

Effect of temperature on respiration of larval stages of *Hyas araneus* and *H. coarctatus* (Decapoda, Majidae)

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ABSTRACT: Larvae of the crustaceans *Hyas araneus* L. and *H. coarctatus* Leach were reared in the laboratory at 12°C; their respiration rates were measured at 3, 6, 9, 12, 15 and 18°C. For all stages of *H. araneus* and for the megalopa of *H. coarctatus* the increase in metabolic rates with increasing temperature could be described by Bělehrádek's equation; Q_{10} values decreased in these cases with increasing temperature. In the zoeal stages of *H. coarctatus* the relation between respiration and temperature followed an exponential model, and the Q_{10} values remained constant (Zoea I) or increased (Zoea II) with increasing temperature. At 3°C, equivalent stages of the 2 species had almost identical respiration rates (R , per individual); weight-specific metabolic rates (QO_2) were higher in *H. coarctatus*. The rate of increase in R with increasing temperature was conspicuously lower in *H. coarctatus* than in *H. araneus*. At 18°C the former species had R values 30% (Zoea I), 37% (Zoea II), and 16% (megalopa) below those in the latter species. Since there were similar differences in biomass (measured as dry weight, carbon, nitrogen, and hydrogen content) between corresponding stages of the 2 species, QO_2 values became very similar at 18°C. The significance of the moult cycle and of adaptation is discussed in relation to the general results obtained from comparable investigations on crustacean larval metabolism.

INTRODUCTION

Influence of environmental factors on metabolic requirements of decapod larvae has been studied in a number of species (for review see Schatzlein & Costlow 1978, Dawirs 1983, 1984). In most cases, respiration (both per individual and per unit of weight) increases with increasing temperature (Kinne 1970, Precht et al. 1973), but the response may vary within a range of temperatures (e.g. Schatzlein & Costlow 1978) and between developmental stages or related species (e.g. Sastry & McCarthy 1973, Sastry & Vargo 1977).

Changes of respiration (at 12°C) during the course of larval development and growth of the spider crabs *Hyas araneus* and *H. coarctatus* were described by Anger & Jacobi (1985) and Jacobi & Anger (1985). In the present study, metabolic rates of larvae of these species were measured in the laboratory at 6 different

constant temperatures in order to compare responses between stages and species.

MATERIALS AND METHODS

Larvae of *Hyas araneus* and *H. coarctatus* were obtained and reared at 12°C as described by Anger et al. (1983), Anger & Jacobi (1985), and Jacobi & Anger (1985). Samples of larvae were taken approximately in the middle of their moult cycles, i.e. 6 d after Zoea I hatching or moulting, and 11 d after megalopal moulting. In part of these samples, dry weight (W), carbon (C), nitrogen (N), and hydrogen (H) were measured with standard techniques (Anger et al. 1983), and the energy content was calculated from C (Salonen et al. 1976). Another aliquot part of the larval sample was used for the measurement of respiration rate at 6 different temperatures (3, 6, 9, 12, 15, and 18°C), applying the Winkler method (Grasshoff 1976, Anger & Jacobi 1985). Before each experiment, the larvae were adapted to the experimental temperatures for 2 h, without food.

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RESULTS

All measurements of biomass in 6 d old zoeae and 11 d old megalopae of both species are compiled in Table 1. The values found for the megalopa of *Hyas araneus* and those for the Zoea II and megalopa stage of *H. coarctatus* were significantly lower than the corresponding values given by Anger & Jacobi (1985) and Jacobi & Anger (1985), respectively. In all other cases there was good correspondence in estimates of biomass and energy found in these different studies.

The relative composition of the larvae was very similar in the 2 species, but the absolute amounts were quite different: the zoeae of *Hyas coarctatus* had consistently about 30% less biomass and energy per individual than those of *H. araneus*. This difference decreased to less than 20% in the megalopa stage.

Individual (R) and weight-specific (QO_2) respiration

rates (Table 2), without exception, increased with increasing temperature in all larval stages of both species. The Q_{10} values for 4 different temperature ranges of 6 C° each are compiled in Table 3. This index of metabolic response generally decreased with increasing temperature in *Hyas araneus*. In *H. coarctatus*, in contrast, such a trend was found only in the megalopa. In Zoea I of this species, Q_{10} values remained almost constant; in Zoea II they increased with increasing temperature (Table 3).

The inconsistency of these trends consequently also affected the regression models describing the relation between respiration (R) and temperature (T ; in °C). In most cases the best fit between measured and predicted data was obtained with Bělehrádek's (1935, 1957) equation:

$$R = b (T - \alpha)^m, \quad (1)$$

Table 1. *Hyas araneus* and *H. coarctatus*, larval stages. Dry weight (W), carbon (C), nitrogen (N), hydrogen (H) (all in μg ; C , N , H also in % of W), C/N and C/H ratios, energy content (in Joules, J) per individual and per mg W ; \bar{x} , \pm : arithmetic mean, standard deviation; n : number of replicate analyses; n' : total number of individuals analysed

Parameter	<i>Hyas araneus</i>			<i>Hyas coarctatus</i>			
	Zoea I	Zoea II	Megalopa	Zoea I	Zoea II	Megalopa	
W (μg)	\bar{x}	128.6	276.5	470.7	91.1	194.0	381.9
	\pm	3.8	14.2	60.6	3.2	9.1	72.8
C (%)	\bar{x}	38.8	41.1	34.9	35.8	36.9	34.1
	\pm	0.5	0.9	1.1	0.7	1.3	1.7
C (μg)	\bar{x}	50.0	113.7	164.6	32.6	71.6	131.3
	\pm	1.7	6.9	24.2	1.4	4.5	30.2
N (%)	\bar{x}	7.3	8.1	7.5	7.3	7.7	7.3
	\pm	0.1	0.2	0.4	0.2	0.3	0.3
N (μg)	\bar{x}	9.4	22.4	35.5	6.6	14.9	27.8
	\pm	0.4	1.0	4.8	0.2	0.9	5.1
H (%)	\bar{x}	5.5	6.0	4.9	5.1	5.5	4.8
	\pm	0.2	0.2	0.3	0.2	0.3	0.6
H (μg)	\bar{x}	7.1	16.5	22.9	4.6	10.6	18.6
	\pm	0.4	1.3	4.3	0.3	0.8	5.5
C/N	\bar{x}	5.29	5.08	4.63	4.93	4.79	4.68
	\pm	0.05	0.11	0.18	0.08	0.04	0.27
C/H	\bar{x}	7.09	6.90	7.22	7.05	6.76	7.17
	\pm	0.23	0.15	0.34	0.14	0.17	0.57
J ind ⁻¹	\bar{x}	1.80	4.21	5.67	1.13	2.52	4.49
	\pm	0.07	0.28	0.88	0.05	0.18	1.11
J mg ⁻¹	\bar{x}	14.0	15.2	12.0	12.4	13.0	11.6
	\pm	0.3	0.5	0.5	0.3	0.6	0.8
n		13	13	13	13	11	20
n'		52	26	13	91	66	20

Table 2. *Hyas araneus* and *H. coarctatus*, larval stages. Individual (R) and weight-specific (QO_2) respiration rates, in $\mu\text{g O}_2\text{h}^{-1}$ individual $^{-1}$ and $\mu\text{g O}_2\text{h}^{-1}\text{mg}^{-1}$, respectively, in relation to temperature ($^{\circ}\text{C}$). \bar{x} , \pm SD: arithmetic mean \pm standard deviation ($n = 8$)

			Temperature ($^{\circ}\text{C}$)					
			3	6	9	12	15	18
<i>Hyas araneus</i>								
Zoea I	R	\bar{x}	0.097	0.205	0.236	0.268	0.315	0.320
		\pm	0.015	0.022	0.020	0.012	0.021	0.035
	QO_2		0.75	1.59	1.83	2.08	2.44	2.48
Zoea II	R	\bar{x}	0.227	0.377	0.504	0.583	0.618	0.798
		\pm	0.008	0.042	0.027	0.057	0.048	0.155
	QO_2		0.82	1.37	1.83	2.11	2.24	2.89
Megalopa	R	\bar{x}	0.270	0.412	0.631	0.698	0.770	0.846
		\pm	0.054	0.051	0.160	0.116	0.117	0.065
	QO_2		0.57	0.88	1.34	1.48	1.64	1.80
<i>Hyas coarctatus</i>								
Zoea I	R	\bar{x}	0.103	0.122	0.147	0.163	0.207	0.225
		\pm	0.010	0.010	0.008	0.012	0.015	0.041
	QO_2		1.13	1.34	1.61	1.79	2.27	2.47
Zoea II	R	\bar{x}	0.219	0.256	0.282	0.327	0.408	0.502
		\pm	0.019	0.021	0.020	0.023	0.020	0.030
	QO_2		1.13	1.32	1.45	1.68	2.10	2.59
Megalopa	R	\bar{x}	0.275	0.382	0.455	0.648	0.670	0.712
		\pm	0.062	0.027	0.074	0.063	0.101	0.122
	QO_2		0.72	1.00	1.19	1.70	1.75	1.86

where b , α , and m = fitted constants; b = intercept with R -axis in the linearized (logarithmic) form of Eq. (1). Thus it is a scaling constant defining shifts along the R axis. Since the weight-specific metabolic rate (QO_2) is defined as RW^{-1} , constant b for QO_2 is obtained by dividing the b value for R by W (from Table 1, but expressed in mg). Constant α is termed the 'biological zero' (Bělehrádek 1935, 1957), i.e. the temperature at which R theoretically becomes zero. The coefficient m expresses the overall degree of curvilinearity in relation to T .

This model was applied to all larval stages of *Hyas*

araneus and to the megalopa of *H. coarctatus*. All fitted parameters of Eq. (1) are given in Table 4.

The biological zero (α) was highest in Zoea I of *Hyas araneus*, intermediate in the following stages of this species, and much lower in the megalopa of *H. coarctatus*. The constant m shows the opposite trend (Table 4).

The shape of the curves represented by Eq. (1) is shown, as an example, for the larval stages of *Hyas araneus* in Fig. 1. It can be seen that these curves are not parallel but increasingly divergent with increasing temperature. In particular, the metabolic response pat-

Table 3. *Hyas araneus* and *H. coarctatus*, larval stages. Q_{10} values for 4 different 6°C temperature ranges

Temperature range ($^{\circ}\text{C}$)	<i>Hyas araneus</i>			<i>Hyas coarctatus</i>		
	Zoea I	Zoea II	Megalopa	Zoea I	Zoea II	Megalopa
3-9	4.40	3.78	4.12	1.81	1.52	2.31
6-12	1.56	2.06	2.40	1.62	1.50	2.41
9-15	1.62	1.40	1.39	1.77	1.85	1.91
12-18	1.35	1.69	1.38	1.71	2.05	1.17

Table 4. *Hyas araneus* and *H. coarctatus*, larval stages. Parameters of Eq. (1) and (2) for individual (R) and weight-specific (QO_2) respiration rate in relation to temperature ($^{\circ}C$). r : correlation coefficient (in all cases significantly different from zero; $P < 0.001$)

Parameter	<i>Hyas araneus</i>			<i>Hyas coarctatus</i>		
	Zoea I	Zoea II	Megalopa	Zoea I	Zoea II	Megalopa
b (R)	0.140	0.149	0.189	0.089*	0.181*	0.097
b (QO_2)	1.089	0.539	0.402	0.977*	0.933*	0.254
m	0.305	0.569	0.528	0.053*	0.054*	0.686
α	2.7	0.9	1.1	—	—	-1.5
r	0.998	0.994	0.992	0.994*	0.991*	0.986

* Parameters for Eq. (2); all others for Eq. (1)

tern of the Zoea I stage is much different from that in the 2 following instars.

Respiration in the zoeal stages of *Hyas coarctatus* in relation to temperature followed an exponential model [Eq. (2)] rather than Bělehrádek's equation [Eq. (1)]:

$$R = b \cdot e^{mt}, \quad (2)$$

where R , T , b , and m = defined as above; e = base of natural logarithms. Constant b can be calculated for QO_2 as described for Eq. (1). An equally good relation between measured and predicted data as that of Eq. (2) is given by the Arrhenius equation (e.g. Hirche 1984). Since the latter is more complicated, and does not yield

a better description of the above relation, Eq. (2) was adopted here.

Respiration (R) curves of *Hyas coarctatus* larvae intersect those of same-stage *H. araneus* larvae near $T = 3^{\circ}C$. With increasing T , the R of *H. araneus* increasingly diverges from that of *H. coarctatus*. This pattern can be observed in all larval stages (Table 2). At the highest temperature ($18^{\circ}C$) R values of *H. coarctatus* were 30% (Zoea I), 37% (Zoea II), and 16% (megalopa) below those of *H. araneus*. Since similar differences were found in biomass, as indicated earlier, the weight-specific metabolic rates (QO_2) of equal stages at $18^{\circ}C$ were very similar in the 2 species (Table 2).

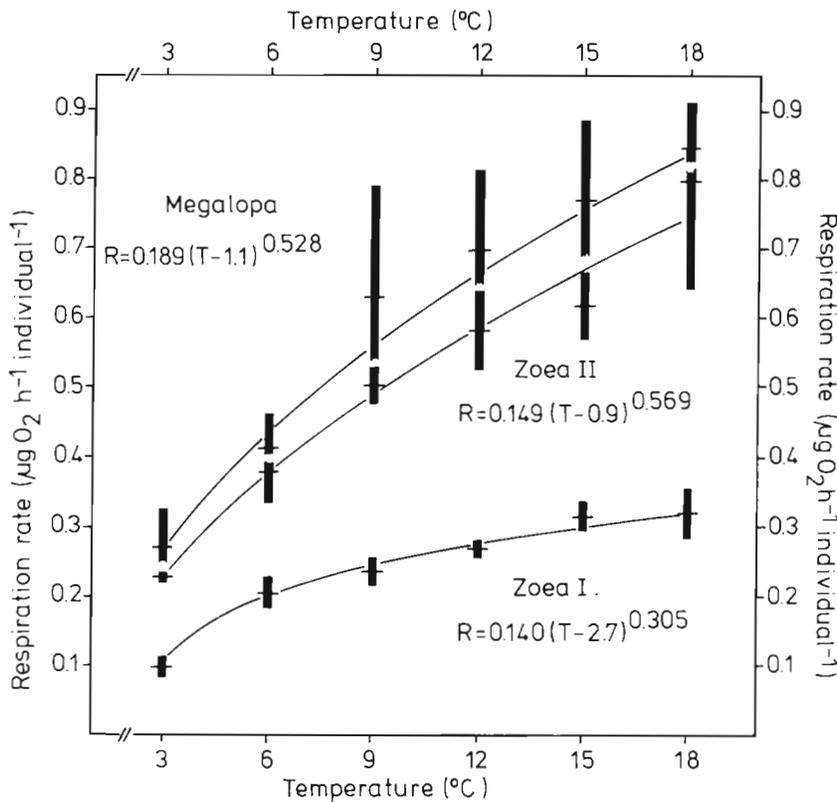


Fig. 1 *Hyas araneus*. Respiration rate (R ; $\mu g O_2 h^{-1} individual^{-1}$) of larval stages in relation to temperature (T ; $^{\circ}C$). Arithmetic mean \pm standard deviation

DISCUSSION

Respiration values (R , QO_2) and metabolic response to changes in temperature (Q_{10}) found in larval stages of *Hyas araneus* and *H. coarctatus* fall within the range observed for decapod larvae and other planktonic crustacea of different size, geographic origin, and systematic position (e.g. Vernberg & Costlow 1966, Sastry & McCarthy 1973, Ikeda 1974, Sastry & Vargo 1977, Schatzlein & Costlow 1978, Moreira et al. 1980, 1981, Laughlin & Neff 1981, Vernberg et al. 1981, Dawirs 1983, Paul & Nunes 1983, Hirche 1984, McNamara et al. 1985). Despite this abundance of studies on metabolism in relation to temperature, there exists by no means a general view of this relation in planktonic crustaceans in general or in any crustacean sub-group. This study too was unable to demonstrate a pattern common to all the larval stages of 2 closely related species. This is particularly conspicuous in the Q_{10} values (Table 3): their trends with changing ranges of temperature differed in the zoeal stages of *Hyas coarctatus* from that in the megalopa of the same species, and from those in all stages of *H. araneus*. Deviating trends in early larval stages were also found in *Cancer borealis* (Sastry & McCarthy 1973) and *Carcinus maenas* (Dawirs 1983). If there are general response patterns that can be described and predicted by a single model or a few models, such future generalization requires many further comparative investigations. These should consider more experimental temperatures and wider ranges of temperature than most of the above studies have used.

The data presented here allow us to formulate some relations between the metabolism of *Hyas* larvae and temperature as well as body weight. The latter relation – as has been discussed in most of the above-mentioned literature – is in general a linear function between log respiration and log weight (for recent discussion see e.g. Vernberg et al. 1981). These authors write 'among decapod larvae, especially during the developmental sequence, this relationship is not well understood'. Anger & Jacobi (1985) and Jacobi & Anger (1985) have shown that this is caused by a general lack of consideration and understanding of the larval moult cycle. The present results are strictly valid only for 6 d (Zoea I and II) or 11 d (megalopa) old larvae reared at constant 12°C. For most of the data given in the above-listed literature the larval age within the moult cycle had not even been recorded. Since there can be great changes of metabolism under constant conditions during each moult cycle, the relations between respiration and both temperature and biomass should also be studied in different stages of the moult cycle. Such studies may reveal that the metabolic response (e.g. Q_{10} value) can be quite differ-

ent in early postmoult or late premoult larvae, as compared to larvae in intermoult or early premoult (as in the present study), because physiological stability is higher in the latter than in the former stages.

Another factor which may complicate the interpretation of experimental data on metabolism is adaptation (i.e. both acclimation and acclimatization; for general discussion see e.g. Prosser 1958, Kinne 1970, Alderdice 1972, 1976, Precht et al. 1973). Our relatively high respiration values for *Hyas coarctatus* larvae at low temperatures (Table 2) seem to suggest that this species is more cold-adapted than *H. araneus*. Patterns of development rate of these species in relation to temperature (Anger 1984), and geographic distribution (Christiansen 1982), however, do not support such an interpretation in this particular case (see also recent criticism of the concept of metabolic adaptation to low temperatures by Hirche 1984). Additional studies must demonstrate the significance of the moult cycle, of adaptation phenomena, and of possible 'other temperature-dependent compartments of metabolic demand' (Alderdice 1976) for interpretation and modelling of larval crustacean energetics.

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LITERATURE CITED

- Alderdice, D. F. (1972). Factor combinations: Responses of marine poikilotherms to environmental factors acting in concert. In: Kinne O. (ed.) Marine ecology, Vol. I, Environmental factors, Part 3. Wiley, London, p. 1659–1722
- Alderdice, D. F. (1976). Some concepts and descriptions of physiological tolerance: rate-temperature curves of poikilotherms as transects of response surfaces. *J. Fish. Res. Bd Can.* 33: 299–307
- Anger, K. (1984). Development and growth in larval and juvenile *Hyas coarctatus* (Decapoda, Majidae) reared in the laboratory. *Mar. Ecol. Prog. Ser.* 19: 115–123
- Anger, K., Jacobi, C. C. (1985). Respiration and growth of *Hyas araneus* L. larvae (Decapoda: Majidae) from hatching to metamorphosis. *J. exp. mar. Biol. Ecol.* 88: 257–270
- Anger, K., Laasch, N., Püschel, C., Schorn, F. (1983). Changes in biomass and chemical composition of spider crab (*Hyas araneus*) larvae reared in the laboratory. *Mar. Ecol. Prog. Ser.* 12: 91–101
- Bělehrádek, J. (1935). Temperature and living matter. *Protoblasma Monographien* 8. Borntraeger, Berlin, p. 277
- Bělehrádek, J. (1957). Physiological aspects of heat and cold. *Ann. Rev. Physiol.* 19: 59–82
- Christiansen, M. E. (1982). A review of the distribution of Crustacea Decapoda Brachyura in the Northeast Atlantic. *Quad. Lab. Tecnol. Pesca* 3: 347–354
- Dawirs, R. R. (1983). Respiration, energy balance and development during growth and starvation of *Carcinus*

- maenas* L. larvae (Decapoda: Portunidae). J. exp. mar. Biol. Ecol. 69: 105-128
- Dawirs, R. R. (1984). Respiratory metabolism of *Pagurus bernhardus* (Decapoda: Paguridae) megalopa. Mar. Biol. 83: 219-223
- Grasshoff, K. (1976). Methods of sea water analysis. Verlag Chemie, Weinheim.
- Hirche, H.-J. (1984). Temperature and metabolism of plankton. I. Respiration of Antarctic zooplankton at different temperatures with a comparison of Antarctic and Nordic krill. Comp. Biochem. Physiol. 77A: 361-368
- Ikeda, T. (1974). Nutritional ecology of marine zooplankton. Mem. Fac. Fish. Hokkaido Univ. 22: 1-97
- Jacobi, C. C., Anger, K. (1985). Growth and respiration during the larval development of *Hyas coarctatus* (Decapoda: Majidae). Mar. Biol. 87: 173-180
- Kinne, O. (1970). Temperature: Invertebrates. In: Kinne, O. (ed.) Marine ecology, Vol. I, Environmental factors, Part. 1. Wiley, London, p. 407-514
- Laughlin, R. B., Jr., Neff, J. M. (1981). Ontogeny of respiratory and growth responses of larval mud crabs *Rhithropanopeus harrisi* exposed to different temperatures, salinities and naphthalene concentrations. Mar. Ecol. Prog. Ser. 5: 319-332
- McNamara, J. C., Moreira, G. S., Moreira, P. S. (1985). Thermal effects on metabolism in selected ontogenetic stages of the freshwater shrimps *Macrobrachium olfersii* and *Macrobrachium heterochirus* (Decapoda, Palaemonidae). Comp. Biochem. Physiol. 80A: 187-190
- Moreira, G. S., McNamara, J. C., Moreira, P. S., Weinrich, M. (1980). Temperature and salinity effects on the respiratory metabolism of the first zoeal stage of *Macrobrachium holthuisi* Genofre & Lobao (Decapoda: Palaemonidae). J. exp. mar. Biol. Ecol. 47: 141-148
- Moreira, G. S., McNamara, J. C., Hiroki, K., Moreira, P. S. (1981). The effect of temperature on the respiratory metabolism of selected developmental stages of *Emerita brasiliensis* Schmitt (Anomura, Hippidae). Comp. Biochem. Physiol. 70A: 627-629
- Paul, A. J., Nunes, P. (1983). Temperature modification of respiratory metabolism and caloric intake of *Pandalus borealis* (Krøyer) first zoeae. J. exp. mar. Biol. Ecol. 66: 163-168
- Precht, H., Christopherson, J., Hensel, H., Larcher, W. (1973). Temperature and life. Springer, Berlin
- Prosser, C. L. (1958). General summary: the nature of physiological adaptation. In: Prosser, C. L. (ed.) Physiological adaptation. Am. Physiol. Soc., Washington, p. 167-180
- Salonen, K., Sarvala, J., Hakala, I., Viljanen, M.-L. (1976). The relation of energy and organic carbon in aquatic invertebrates. Limnol. Oceanogr. 21: 724-730
- Sastry, A. N., McCarthy, J. F. (1973). Diversity in metabolic adaptation of pelagic larval stages of two sympatric species of brachyuran crabs. Neth. J. Sea Res. 7: 434-446
- Sastry, A. N., Vargo, L. S. (1977). Variations in physiological responses of crustacean larvae to temperature. In: Vernberg, F. J., Calabrese, A., Thurberg, F. P., Vernberg, W. B. (ed.) Physiological responses of marine biota to pollutants. Academic Press, New York, p. 401-423
- Schatzlein, F. C., Costlow, J. D. (1978). Oxygen consumption of the larvae of the decapod crustaceans, *Emerita talpoida* (Say) and *Libinia emarginata* Leach. Comp. Biochem. Physiol. 61A: 441-450
- Vernberg, F. J., Costlow, J. D. (1966). Studies on the physiological variation between tropical and temperate-zone fiddler crabs of the genus *Uca*. IV. Oxygen consumption of larvae and young crabs reared in the laboratory. Physiol. Zool. 39: 36-52
- Vernberg, W. B., Moreira, G. S., McNamara, J. C. (1981). The effect of temperature on the respiratory metabolism of the developmental stages of *Pagurus criniticornis* (Dana) (Anomura: Paguridae). Mar. Biol. Lett. 2: 1-9