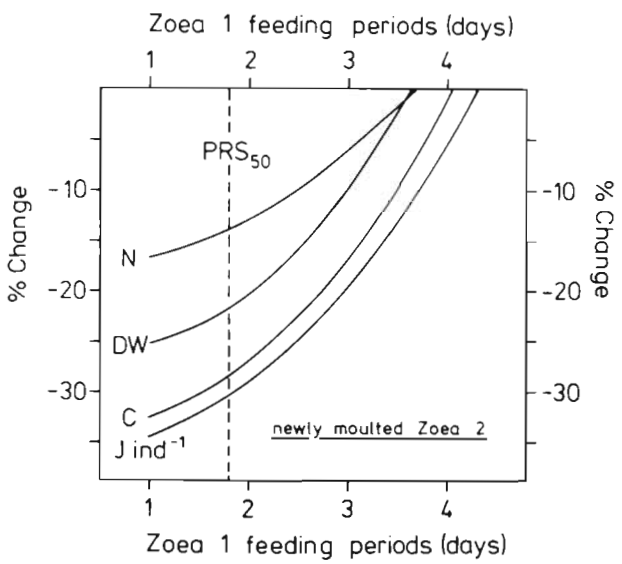

Fig. 3. *Carcinus maenas*. Individual dry weight (DW), carbon (C), nitrogen (N), and energy (J ind^{-1}) losses towards ecdysis, after periods of limited initial feeding of Zoea 1; percentage differences between biomass (DW, C, N) or energy (J ind^{-1}) of newly moulted Zoea 2 and that which Zoea 1 attained at times when feeding ceased. PRS_{50}: point-of-reserve-saturation

vae, if sufficient food is available, and reach a maximum before slightly decreasing in late premoult. Quadratic equations describe this pattern with best fits of original and predicted values.

Besides significant responses to varying water temperatures (Dawirs et al. 1986), *Carcinus maenas* larval growth seems inherently variable. Characteristic growth data of Zoea 1 hatched from 2 different female crabs are compared in Table 3. Larvae from Hatch B (Dawirs et al. 1986) show considerably higher absolute and relative growth than those derived from Hatch A (present study), although development started with comparable amounts of individual DW, C, N, and energy. Similar relations were found in *Hyas araneus* Zoea 1, with only little variation in biomass of newly hatched larvae and considerable differences in late premoult (Kunisch & Anger 1984).

Carcinus maenas larvae are clearly planktotrophic, and must feed for certain minimum periods in order to moult to Zoea 2. If Zoea 1 larvae are fed only for limited periods, ecdysis is delayed both in this stage and, even more pronounced, in the following Zoea 2 stage, though food supply is not limited in the latter (see Dawirs 1984). During this delay, Zoea 1 larvae lose energy and biomass in all constituents. The longer the initial feeding periods last, the less reserves are used during subsequent shorter delays of normal instar duration.

Minimum initial feeding times necessary to guarantee at least occasional moulting to the following instar have to exceed about 20 % of the Zoea 1 development under optimum feeding conditions (PRS_0; Dawirs 1984). Minimum amounts of individual biomass and energy are, therefore, accumulated during an initial 1 d feeding period at 18 °C, with about 23 to 37 % that of newly hatched larvae. This equals about 44 to 56 % of maximum growth (MG), which occurs after 3 to 4 d under optimum feeding conditions. When food supply is ceased after 1 d, newly moulted Zoea 2 larvae exhibit 43 to 52 % less biomass and energy than those which develop from continuously fed Zoea 1 larvae. After minimum time-limited food supply the Zoea 1 may moult with even less individual biomass and energy than newly hatched larvae.

The PRS_{50} occurred after about one-third of the moult cycle (1.8 d) with individual growth values of 70 to 84 % of MG. Larvae with no chance to feed beyond this point moult with 31 to 41 % less biomass and energy than continuously fed Zoea 1 larvae. Future investigations should ascertain whether Zoea 2 can compensate for these growth deficits during their considerably extended moult cycles.

Intermoult (C) passes to premoult (D_0) (terminology in Drach 1939) after about one-third of larval moult cycles (Freeman & Costlow 1980, Anger 1983), corre-

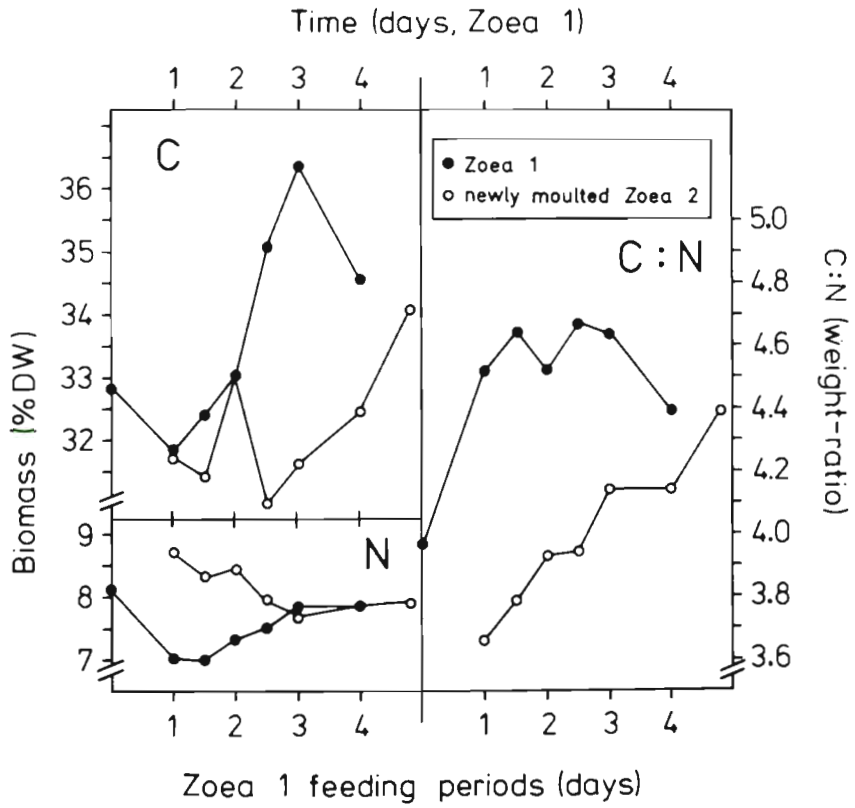

Fig. 4. *Carcinus maenas*. Dry weight (DW)-related percentages of carbon (C) and nitrogen (N), and C:N ratios during the moult cycle of Zoea 1, and in newly moulted Zoea 2 in relation to length of initial feeding periods of Zoea 1. Continuously fed Zoea 1 moult to the Zoea 2 after 4.8 d (Dawirs 1985)

Table 3. *Carcinus maenas*. Characteristic growth data of Zoea 1 at 18 °C, hatched from 2 different females. A: present study; B: Dawirs et al. (1986); B_0: individual biomass or energy at hatching; B_{max}: maximum attained biomass or energy; MG: maximum growth; DW: dry weight (µg); C: carbon (µg); N: nitrogen (µg); J ind^{-1}: individual energy content (Joule)

Study	Parameter	B_0 (µg/J)	B_{max} (µg/J)	MG (µg/J)	MG (%)
A	DW	11.64	18.64	7.00	60
	C	3.79	6.47	2.68	71
	N	0.91	1.43	0.49	52
	J ind^{-1}	0.128	0.222	0.094	73
B	DW	11.08	19.29	8.21	74
	C	3.93	7.08	3.15	80
	N	0.95	1.63	0.68	72
	J ind^{-1}	0.136	0.244	0.108	79

sponding very well with the PRS. Anger (1984) introduced a 'D_0 threshold', after which larval development proceeds independently of further food supply (see Dawirs 1984). At this point, *Carcinus maenas* Zoea 1 have attained about 80 % MG by ingestion of 71 % of total food consumed (see Dawirs & Dietrich 1986). During the subsequent premoult, which lasts about twice as long as the preceding post and intermoult periods combined, MG is accomplished by the remaining 29 % of total food intake.

Growing Zoea 1 larvae accumulate C at higher rates than N, which seems to characterize larval growth of brachyuran crabs as shown for *Hyas araneus* (Anger & Dawirs 1982, Anger & Jacobi 1985), *Hyas coarctatus* (Jacobi & Anger 1985), and *Carcinus maenas* (Dawirs et al. 1986). It can thus be assumed that overall relatively more lipid than protein is incorporated during the moult cycle, although crab larvae consist of much more protein than lipid (see Anger et al. 1983, Dawirs et al. 1986). C:N ratios are used to discuss changing relative compositions of protein and lipid (for reference see Dawirs et al. 1986). More lipid is incorporated than protein until the onset of premoult, but vice versa during subsequent periods of the moult cycle, where N-based are higher than C-based gross growth efficiencies (K_1). Similar relations are found in all larval instars of *C. maenas* (Dawirs et al. 1986) and *H. araneus* (Anger & Dawirs 1982, Anger & Jacobi 1985).

Starving *Carcinus maenas* Zoea 1 metabolize C at higher rates than N, and C:N ratios decrease towards ecdysis. DW-related N-content increases when initial feeding is limited to less than 3 d, while relative C-content decreases. Lipid, which was stored from early feeding, is primarily reclaimed and metabolized if food is no longer available. Starving Zoea 1 larvae require higher relative amounts of lipid to finish the moult

cycle if less reserves were accumulated previously. Considerably extended moult cycles of subsequent feeding Zoea 2 larvae may therefore be due to prolonged times of food intake. This may be necessary primarily to replenish lipid reserves, rather than to recover from physiological damage caused by starvation (see Dawirs 1984).

Similar relations were found in the megalopa stage of *Pagurus bernhardus*, which phylogenetically have lost the ability to consume food but nevertheless develop and metamorphose successfully (Dawirs 1981). These megalops metabolize mainly lipids, which are accumulated during previous zoea stages. The *Carcinus maenas* megalopa reveals a very distinct parabolic growth pattern (Dawirs et al. 1986), similar to that of *Hyas araneus* (Anger & Dawirs 1982, Anger & Jacobi 1985) and *Hyas coarctatus* (Jacobi & Anger 1985), losing considerable amounts of biomass and individual energy after little more than half of the moult cycle. Since the megalopa continues feeding at this time, energy input obviously no longer meets metabolic requirements (see Anger & Dietrich 1984, Dawirs & Dietrich 1986). Lipid was found to be the chief energy source for metabolism during this period of the moult cycle.

Carcinus maenas larvae are thus able to accumulate sufficient lipid reserves during limited periods of food supply. This protects the Zoea 1 against natural food shortages, and ensures successful development during periods of food deprivation. Storch & Anger (1983) found large lipid inclusions in R-cells (hepatopancreas) of well-fed *Hyas araneus* Zoea 1, which were metabolized during starvation. *C. maenas* and *H. araneus* Zoea 1 larvae, which were not fed at all, metabolized relatively more protein than lipid and always died after certain periods (Anger & Dawirs 1982, Dawirs 1983). Since it is of minor ecological significance to know how long it takes larvae to die under starvation, experiments have instead been designed to find out for how long natural food shortages may last while still allowing crab larvae to recover, moult to the next stage and develop successfully through metamorphosis (Anger & Dawirs 1981, Dawirs 1984). To investigate ecologically significant biomass and energy losses, starving *Carcinus maenas* larvae were refed and successfully moulted to the next instar (Dawirs unpubl.). Furthermore, it should be interesting to know to what extent biomass and energy, including protein and lipid, accumulate during these subsequent periods of recovery. These questions should be answered for a better understanding of more ecologically relevant energy budgets, since changing nutrient supply as well as varying water temperature seem to be important factors influencing larval development in boreal seas (see Ikeda 1974).

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