Effects of nutrition (herbivore vs carnivore) on energy charge and nucleotide composition in *Hyas araneus* larvae

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ABSTRACT: Growth rate expressed as dry weight, elemental composition (C, N, H), protein content and nucleotide composition (ATP, ADP, AMP, CTP, GTP and UTP) as well as adenosine were measured in laboratory cultured *Hyas araneus* larvae fed two different diets. One group was fed freshly hatched *Artemia* sp. nauplii, the other the diatom *Odontella (Biddulphia) sinensis.* Growth rate was reduced in the *O. sinensis*-fed group, reaching 20 to 50 % of the growth rate of *Artemia*-fed larvae. In all cases, some further development to the next instar occurred when larvae were fed *O. sinensis*, although at reduced levels compared to *Artemia*-fed larvae. The adenylic energy charge was quite similar for the two nutritional conditions tested and therefore does not reflect the reduced growth rate in *O. sinensis*-fed larvae. The individual nucleotide content was clearly reduced in *O. sinensis*-fed larvae, reflecting the nutritional conditions already during early developmental periods. These reduced amount of nucleotides in *O. sinensis*-fed larvae were most obvious when adenylic nucleotide contents were pooled. Pooled adenylic nucleotides were found to be correlated with the individual content of carbon and protein, showing significant differences at both nutritional conditions tested.

INTRODUCTION

Adenylic energy charge (AEC) was first used as a measurement of the energy directly available to cells (Atkinson & Walton, 1967; Bomsel & Pradet, 1967), and it was later adopted by Ivanovici (1980a) and Romano & Daumas (1981) as an index for estimating the physiological condition of organisms. A previous study of the nucleotide composition of decapod larvae showed that the AEC was generally unaffected by food conditions (Harms et al., 1990b). It was suggested in that study that the individual amount of adenylate nucleotides might be a more useful indicator of the well-being of decapod larvae, supporting Atkinson's original hypothesis that the AEC might be a relatively conservative property and that changes in AEC are always accompanied if not preceded by changes in the quantity of adenylate nucleotides (Atkinson, 1968). To evelute these previous results, the elemental composition, protein and nucleotide content of *Hyas araneus* larvae fed two different diets (herbivore vs carnivore) were analysed. The nutritional conditions used here have already been studied in more detail in previous reports (Harms & Seeger, 1989; Harms & Anger, 1990; Harms et al., 1990a). The two diets were chosen because of their difference in nutritional value, which facilitates the detection of variations in nucleotide content and/or AEC related to growth conditions.

MATERIALS AND METHODS

Handling of larvae

Ovigerous females of *Hyas araneus* were collected near Helgoland (North Sea, German Bight). Females were maintained individually in flow-through aquaria until freshly hatched, actively swimming larvae could be collected in sieves which received water from an overflow. The larvae were reared in mass cultures (Zoea I: 50; Zoea II: 30 and Megalopa 10 individuals) at a constant temperature of 12 °C in 1-μm-filtered natural seawater (30 to 32 ‰ S, 12 h light: 12 h dark) with two different diets. The data for each larval stage were collected from a larval hatch originating from one female. In order to obtain zoea II and megalopa stages, larvae were cultivated by standard methods using *Artemia* sp. nauplii as food (Anger et al., 1983), until they reached these stages. Each experiment (zoea I, II and megalopa) started with freshly moulted larvae (day zero of the experiment). In each experiment, larvae were divided into two groups. One group was fed freshly hatched *Artemia* sp. nauplii (Bay Brand, San Francisco, USA), the other diatoms *Odontella (Biddulphia) sinensis*. The food concentration in the *Artemia*-fed group was $\approx$ 10 nauplii $\cdot$ ml^{-1} = 7.6 μg C $\cdot$ ml^{-1}. The *O. sinensis*-fed group received a food concentration of 60 cells $\cdot$ ml^{-1} = 1 μg C $\cdot$ ml^{-1} (for more details see Harms et al., 1990a). The culture medium was changed daily for the *O. sinensis* and every second day for the *Artemia*-fed group.

Biochemical analyses

Larval growth and nucleotide composition were measured in each larval stage at regular intervals (every second day in zoea I and II, every third day in megalopa) in aliquot samples of larvae from the same hatch and of the same age within a given moult cycle. Samples were stored at −80 °C for later analyses. Parallel measurements comprised the following: dry weight (W), carbon (C), nitrogen (N), and hydrogen (H), protein and nucleotide composition. W, C, N and H were measured in eight replicates, with freeze drying weighing on a Mettler UM3 microbalance, and subsequent combusting in an Elemental Analyser Model 1106 (Carlo Erba Science), following the methods described by Anger et al. (1989).

In order to measure nucleotides and protein content, three replicate samples of 50 (Zoea I and II) to 20 (megalopa) larvae were homogenized in 1.5 ml of cold 0.5 M Trichloroacetic acid. The cooled samples stood 10 min for protein precipitation and nucleotide extraction before being centrifuged for 15 min at 4300 rpm. The supernatant was decanted and neutralized (v/v) with a mixture of Trioctylamin and Freon (0.5 M). The water phase was used immediately after careful mixing for analysis of nucleotide content by HPLC (for details see Moal et al., 1989). In addition to the three adenylic nucleotides (AN) ATP, ADP and AMP, also CTP, GTP, UTP and adenosine could be detected in most cases. The pellet was resuspended in 1.0 ml 1 N NaOH and was left at 4 °C for at least 12 h, before analysing total protein by the Folin Ciocalteau method (Lowry et al., 1951).

Artemia-fed megalopa were analysed twice. During the first experiment (Experiment I), no comparable data for *O. sinensis*-fed larvae could be obtained, because infections occurred in the algae cultures early in the experiment. Therefore, a second experiment (Experiment II) was performed. Experiment I is included in some figures

when of special interest and marked as Experiment I. Experiment I data were also included in the data pool for regression analysis.

Error bars ($\bar{x} \pm$ SD) are given in Tables and Figures only, when directly measured values are displayed, not in those calculated from two independently measured data series (for instance, nucleotide content · mg protein^{-1} (Table 2), AEC (Fig. 4) and ΣAN (Fig. 5).

RESULTS

Growth rate

Larval growth was measured as dry weight (W), carbon (C), nitrogen (N), hydrogen (H) and protein. W and protein content are given in Table 1. The changes in absolute biomass per individual during the larval development is shown for C in Figure 1. Increase in N content is documented as total net gain during each larval instar (Fig. 2). The individual amount of N at both nutritional conditions can be estimated from the protein content by using the regression equation given by Anger et al. (1989). The individual content for H, which is not presented here, might be estimated from C, using the regression equation also given by Anger et al. (1989).

During each larval stage, W, C, N and protein increased under both nutritional conditions tested, except for protein in *Odontella (Biddulphia) sinensis*-fed megalopa (Fig. 2). The gain in organic material was highest in the *Artemia*-fed group, reaching slightly higher net gain values in W, C and N, compared to data presented by Harms et al. (1990a). The net gain in protein was low compared to earlier data (Harms et al., 1990a). The percentage gain of biomass decreased in *Artemia*-fed larvae from instar to instar. Larvae fed *O. sinensis* had a lower biomass increase compared to *Artemia*-fed larvae (Fig. 2). The absolute and percentage increase of biomass was highest in the zoea II, except for W and protein which was accumulated in higher quantities in the megalopa and the zoea I, respectively. The biomass increase in the zoea I reached approximately one-fifth, except for protein which reached one-third, of the biomass accumulation of *Artemia*-fed larvae. The growth rate in the zoea II reached approximately 55 to 65 % of the values of *Artemia*-fed larvae, except for protein which reached only 20 %. The biomass increase in *O. sinensis*-fed megalopa varied between 16 % (C), 36 % (N) and 53 % (W) compared to *Artemia*-fed megalopa. Protein decreased (−9 %) in the megalopa when fed *O. sinensis*. The net gain of biomass in *O. sinensis*-fed larvae reported here, is above the values reported in an earlier study (Harms et al., 1990a). This is especially true for W, C and N in the zoea II and megalopa stages. Further development to the next larval instar could be observed in all experiments, although developmental success of *O. sinensis*-fed larvae was low compared with the *Artemia*-fed group. The developmental success of *O. sinensis*-fed larvae decreased from zoea I to megalopa.

The growth measured as W, protein and C (Table 1 and Fig. 1) ceased in all instars in late premoult. This final phase of constant or decreasing biomass is part of the normal growth pattern of the larvae, and is always much longer in the megalopa stage than in zoeal stages (see Anger et al., 1990). This decrease in biomass was observed earlier in the moulting cycle when larvae were fed with the diatom *O. sinensis* (Fig. 1).

Table 1. *Hyas araneus*. Dry weight (W, µg individual^{-1}), and protein content (µg individual^{-1}) during time (days) of development in subsequent larval stages reared under different nutritional conditions at constant temperature (12 °C) * * Larvae developed to the next instar after being fed with *Odontella (Biddulphia) sinensis* in the previous larval stage; x̄, ±SD: arithmetic mean, standard deviation; number of analyses = 8 for W, = 3 for protein

Larval stage	Age (days)	Dry weight				Protein			
		Artemia sp.		*O. sinensis*		*Artemia* sp.		*O. sinensis*	
		x̄	±SD	x̄	±SD	x̄	±SD	x̄	±SD
Zoea I	0	68.46	2.07	68.46	2.07	19.17	1.66	19.17	1.66
	2	108.96	5.46	87.75	1.93	25.64	1.65	19.36	2.33
	4	105.70	3.58	102.75	5.15	31.63	0.62	24.47	2.85
	6	140.81	3.68	112.02	6.50	37.16	0.47	31.73	5.03
	8	145.02	11.80	121.49	17.30	47.72	3.09	32.11	2.82
	10	170.26	12.10	89.27	3.30	44.09	1.37	30.81	1.50
	12			95.99	6.37			30.16	1.65
	14			102.86	3.78			27.64	1.98
Zoea II**	0			145.80	6.31			34.89	1.61
Zoea II	0	161.23	5.70	161.23	5.70	50.56	1.28	50.56	1.28
	2	242.47	8.82	206.74	15.30	62.50	1.21	58.24	0.62
	4	265.37	18.67	217.42	19.54	71.52	1.70	59.39	4.46
	6	299.84	14.32	252.72	18.98	76.01	7.02	57.89	0.75
	8	329.13	25.33	242.02	24.42	88.49	0.19	52.23	4.01
	10	348.31	13.71	244.04	30.60	76.35	8.20	63.82	0.53
	11	350.73	12.00	286.97	10.08	85.27	2.92	62.89	3.83
	12	343.01	7.09	288.19	21.16	89.02	0.19	65.86	8.23
	13			289.41	14.24			57.79	4.82
Megalopa**	0			278.24	15.42			72.13	0.51
Megalopa	0	322.53	13.52	322.53	13.52	101.93	12.81	101.93	12.81
	3	529.69	51.09	402.29	22.83	143.91	6.71	92.55	25.08
	6	574.06	42.09	507.45	44.48	177.82	20.87	100.97	2.76
	9	566.11	30.41	526.14	56.62	195.14	8.05	113.28	3.61
	12	626.65	68.67	529.39	39.52	219.23	14.03	111.10	24.88
	15	554.72	36.67	485.19	38.47	178.26	35.37	100.84	1.87
	18	642.43	77.37	482.77	62.17	143.90	6.66	115.51	12.36
	21	552.49	34.03	431.11	41.64	140.34	1.09	90.21	1.38
	24	573.11	32.48	454.57	65.24	134.94	2.48	93.03	0.93

Nucleotide composition

The nucleotide composition for both nutritional conditions tested is given in Table 2 as concentrations · mg protein^{-1}. Besides the three adenosine nucleotides (AN), adenosine and the three triphosphates CTP, UTP and GTP could be detected. The column separation for UTP and GTP was sometimes inadequate and these analyses are marked with an asterisk. The protein specific nucleotide concentrations were very similar for both diets tested and stayed quite constant throughout each moulting cycle.

The individual AN content is given in Figure 3. The variation of the three replicates is normally below 5 %, so that error bars are not visible. Higher standard deviations are found in ATP analyses. The increase in ATP was most advanced in *Artemia*-fed larvae.
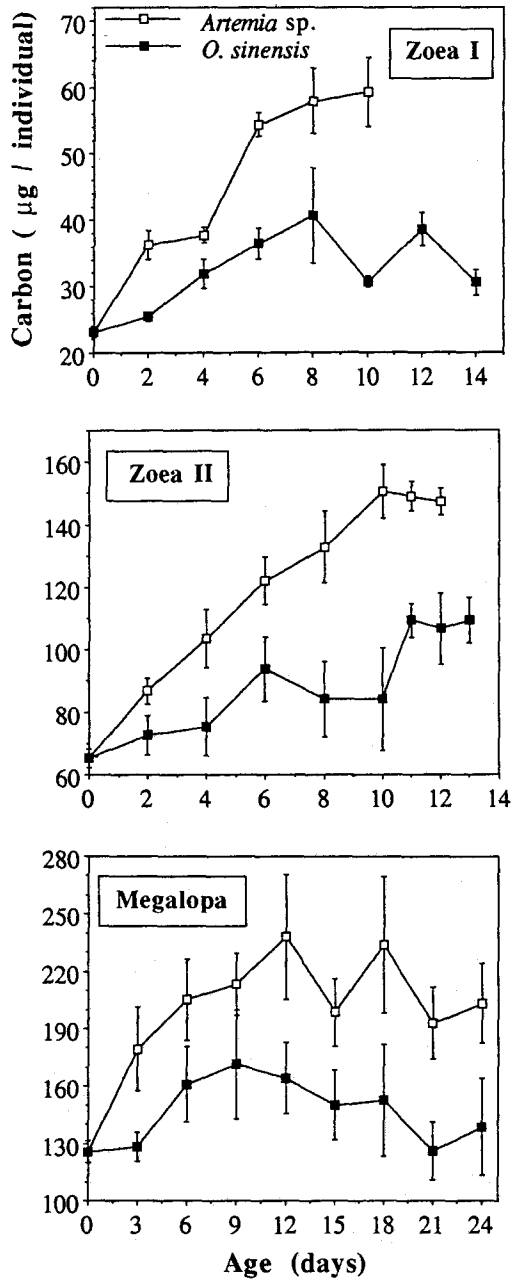
Fig. 1. *Hyas araneus*. Carbon content (μg · individual^{-1}; x ± SD; n = 8) during the course of the moulting cycle in subsequent larval stages fed two different diets

Table 2. *Hyas araneus.* Protein specific nucleotide (AMP, ADP, ATP, CTP, UTP, GTP) and adenosine concentrations during time (days) of development in subsequent larval stages reared under different nutritional conditions at constant temperature (12 °C). * Analyses with inadequate separation. ** Larvae developed to the next instar after being fed in the previous larval stage with *Odontella (Biddulphia) sinensis*

Larval stage/ Diet	Age (days)	AMP	ADP	ATP	CTP	UTP	GTP	Adenosine
Zoea I								
Artemia sp.	0	0.95	2.08	14.16	1.35	1.47	1.08	–
	2	0.90	1.70	11.61	1.15	0.91 *	1.70 *	3.02
	4	1.51	1.85	15.93	1.16	2.98	1.34	3.07
	6	1.05	2.52	15.93	1.40	1.56	1.15	0.87
	8	1.55	3.53	11.44	1.37	2.85	1.26	0.76
	10	0.74	4.05	13.48	1.35	2.64	0.87	2.47
O. sinensis	0	0.95	2.08	14.16	1.35	1.47	1.08	–
	2	0.74	1.92	10.84	–	1.24	0.94	–
	4	0.97	1.87	13.24	1.04	2.13	1.29	1.54
	6	1.47	2.84	12.34	1.41	1.83	1.13	0.97
	8	0.87	3.70	10.60	1.68	2.08	1.12	2.11
	10	0.74	3.92	10.86	1.08	1.78 *	0.75 *	2.30
	12	0.94	1.75	13.37	1.41	2.05	1.13	–
	14	0.35	1.18	14.02	0.98	1.05	0.84	0.88
Zoea II **	0	1.46	3.94	10.77	2.28	0.99	0.69	–
Zoea II								
Artemia sp.	0	1.82	2.95	12.34	0.94	1.45	1.02	0.55
	2	2.38	2.64	14.91	2.58	2.01	1.28	0.54
	4	1.25	2.42	12.45	1.80	4.43	1.06	–
	6	0.97	2.64	16.06	2.96	6.02 *	1.55 *	0.45
	8	1.11	2.10	15.40	0.50	5.82 *	1.26 *	0.37
	10	1.60	2.59	17.29	1.53	1.49	1.22	0.48
	11	0.91	2.09	16.93	1.10	4.21	1.47	0.40
	12	0.92	1.05	14.27	0.78	3.13	1.25	0.77
O. sinensis	0	1.82	2.95	12.34	0.94	1.45	1.02	0.55
	2	1.30	2.52	12.89	2.61	2.54	1.06	–
	4	1.52	2.89	12.99	2.58	2.91	1.07	–
	6	2.24	3.60	16.69	2.85	3.75	1.36	0.60
	8	1.69	2.86	15.73	1.58	3.43	1.56	0.65
	10	1.29	3.63	16.44	1.51	3.43	1.41	0.57
	11	1.28	1.42	17.74	0.97	4.22	1.59	0.81
	12	1.58	2.75	14.29	0.69	–	–	0.91
	13	2.33	4.75	14.43	0.46	2.33	0.39	1.04
Megalopa **	0	2.47	3.01	11.54	0.54	1.75	1.20	0.82
Megalopa								
Artemia sp.	0	1.65	1.70	11.42	0.57	1.56	0.91	1.21
	3	1.39	1.26	9.73	0.82	1.89	0.78	1.22
	6	1.12	1.18	11.42	0.74	2.30	0.88	1.19
	9	1.04	1.23	10.96	0.93	1.95	0.82	0.68
	12	4.19	3.37	4.64	0.99	0.87	0.48	0.52
	15	0.95	1.01	12.43	0.90	2.48	0.91	0.41
	18	1.33	1.86	15.18	0.96	2.51	1.09	0.75
	21	3.32	4.00	10.54	0.99	1.49	0.78	0.61
	24	1.66	2.34	15.01	1.03	1.89	1.07	1.14

Table 2 (contd)

Larval stage/ Diet	Age (days)	AMP	ADP	ATP	CTP	UTP	GTP	Adenosine
Megalopa								
O. sinensis	0	1.65	1.70	11.42	0.57	1.56	0.91	1.21
	3	1.94	1.82	10.87	0.74	1.15	0.84	0.63
	6	2.10	1.69	20.71	1.03	3.86	1.50	0.81
	9	2.85	3.51	11.01	0.90	1.47	0.90	0.70
	12	1.66	2.54	19.31	0.84	2.76	1.13	0.62
	15	1.34	2.14	17.80	1.36	2.97	1.26	0.75
	18	1.11	2.30	16.42	0.43	2.43	1.33	0.60
	21	1.40	2.60	16.39	0.67	1.18	1.18	0.84
	24	10.27	5.68	3.05	1.33	0.68	0.43	0.79

Experiment I and II on *Artemia*-fed megalopa showed similar nucleotide contents during the larval development, except for 12-day old megalopa in Experiment II. A net gain of ATP was also found in the *O. sinensis*-fed larval stages. However, the individual amount of nucleotides in *O. sinensis*-fed larvae were always reduced compared to *Artemia*-fed larvae. This trend was already established during early developmental processes, showing that nutritional conditions had an immediate influence on the levels of nucleotides and therefore on the energy available to the larvae. The percentage proportion of ATP to the total AN pool varied with a few exceptions between 75 to 92 %, under both nutritional conditions tested.

The adenylic energy charge (AEC) was calculated from the mean values of individual AN content presented in Figure 3. In zoea I, AEC decreased in 8-day old *Artemia*-fed larvae (equal to D_0 of the moulting cycle), recovering slightly later (Fig. 4). A similar pattern was observed in *O. sinensis*-fed larvae, the decrease occurring somewhat earlier, whereas the later increase was much more obvious because of their prolonged developmental duration. In the zoea II, AEC increased in *Artemia*-fed larvae throughout larval development. *O. sinensis*-fed larvae showed a similar increase in the AEC, reaching similar values to *Artemia*-fed larvae at day 11; however, during late premoult of the moulting cycle, AEC declined rapidly from 0.89 to 0.78. A similar decrease in AEC (0.85 to 0.32) was observed in the late premoult period of *O. sinensis*-fed megalopa, whereas no differences in the AEC were observed during earlier developmental periods between both nutritional conditions tested. The AEC of *Artemia*-fed megalopa in Experiment I and II are generally in good agreement, except a decrease to 0.5 on day 12 in Experiment II (recovering three days later to the previous level) and a somewhat lower initial value in Experiment I. Generally the AEC did not reflect the differences between the two nutritional conditions tested. Only in late premoult periods of the moulting cycle could a sharp decrease in AEC be observed when larvae were fed suboptimally with *O. sinensis*.

The differences between the two diets were most obvious when individual contents of adenosine nucleotides were pooled (Fig. 5). The differences between the two nutritional diets are significant, due to the low variation between the three replicates (see above). The individual nucleotide contents reflected the nutritional status of the larvae earlier than changes in the AEC did.
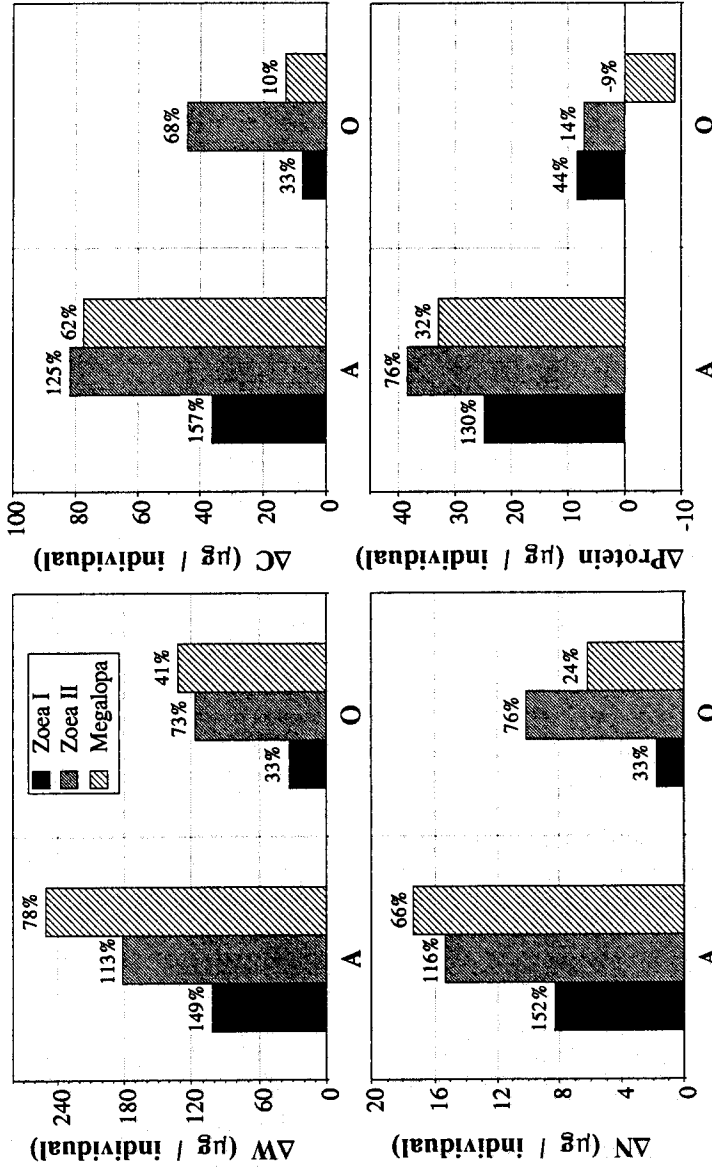
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Fig. 2. *Hyas araneus*. Gain or loss (Δ, change given in μg · individual^{-1}, and as percentage change, related to early postmoult values) in dry weight (W), carbon (C), nitrogen (N) and protein in subsequent larval stages fed two different diets [A: *Artemia* sp.; O: *Odontella (Biddulphia) sinensis*]
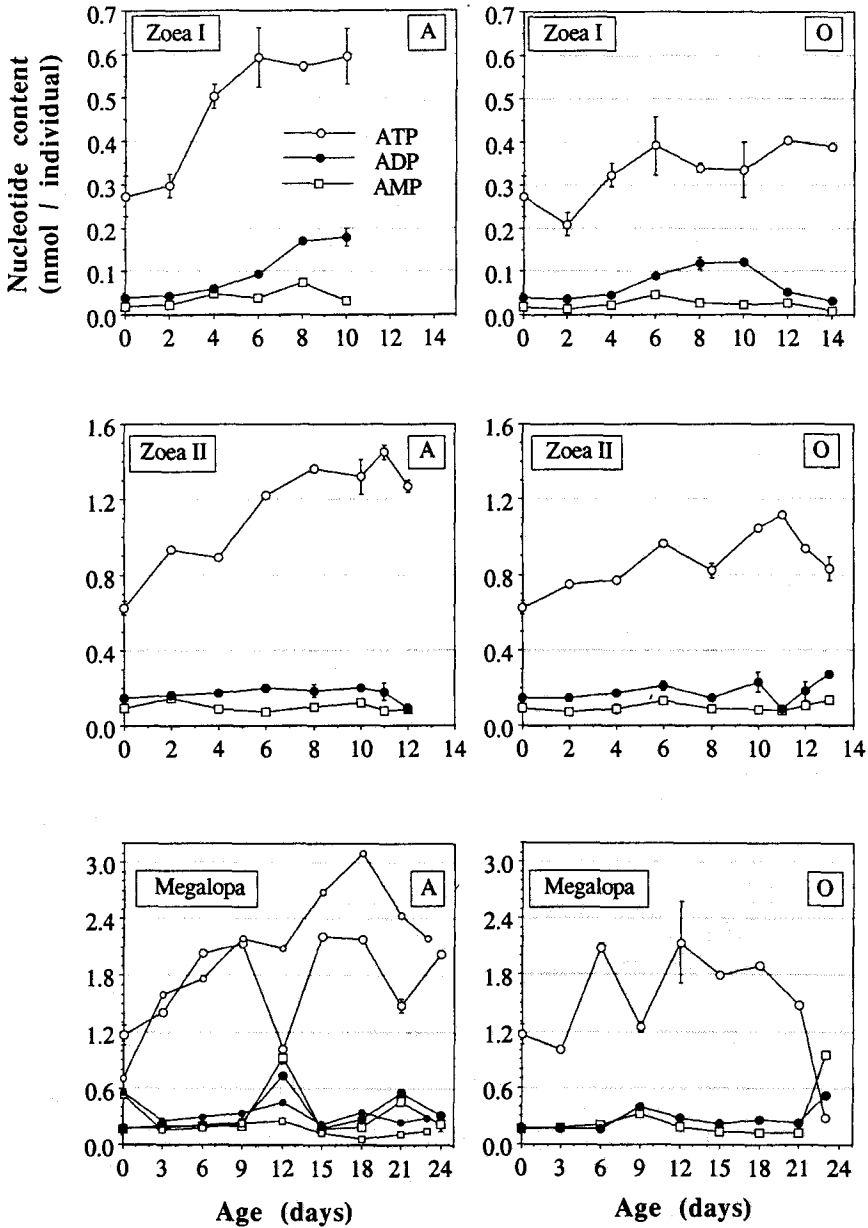
Fig. 3. *Hyas araneus*. Individual adenylate nucleotide content (ATP, ADP, AMP; $\bar{x} \pm$ SD, n = 3) during the course of the moulting cycle in subsequent larval stages fed two different diets [A: *Artemia* sp.; O: *Odontella (Biddulphia) sinensis*]. Results of Experiment I are also shown in the diagram (small signs)

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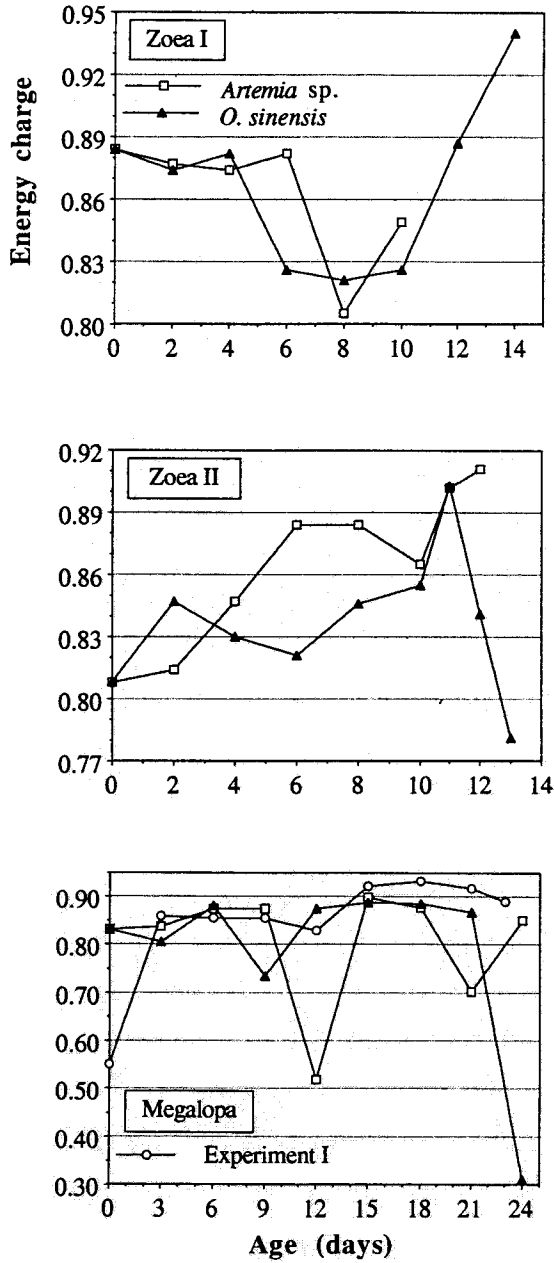
Fig. 4. *Hyas araneus*. Adenylate energy charge (AEC) [(ATP + ½ADP)/(ATP + ADP + AMP)] during
the course of the moulting cycle in subsequent larval stages fed two different diets. Results of
Experiment I are also shown in the diagram
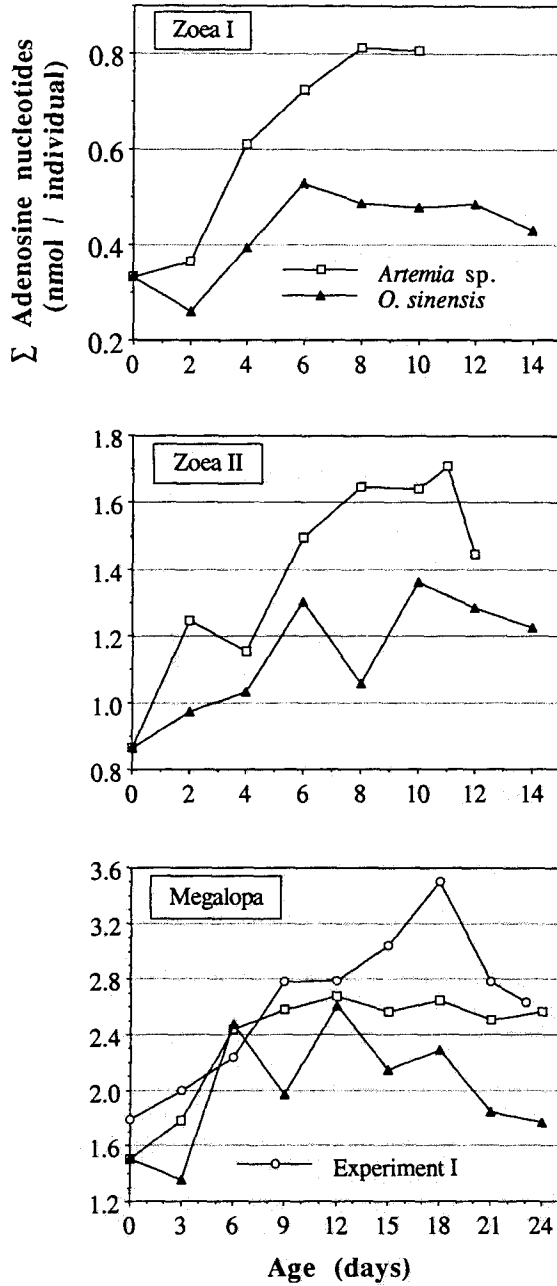
Fig. 5. *Hyas araneus*. Pooled adenylate nucleotide content (ATP + ADP + AMP) during the course of the moulting cycle in subsequent larval stages fed two different diets. Results of Experiment I are also shown in the diagram

No correlations could be found between the individual content of ATP and one of the other triphosphates, nor between the three triphosphates. Correlation was found between the pooled contents of the three triphosphates CTP, GTP and UTP and the ATP content (Σ CTP + GTP + UTP = 0.078 + 0.27 ATP; r = 0.85; n = 55; P < 0.001). Instead of using a linear regression, a somewhat better correlation can be found by using a power function (Σ CTP + GTP + UTP = −0.47 ATP$^{0.919}$, R = 0.919).

Relationship between growth and nucleotide composition

The nutritional conditions, as shown above, were reflected both in growth and nucleotide composition. It was found that the content of nucleotides are correlated with the contents of C and protein (Table 3). The weakest correlations were found between the

Table 3. *Hyas araneus*. Larval stages (zoea I to megalopa); parameter for linear regression [y = a + b x] describing relationships between biochemical components [x = carbon, protein und Joule individual^{-1} (J ind^{-1})] and nucleotide concentrations [y = ATP, ΣAN, ΣCGU] for pooled data of the two nutritional conditions tested. ΣAN: sum of adenosin nucleotides (AMP + ADP + ATP); ΣCGU: sum of CTP + GTP + UTP; intercept a and slope b ± standard deviations, r: correlation coefficient; level of significance in all cases P < 0.001; number of paired data n = 58, for ΣCGU n = 56

		a	±	b	±	r
Carbon	ATP	0.094	0.081	0.085	0.0005	0.905
	ΣAN	0.179	0.058	0.011	0.0004	0.965
	ΣCGU	0.087	0.032	0.002	0.0002	0.846
Protein	ATP	0.150	0.104	0.012	0.0010	0.843
	ΣAN	0.197	0.081	0.015	0.0008	0.935
	ΣCGU	0.096	0.036	0.003	0.0003	0.804
J ind^{-1}	ATP	0.131	0.083	0.234	0.0150	0.897
	ΣAN	0.232	0.067	0.293	0.0130	0.952
	ΣCGU	0.096	0.032	0.067	0.0058	0.842

sum of the three triphosphates CTP, GTP and UTP and the biochemical compounds C and protein. The highest correlation coefficients were found for the relationship between Σ AN and C and protein. For these two cases, separate correlations for the two nutritional conditions tested are given in Figure 6. The correlation constants differed slightly but significantly with the nutritional status of the larvae.

The total weight of the measured adenosine nucleotides amounted to 0.16–0.28 % of W, varying only slightly between the larval stages and nutritional conditions. Variation was predominantly observed within the single larval stages, with lowest values (0.16–0.18 %) on day two or three and slightly higher values (0.21–0.28 %) during later development.

DISCUSSION

The two diets tested here have been previously used in a variety of studies to estimate energy budgets of laboratory reared decapod larvae (Harms & Anger, 1990; Harms et al., 1990a). The algae diet *(Odontella [Biddulphia] sinensis)* had been found to
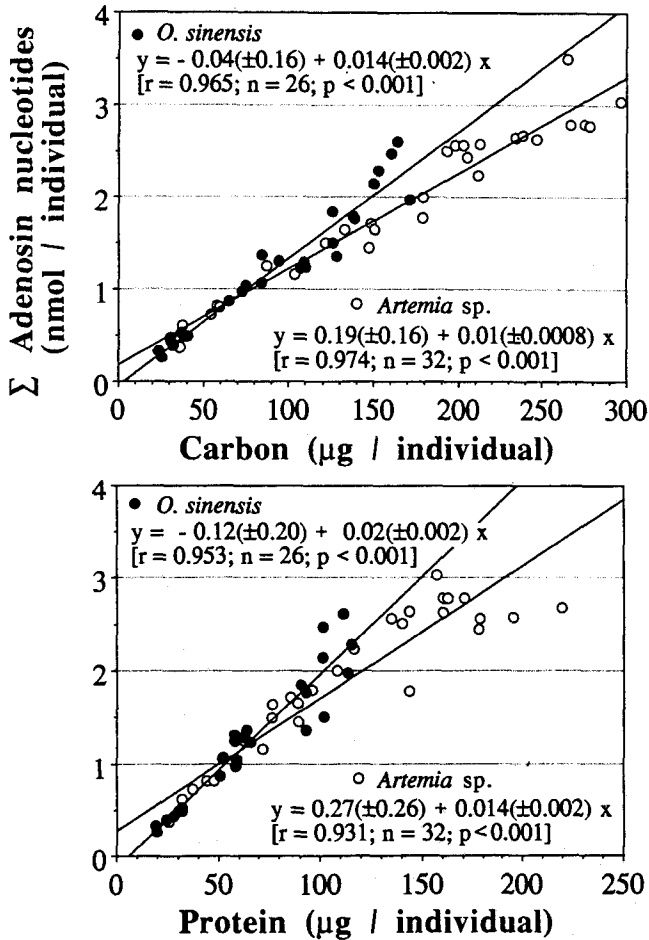
Fig. 6. *Hyas araneus*. Carbon and protein concentrations related to the adenosine nucleotide pool for the two different nutritional conditions tested. Intercept with y-axis and slope of least-square regression lines given with 95 % confidence intervals; r, correlation coefficient; n, number of paired data; P, level of significance for r ≠ 0

be sufficient for some further development to the next larval instars (Harms & Seeger, 1989), but larvae failed to complete the entire development successfully up to the juvenile instar when fed exclusively on this diet. In this study, further development to the next instar could be observed in all cases. Developmental success decreased in *O. sinensis*-fed megalopa, which corresponds to the low increase of the elemental composition (C, H, N) and protein content in this larval stage. This study again demonstrates and quantifies the ability of larval crabs to convert phytoplankton biomass (see also Harms et al., 1990a). The growth of *O. sinensis*-fed larvae reported here are higher than in previous experiments (Harms et al., 1990a). The algae diet allowed some net gain in organic constituents, except for protein in the megalopa stage. However, *O. sinensis* supplies suboptimal nutrition compared to *Artemia* sp. nauplii.

Decapod larval development is characterized by a sequence of morphologically different instars, which are separated by moults. The time between two moults can be further divided into a series of internal physiological and anatomical alterations, the moulting cycle as described by Drach (1939) and Drach & Tschernigovtzeff (1967) and which was adapted by Anger (1983) to brachyuran decapod larvae. Major biochemical changes, especially in the nucleotide composition, has been found to take place in late premoult of the moulting cycle. This is especially pronounced when larvae are fed a suboptimal diet (Figs 3, 4), indicating that during this period of the moulting cycle, energy consuming processes are taking place.

The AEC is proposed as an index of the energy potentially available for cellular metabolism (Atkinson, 1977; Dickson & Franz, 1980). Any factor which upsets homeostasis should be reflected in an altered AEC. The maximum value of the AEC is 1, but it is found to be normally maintained between 0.80 and 0.94 in unstressed organisms (Ivanovici, 1980b; Vetter & Hodson, 1982). The values for the AEC observed here varied with a few exceptions (*O. sinensis*-fed zoea II and megalopa in late premoult stage, and 12-day old *Artemia*-fed megalopa) within this range, showing that suboptimal feeding conditions are not reflected in the AEC. The maintenance of a high AEC might be the result of rapid extramitochondrial resynthesis of 1 mol ATP and 1 mol of AMP from 2 mol of ADP by adenylate kinase. The resulting AMP is then rapidly deaminated to inosine monophosphate (Chapman et al., 1976; Driedzic & Hochachka, 1976). The maintenance of a high AEC in suboptimally fed larvae may facilitate a rapid resumption of synthetic activity when larvae regain access to high quality food.

The individual AN content of *Hyas araneus* larvae is affected by nutritional conditions at an early stage of the developmental process. This is made most obvious by the pooled AN data (Fig. 5). Similar results had been observed in a previous study (Harms et al., 1990b), where decreasing adenylate pools were reported in starving *Carcinus maenas* larvae while the AEC was maintained constant. Literature reports on changes in ATP contents are contradictory. Decreasing ATP contents were reported for starving adult crayfish *Orconectes inermis inermis* (Dickson & Giesy, 1982). However, in contrast to this the same authors reported increasing ATP levels in starved crayfish *Procambrus clarkii*. Increasing ATP values were also reported for food-deprived fish (Dehn, 1985). Schirf et al. (1987) showed that different organs of starved crayfish *P. clarkii* respond differently to nutritional stress. The ATP pool increased in the muscles although the AEC was unaffected, while it decreased in the hepatopancreas.

Nucleotide concentrations in *H. araneus* larvae reached values between 0.16 to 0.28 % of W. The concentrations found for *C. maenas* larvae were somewhat higher, varying from 0.20 to 0.56 % of W (Harms et al., 1990b). Higher values were reported for North Atlantic krill varying from 0.40 to 1.3 % (Saether & Mohr, 1987). ATP contribute up to 75–92 % of this weight proportion, which stands in good agreement with the weight relationships reported by Harms et al. (1990) and Saether & Mohr (1987).

The results presented here show that the AEC was generally unaffected by the two food conditions tested. These findings are not restricted to Decapoda. Vetter et al. (1986) found that AEC was kept constant in fishes, and that the nucleotide content decreased in response to the stress situations. The individual amount of adenylate nucleotide might be a more sensitive indicator of the well-being of organisms. The findings reported here thus support Atkinson's original hypothesis (Atkinson, 1968) that the AEC is a relatively

conservative property and that changes in AEC are always accompanied if not preceded by changes in the quantity of adenylate nucleotides.

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