

## EFFECTS OF NUTRITION (HERBIVORE VS. CARNIVORE) ON THE ENERGY BUDGET OF A BRACHYURAN MEGALOPA \*

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### SUMMARY

Megalopa larvae of a spider crab, *Hyas araneus*, were reared in the laboratory under constant 12°C, 32‰S, with diatoms (*Biddulphia sinensis*) given as food. Oxygen consumption, nitrogen excretion, and growth were measured in regular intervals during the moult cycle. Growth was measured as change in dry weight, carbon, nitrogen, hydrogen, protein, and lipid. Estimates of energy accumulation obtained independently from either carbon or biochemical components gave similar values of growth. The present results are compared with earlier data measured in carnivorous (*Artemia*-fed) larvae (ref. 10). In larvae fed with *B. sinensis*, accumulation of biomass amounted to only ca 8% of that in the *Artemia*-fed group. Energy loss by excretion increased in carnivorous larvae during the first days, then it remained stable throughout the rest of the moult cycle. It was low in larvae fed with diatoms, but increased at the end of the moult cycle, reaching similar values as in the *Artemia*-fed group. Energy loss by respiration was slightly reduced in larvae fed with *B. sinensis*, reaching 82% of the values observed in *Artemia*-fed larvae. Larvae fed with diatoms had high O/N ratios (86–96) at the beginning of the moult cycle, followed by decreasing values (eventually reaching 14 in premoult). This indicates that initially lipids were used as a predominant metabolic substrate, later proteins. Larvae fed with *Artemia* sp. showed O/N ratios varying between 20 and 40, with minimum values in the middle of the moult cycle, indicating in this group chiefly protein catabolism during the intermoult period. Energy budgets for the two different nutritional conditions were calculated. Net growth efficiency ( $K_2$ ) were 13.8 and 1.5 % in larvae fed with *Artemia* nauplii or *B. sinensis*, respectively.

### INTRODUCTION

Nutrition and temperature belong to the principal factors affecting survival, development and growth of decapod larvae (refs. 1–4). Meroplanktonic decapod larvae are considered predominantly carnivorous (ref. 2). It was shown in laboratory experiments that nutritional requirements of larvae were higher than average concentrations of potentially suitable food organisms in the field (for literature see ref. 5). The actual success in growth and survival of larvae in the field may be explained partly by natural patchiness in the distribution of both predator and prey populations (see models presented by refs. 6, 7), possibly combined with physiological adaptations to starvation periods (ref. 5).

Another explanation would be an opportunistic feeding behaviour of decapod larvae, i.e. the ability to switch from carnivorous to herbivorous nutrition when zooplanktonic prey becomes scarce. This ability was already observed in field samples by Lebour (ref. 8). Larvae of seven decapod species that were in laboratory experiments fed exclusively with phytoplankton, showed a prolonged survival time compared to starved controls, and in most cases some further development to successive larval stages (ref. 3). Comparison of ingestion and respiration rates of herbivorously fed

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tanner crab larvae, however, showed that in this case only a minor part (14%) of the larval metabolic demands could be met by ingested phytoplankton carbon (ref. 9).

Energy budgets of laboratory-reared decapod larvae that were fed with *Artemia* sp. nauplii were studied in a number of species (for recent discussion see refs. 10, 11). Exuvial losses and those caused by starvation were studied in detail by Anger and coworkers (refs. 5, 12-16) and Dawirs (refs. 17-18). The data presented here provide a first energy budget for *Hyas araneus* megalopa fed exclusively with phytoplankton, the diatom *Biddulphia sinensis*. These data are compared with earlier data from larvae that were fed with *Artemia* sp. nauplii (refs. 10, 19).

## METHODS

Ovigerous female *Hyas araneus* L. were dredged during winter 1988/89 from ca 30 to 50 meters depth near the island of Helgoland (German Bight, North Sea). They were maintained in flow-through aquaria at ca 3 to 5°C, until freshly hatched larvae could be collected. Larvae were mass-reared to the megalopa stage at constant 12°C and 32‰ salinity (ref. 20), using *Artemia* sp. nauplii (San Francisco Bay Brand) as food. Thereafter, the larvae were fed exclusively with diatoms (*Biddulphia sinensis*) at a concentration of 1 µg C ml<sup>-1</sup> (60 cells ml<sup>-1</sup>). This corresponds to maximum values observed in the field near Helgoland (Hagmeier, pers. comm.), and it was found to exceed in experiments the daily food uptake of larvae. Hence, this *ad libitum* feeding condition allowed a direct comparison of the present data with those from earlier experiments, where *Artemia* sp. nauplii had been given as a food source in non-limiting concentrations (5-10 nauplii ml<sup>-1</sup>). From the fourth day after moulting, the larvae were reared individually in 25 cm<sup>3</sup> vials in order to avoid cannibalism. The culture medium was changed daily.

Experiment A. This experiment comprised simultaneous measurements (larvae from the same hatch) of growth, respiration and nitrogen excretion in megalopa larvae of *Hyas araneus* fed with the diatom *Biddulphia sinensis*. Additionally, 25 megalopa were reared individually with *Artemia* sp. nauplii, and another 25 with *B. sinensis*, for determination of development durations and survival rates at these two nutritional conditions.

Measurements of growth. Megalopa of the same age were sampled from culture bowls for measurements of growth (dry weight, carbon, nitrogen, hydrogen, protein, lipid; details of methods: refs. [20]). Frequency of sampling, number of replicate analyses (n), and total number of larvae analysed (n') are given in Table I. Energy content (E; in Joules, J) was calculated from C (ref. 21).

Measurements of respiration and nitrogen excretion. Aliquot parts of sampled larvae were used for measurements of respiration and excretion rates. Respiration was measured applying the Winkler method (refs. 23, 24), with three individuals incubated for ca 15 h in bottles with ≈ 55 cm<sup>3</sup> filtered sea water (Millipore; 0.45 µm). Prior to the experiments, the larvae were held for 2h in bowls without food to allow for defaecation. Each measurement included eight replicate experiments (with larvae) and five replicate blanks (without larvae).

Table 1. Biomass data for *Hyas araneus megalopa* fed with the diatom *Biddulphia sinensis* at 12°C. W: dry weight, C: carbon, N: nitrogen, H: hydrogen in  $\mu\text{g ind}^{-1}$ ; C, N, H also in % of W; C/N and C/H ratios; E: J mg W<sup>-1</sup> and E: J ind.<sup>-1</sup>; x,  $\pm$ SD: arithmetic mean, standard deviation; n: number of replicate analyses; N: total number of individuals analysed.

Age (d)	W ( $\mu\text{g/ind.}$ )		C (%)		N (%)		H (%)		C ( $\mu\text{g/ind.}$ )		N ( $\mu\text{g/ind.}$ )		H ( $\mu\text{g/ind.}$ )		C/N		C/H		E (J/mg W)		E (J/ind.)		n
	x	$\pm$ SD	x	$\pm$ SD	x	$\pm$ SD	x	$\pm$ SD	x	$\pm$ SD	x	$\pm$ SD	x	$\pm$ SD	x	$\pm$ SD	x	$\pm$ SD	x	$\pm$ SD	x	$\pm$ SD	
Megalopa																							
0	328.2	23.7	43.8	1.3	8.2	0.3	6.5	0.3	143.8	9.7	27.0	1.9	21.5	2.0	5.3	0.2	6.7	0.3	16.7	0.7	5.5	0.4	8
3	456.9	54.6	34.4	0.8	6.4	0.3	5.1	0.2	157.2	20.5	29.0	3.2	23.6	3.6	5.4	0.2	6.7	0.2	11.7	0.4	5.4	0.7	8
6	457.2	62.8	33.8	0.5	6.5	0.4	5.3	0.2	154.3	21.0	29.3	3.3	24.0	3.0	5.2	0.3	6.4	0.1	11.5	0.2	5.2	0.7	8
9	520.2	57.9	33.5	4.3	6.9	0.3	6.8	0.3	174.0	29.9	35.7	3.9	35.7	5.0	4.9	0.6	4.9	0.6	11.4	1.9	5.9	1.2	8
12	528.3	36.6	36.2	0.9	7.3	0.3	7.3	0.3	191.3	15.7	38.8	1.9	38.6	3.2	5.0	0.2	5.0	0.1	12.6	0.4	6.7	0.6	8
16	485.2	31.0	34.2	1.0	7.5	0.3	5.2	0.2	165.9	10.2	36.2	2.0	25.1	1.7	4.6	0.1	6.6	0.1	11.7	0.5	5.7	0.4	8
20	526.1	63.9	35.6	1.1	7.6	0.3	7.3	0.3	187.8	26.4	39.9	5.5	38.6	5.8	4.7	0.2	4.9	0.1	12.4	0.6	6.5	1.0	8
24	529.3	64.7	34.3	1.6	7.8	0.4	5.3	0.4	182.0	28.1	41.4	6.1	28.4	4.8	4.4	0.1	6.4	0.3	11.7	0.8	6.2	1.1	8
28	437.3	51.8	31.8	2.3	7.3	0.7	5.0	0.5	139.6	24.5	32.2	6.2	22.0	4.1	4.4	0.2	6.3	0.2	10.5	1.1	4.6	0.9	6
Crab I																							
0	469.3	83.5	34.427		8.2	0.9	5.1	0.5	160.6	25.6	37.9	4.4	23.9	3.6	4.2	0.3	6.7	0.2	11.8	1.3	5.5	0.9	8

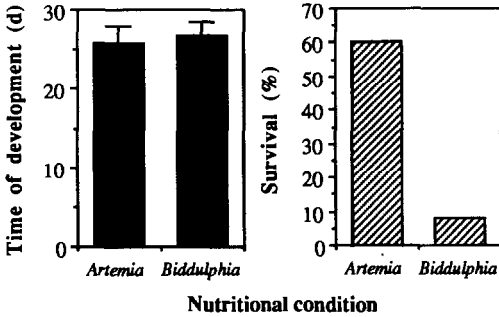


Fig. 1. Development time and survival rate of *Hyas araneus* megalopa fed with *Artemia* sp. nauplii or a diatom, *Biddulphia sinensis*.

The decrease of oxygen concentration in the experiments was <15%, which is believed not to affect larval respiration (ref. 24). Parallel to oxygen consumption, ammonia excretion was measured under identical conditions (ref. 10), applying the analytical procedure described by Solarzano (ref. 25).

**Experiment B.** Growth data of *Hyas araneus* megalopa fed with *Artemia* sp. nauplii were taken from "Experiment A", respiration and excretion data from "experiment B" in Anger et al. (ref. 10).

## RESULTS

**Development duration.** Individually reared megalopa of *Hyas araneus* moulted under both experimental conditions (fed with either *Artemia* sp. or *Biddulphia sinensis*) to the first crab instar, without showing a significant difference in development time:  $25.8 \pm 2.0$  and  $26.7 \pm 1.8$  days, respectively (Fig. 1). A significant difference, however, was found in survival rates, amounting to 60 and 8%, respectively (Fig. 1). In mass cultures fed with *B. sinensis*, a higher percentage (15%) of the megalopa moulted to the juvenile.

**Metabolism.** The metabolic rates in megalopa fed with *Biddulphia sinensis* is given in Table 2. A comparison of the weight-related metabolism (Fig. 2) shows at both nutritional conditions compared here (*Artemia* sp. or *Biddulphia sinensis*) similar variations during time of development. Metabolism of *B. sinensis*-fed larvae was only at the end of development significantly reduced, to 59% of that measured in the *Artemia*-fed group. Cumulative metabolic energy loss per individual was only slightly reduced in larvae fed with *B. sinensis*, with 82% of that in *Artemia*-fed larvae (see Fig. 8).

**Excretion.** Excretion rates of larvae fed with *Biddulphia sinensis* are given in Table 2. Weight-related excretory energy loss (Fig. 2) remained here low during the first days, then it increased continually during time of development. Excretion was always higher in megalopa fed with *Artemia* sp. nauplii than in those fed diatoms, with maximum values found in the middle of the moult cycle.

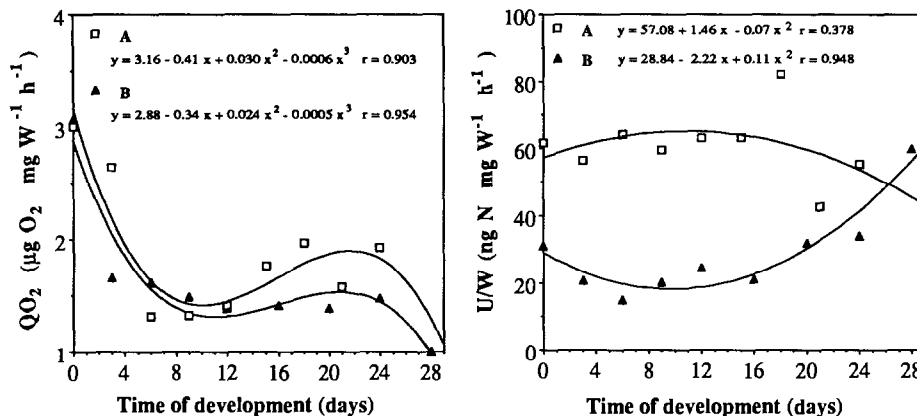


Fig. 2. Weight-related rates of respiration (left) and excretion (right) in *Hyas araneus* megalopa fed with *Artemia* sp. nauplii (A; for more details see ref.10) or a diatom, *Biddulphia sinensis* (B).

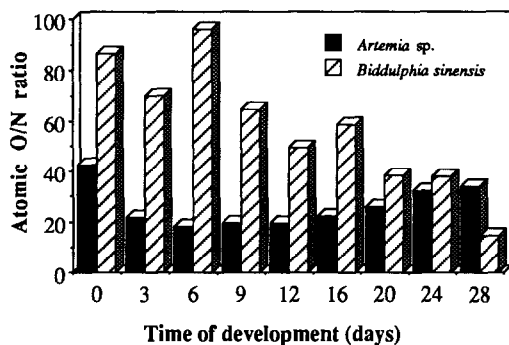


Fig. 3. Atomic O/N ratio in *Hyas araneus* megalopa fed with *Artemia* sp. nauplii (for more details see ref.10) or a diatom, *Biddulphia sinensis*.

**Atomic O/N ratio.** The O/N ratio indicates variation in predominant metabolic substrates utilized by megalopa fed either *Artemia* sp. nauplii or *Biddulphia sinensis*. Maximum values (86-96) were found in postmoult larvae fed with diatoms (Fig. 3). After day 6 they decreased at a constant rate, eventually reaching lower values (14) than in *Artemia*-fed larvae (30). This suggests here an initial utilization of lipids and/or carbohydrates as a predominant metabolic substrate, followed by protein catabolism. Megalopa fed with *Artemia* sp. nauplii used a mixed metabolic substrate, with a clear dominance of protein catabolism throughout major portions (intermoult, early premoult) of the moult cycle.

Table 2. Oxygen uptake (R) and ammonium excretion (U) of *Hyas araneus* megalopa when fed with the diatom *Biddulphia sinensis* (n' and n'': replicate of experiments; N' and N'': number of larvae analyzed; x,  $\pm$ SD: arithmetic mean, standard deviation). Comparable data for *Artemia* sp. fed *Hyas araneus* megalopa are published in ref. 10.

Age (d)	R ( $\mu\text{g O}_2$ / h ind.)		n'	N'	U ( $\mu\text{g N}$ / h ind.)		n''	N''
	x	$\pm$ SD			x	$\pm$ SD		
0	1.007	0.048	8	24	10.20	2.32	8	24
3	0.758	0.046	8	24	9.53	2.55	8	24
6	0.741	0.149	8	24	6.73	0.86	8	24
9	0.776	0.091	8	24	10.52	1.36	8	24
12	0.731	0.033	8	24	12.97	2.09	8	24
16	0.685	0.049	8	24	10.23	2.20	8	24
20	0.730	0.087	8	24	16.67	5.60	8	24
24	0.782	0.083	8	24	18.01	4.01	8	24
28	0.438	0.152	6	24	26.14	9.05	8	24

Table 3. Protein and lipid content of *Hyas araneus* megalopa when fed with the diatom *Biddulphia sinensis* (n' and n'': replicate of experiments, N' and N'': number of larvae analyzed; x,  $\pm$ SD: arithmetic mean, standard deviation). Comparable data for *Artemia* sp. fed *Hyas araneus* megalopa are published in ref. 10.

Age (d)	Protein ( $\mu\text{g}/\text{ind.}$ )		n'	N'	Lipid ( $\mu\text{g}/\text{ind.}$ )		n''	N''
	x	$\pm$ SD			x	$\pm$ SD		
0	64.5	9.6	3	15	63.7	5.1	3	45
3	71.8	5.5	3	15	48.9	7.4	3	45
6	71.2	4.8	3	15	49.2	10.4	3	45
9	95.7	8.5	3	15	39.5	5.5	3	45
12	128.7	10.1	3	15	49.2	7.0	3	45
16	132.5	7.6	3	15	36.7	4.0	3	45
20	122.3	3.4	3	15	44.6	9.9	3	45
24	133.1	10.6	3	15	26.8	4.8	3	45
28	103.7	5.5	3	15	21.3	1.2	3	45

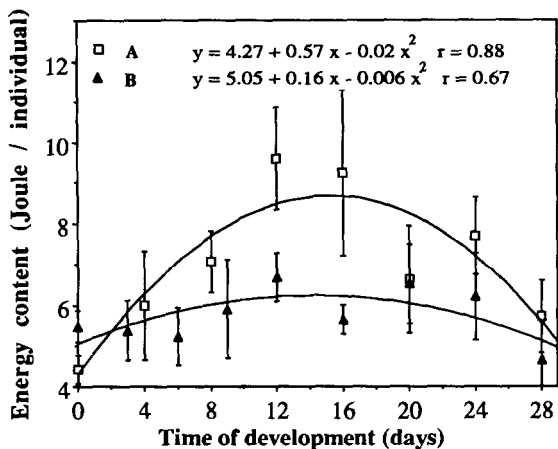


Fig. 4. Accumulation of energy (Joule/individual) in *Hyas araneus* megalopa fed with *Artemia* sp. nauplii (A; for more details see ref.10) or a diatom, *Biddulphia sinensis* (B). Food availability was not a limiting factor under either condition.

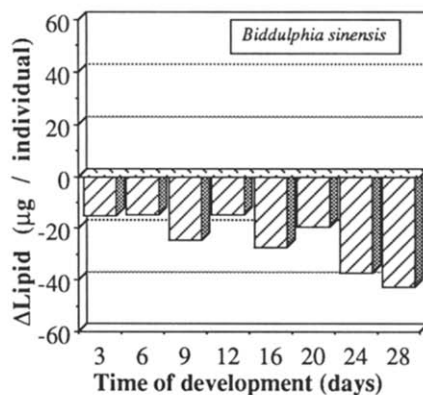
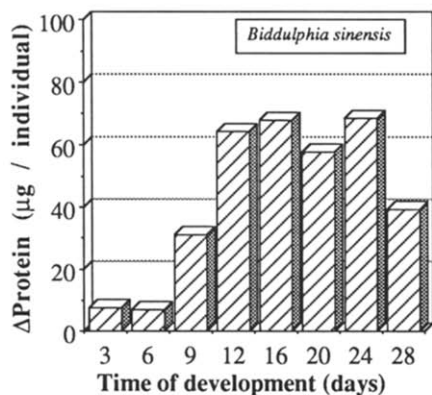
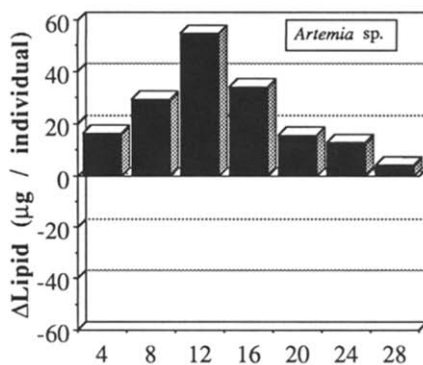
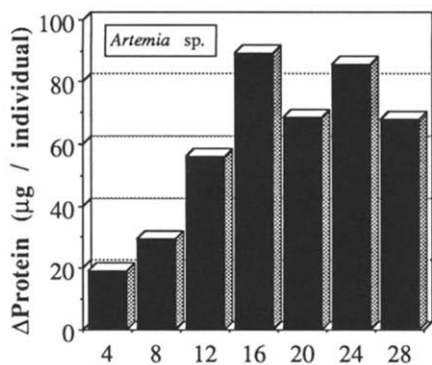


Fig. 5. Changes ( $\Delta$ ,  $\mu\text{g}$ ) in the protein content of *Hyas araneus* megalopa fed with *Artemia* sp. nauplii (details: ref. 10) or a diatom, *Biddulphia sinensis*.

Fig. 6. Changes ( $\Delta$ ,  $\mu\text{g}$ ) in the lipid content of *Hyas araneus* megalopa fed with *Artemia* sp. nauplii (details: ref. 10) or a diatom, *Biddulphia sinensis*.

**Growth patterns.** Biomass increase in megalopa that were fed with diatoms is shown in Tables 1 and 3. Patterns of growth were similar at both nutritional conditions (Fig. 4), with maximum biomass in the middle of the moult cycle. Compared to *Artemia*-fed megalopa (for details see ref. 10), a clearly reduced growth was found in those fed *Biddulphia sinensis*.

No major differences were found in the protein content of larvae reared under either nutritional condition (Fig. 5; details: Table 3; ref. 29). There was nearly no increase in the protein fraction during the first 6 days of the moult cycle, but high accumulation during the later intermoult period. The protein content decreased prior to metamorphosis to the first crab instar.

The lipid content of *Artemia*-fed megalopa increased from the beginning of development, reaching maximum values around day 12 (Fig. 6; ref. 10). Thereafter, a major portion of accumulated lipids was utilized prior to metamorphosis. No accumulation of lipids was found when larvae were fed exclusively with *B. sinensis* (Fig. 6, Table 3). Instead, these larvae catabolized 23% of their initial lipid reserves, mostly in the beginning of development.

**Comparison of energy content estimated from carbon and biochemical constituents.** The energy content of larvae shown in Fig. 4 was calculated from carbon (ref. 21). These values (Table 1; cf. ref. 10) were defined as 100% and then compared with the energy content that may be calculated independently from biochemical composition (ref. 26). Carbohydrate and chitin contents were not measured in this study and had therefore to be estimated from C (ref. 20). These two methods for estimating the energy content of larvae showed in general a good agreement, in both nutritional conditions tested (Fig. 7). The energy content calculated from biochemical composition (expressed as a percentage of values derived from C) varied in larvae fed with *Artemia* sp. nauplii. between 87 and 112%, and in larvae fed with *Biddulphia sinensis* between 81 and 99%.

**Energy budget.** When earlier data on ingestion rate (ref. 19) are included, energy budgets for two distinct nutritional conditions can be calculated. However, cumulative ingestion rate of diatom-fed megalopa measured in the earlier experiment (ref. 19) was below the cumulative assimilation value found in the present study (2.2 vs. 7.0 Joule individual<sup>-1</sup>). Thus the former should be underestimated (for discussion see ref. 19), and no assimilation efficiency or gross growth efficiency could be calculated for megalopa fed with *B. sinensis*.

Net growth efficiency ( $K_2$ ) is given for two distinct time intervals of the moult cycle. The first (days 0-16) is characterized at both nutritional conditions by a positive growth rate (Fig 4). During this time span, 47 and 19% of assimilated energy were used for growth in larvae fed with *Artemia* sp. and *Biddulphia sinensis*, respectively. During complete development, only 14 and 1.5% were channelled into body growth.

Comparison between accumulation (growth) and loss (respiration, excretion) of energy during development of the megalopa (Fig. 8) shows that the total amount of assimilated energy was 30% lower in larvae fed with phytoplankton than in those eating *Artemia*. This difference was caused mainly by a drastic (92%) decrease in growth of herbivorous larvae. Also excretion decreased here significantly (by 65%), whereas energy expenditure by respiration was in diatom-fed larvae reduced by only 18%, as compared to *Artemia*- fed megalopa. In both experimental groups, the megalopa



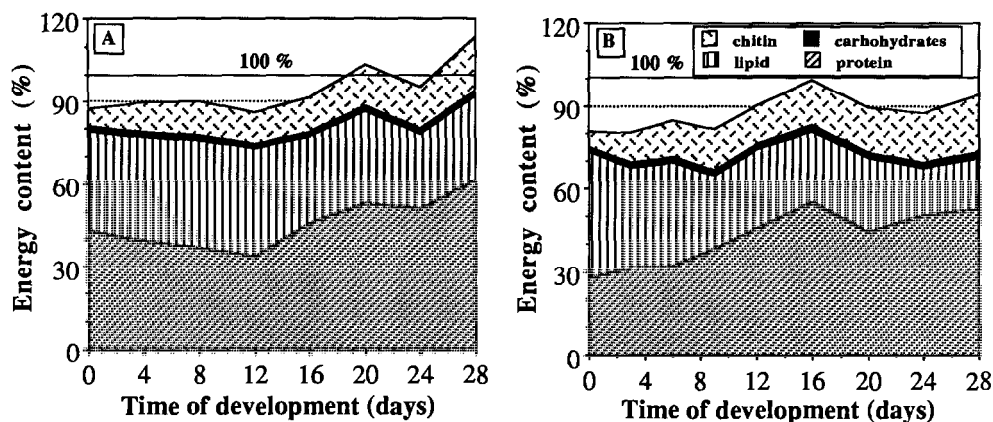


Fig. 7. Comparison of the energy content of *Hyas araneus* megalopa fed with *Artemia* sp. nauplii (A; details: ref. 10) or *Biddulphia sinensis* (B); calculated independently from carbon content (set as 100%) and biochemical composition.

clearly lost much more energy in respiration than it accumulated in growth: 8.1 vs. 1.3 and 6.6 vs. 0.1 Joules individual<sup>-1</sup> in larvae fed with *Artemia* and diatoms, respectively.

## DISCUSSION

The survival of *Hyas araneus* megalopa was strongly affected by nutritional conditions. When fed carnivorously, with *Artemia* sp. nauplii, 60% of the megalopa developed to the first juvenile crab instar, whereas only 8 to 15% reached it when they were fed with phytoplankton. This was still a rather high survival rate, as in earlier experiments with algae as food no development to the juvenile crab could be observed (ref. 19). Such differential survival rates may be caused by differences in the initial energy content of larvae (ref. 10) and/or by variation in the biochemical composition of the phytoplankton given as food (refs. 27-28). It is known from the literature that the chemical composition of algae varies strongly with culture conditions (refs. 29-30), water chemistry (refs. 31-33), temperature (ref. 34), light (refs. 35-36), and age of cultures (ref. 37). Food quantity can be excluded as a limiting factor in our experiments, since both diatoms and brine shrimp nauplii were given in excess quantities. Thus, our comparison of herbivorous and carnivorous feeding conditions refers exclusively to differences in food quality.

The data presented here confirm that *Hyas araneus* megalopa are able to ingest and convert diatoms (cf. refs. 3, 19), and that they can develop through metamorphosis with such a diet. They also provide a first data base for the calculation of an energy budget of decapod larvae reared under suboptimal (exclusively herbivorous) nutritional conditions. *Biddulphia sinensis* was found suitable for such experiments (ref. 19), since it is relatively large ( $\varnothing$  200  $\mu$ m) and chain forming. Slightly uncertain ingestion rates may often be a problem in the calculation of complete energy budgets. Here

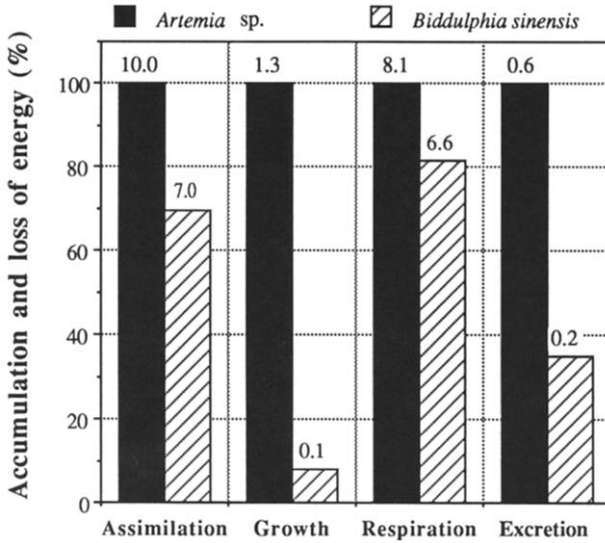


Fig. 8. Accumulation and loss of energy in *Hyas araneus* megalopa fed with *Artemia* sp. nauplii (details: refs. 10) or a diatom, *Biddulphia sinensis*. Numbers above columns: Joules accumulated or loss per individual; percentages: related to values measured in the *Artemia*-fed group (100%).

they were measured in an earlier study, with larvae from a different hatch and diatoms from a different culture (ref. 19). In these experiments, the megalopa larvae lost 16% of their carbon content, and they did not metamorphose to the first juvenile instar with diatoms given as a sole food source (ref. 19). In contrast, carbon content increased in the present study by 15%, showing here a much higher uptake and assimilation of organic material from diatoms.

Respiration rate (R) showed at both nutritional conditions the same pattern of variation throughout the moult cycle. These patterns were observed already in previous studies (refs. 10, 24, 38). When the larvae were fed with diatoms (Table 2), the overall respiratory energy loss was reduced (compared to those eating *Artemia*) by only 18%. Weight-related respiration rates were similar at both nutritional conditions, showing a similar respiratory intensity of tissues.

Low excretion rates and high O/N ratios in megalopa fed with phytoplankton indicate a shift in metabolic substrates, with a decreased catabolism of protein and an increased utilization of lipids and/or carbohydrates. During the final phase of development, excretion rate increased and the O/N ratio decreased, suggesting increasing protein utilization. This concurs with a decreasing protein content during this phase.

The present study demonstrates once again that brachyuran larvae are in principle able to ingest and convert phytoplankton and to develop with a herbivorous diet to the juvenile crab. This supports the hypothesis that they show opportunistic feeding behaviour, utilizing phytoplankton biomass probably also in the field, when suitable zooplankton prey organisms occur in too low concentrations (refs. 10, 19).

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