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Growth and respiration during the larval development of a tropical spider crab, *Libinia ferreirae* (Decapoda: Majidae)

K. Anger[1], J. Harms[1], M. Montú[2], C. Bakker[2]

[1] Biologische Anstalt Helgoland, Meeresstation, D-2192 Helgoland, Federal Republic of Germany
[2] Centro de Biologia Marinha, Universidade Federal do Paraná, 83200 Pontal do Sul, PR, Brazil

ABSTRACT: Larvae of the tropical spider crab *Libinia ferreirae* were reared in the laboratory from hatching to metamorphosis, and their growth (dry weight, DW; ash-free dry weight, AFDW) and respiration rates were measured. Variations in the rates and patterns of growth were compared in 2 hatches (larvae from different females).The larvae of the more viable hatch grew continuously during the 2 zoeal stages and the beginning of the megalopa stage, with particularly high instantaneous growth rates in the beginning of each moult cycle. The megalopa showed decreasing biomass values prior to metamorphosis. Ash content increased significantly during and shortly after each ecdysis, then remained constant (zoeae) or decreased slightly (megalopa). In contrast, organic substance (AFDW), increased throughout most of the moult cycle. Respiration (oxygen consumption per individual) increased during development of the zoeal stages, and in the megalopa it followed a sinusoidal pattern. Weight-specific respiration rates were high near ecdysis and low during the intermoult stages of the moult cycle. Energy partitioning was compared among the different larval instars by calculating amounts of energy accumulation from AFDW and metabolic energy loss from respiration. According to these estimates, net growth efficiency (K_2) decreases from the first to the last larval instar (57, 36, and 7 %, respectively), whereas respiratory losses increase in the same order. *L. ferreirae* has been reported being associated with scyphozoans, and it is speculated that highly increasing mortality as observed during and after metamorphosis might be caused by lack of this specific substrate.

INTRODUCTION

Physiological aspects of larval development have been studied in many decapod crustacean species, although most of them have boreal geographical distributions (for references see e.g. Dawirs 1983). Since Vernberg's & Costlow's (1966) classical paper which included respiration measurements in tropical fiddler crab *Uca* spp. larvae, our knowledge of the physiology of tropical brachyuran larvae has not substantially increased (Schatzlein & Costlow 1978).

Only a few spider crab (Majidae) species have been reared in the laboratory for measurements of larval respiration or growth (in terms of biomass): *Libinia emarginata* (Schatzlein & Costlow 1978), *Hyas araneus* (Anger & Jacobi 1985), *H. coarctatus* (Jacobi & Anger 1985a), and *Inachus dorsettensis* (Anger 1988a). In the present investigation, patterns of larval growth and respiration were analysed in a tropical spider crab, *Libinia ferreirae*. This species is common along the South American Atlantic coast, occurring from Guiana to the state of Santa Catarina in Brazil (Melo 1984). Most records apparently are from the northern and northeastern (tropical) regions of Brazil (Coelho 1971, De Abreu 1980, Melo 1984, Sampaio & Fausto-Filho 1984).

MATERIALS AND METHODS

Obtaining and handling of larvae. Two ovigerous females of *Libinia ferreirae* were dredged during October 1988 from ca 10 m depth, off the beach near Pontal do Sul (Paraná, Brazil). They were maintained in a temperature-controlled laboratory of the Centro de Biologia Marinha (CBM) at ca 25 °C, 32 ‰ S, until larvae hatched from them on 31 October, and from 2 to 3 November, respectively.

Larvae from both hatches were isolated by means of a wide-bore pipette and placed in culture bowls

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(diameter: 11 cm) with ca 400 cm^3 filtered seawater (Whatman GF/C glassfiber filter). Initial population density in the mass cultures was ca 50 zoeae per bowl. Another 30 larvae of the first hatch were placed individually in numbered vials (25 cm^3). In order to ascertain development and mortality rates, moults and deaths in the individual culture were recorded daily. Water and food (freshly hatched San Francisco Bay Brand™ *Artemia* sp.) were changed daily in all cultures. The larvae were reared at 25 ± 1 °C, 32 ± 2 ‰ S, and a 12:12 h L:D light regime.

Development and growth. During the Zoea I development (1st hatch only), larvae were sampled daily from mass cultures and moult-staged microscopically (Anger 1983). Further samples were taken in each stage (from both hatches) and fixed in 4 % formaldehyde-seawater for studies of larval morphology and size increase (to be published elsewhere). Another set of samples was taken every 24 to 72 h (1st hatch) or every 12 h (2nd hatch), respectively, to measure larval biomass (dry weight, DW; ash-free dry weight, AFDW).

Larvae were removed from mass cultures by means of a wide-bore pipette and transferred to filtered seawater. They were then briefly rinsed in distilled water, blotted on filter paper (fluff-free), and dried for 12 h at 60 °C in preweighed silver cartridges. The samples were cooled to room temperature in a desiccator with silica gel, and DW was measured on a Mettler balance to the nearest 0.01 mg. They were then ashed in a muffle furnace at 500 °C for 4 h, cooled, and weighed again.

Every biomass was determined from 5 replicate measurements, with 3 (megalopa) to 50 (Zoea I) larvae each. In the first hatch, a total of 70 DW and AFDW measurements was carried out, using 435 larvae, and in the second hatch 85 measurements with 1695 larvae. The second series of biomass determinations was conducted with a higher temporal resolution and a higher average number of individuals per measurement, in order to quantify more precisely changes in the larval ash content. During this experiment, however, the larvae of the second hatch revealed very low viability and an irregular growth pattern. In spite of this, the results of this 'unsuccessful' experiment are also presented here to show the degree of variation that is possible between 2 hatches of the same species, reared under identical conditions.

Respiration. Every 24 to 72 h, larvae were sampled from mass cultures (parallel to biomass samples; 1st hatch only) and transferred to filtered seawater without food, where they remained for 1 h to allow for defecation. Three (megalopa) to 10 (Zoea I) larvae were carefully pipetted to one Winkler bottle (ca 60 cm^3), which was then closed. Each respiration measurement comprised 8 of such replicate experiments (with larvae) and 4 replicate blanks (without larvae)). Incubation time was ca 12 h. Oxygen was measured applying the Winkler method (Grasshoff 1976). Titrations were carried out with a Metrohm (Switzerland) Dosimat 665 apparatus. The standard error of mean replicate blank values was normally < 0.5 %, indicating a high reproducibility of this technique.

RESULTS

Rates of development and survival

Duration of development at constant 25 °C increased significantly ($p < 0.001$) from the first to the last larval instar, and was significantly shorter in the first juvenile (Crab I) as compared to the megalopa (Fig. 1a). Metamorphosis to the juvenile occurred ca 3 wk after hatching (Fig. 1b).

The course of the moult cycle was followed only in the first larval instar. Stages A to C had a combined length of about 24 h. Only 12 h later, most larvae were already in the transition between early and intermediate premoult (D_0/D_1). The latter stage (D_1) lasted for more than 12 h but normally less than 24 h and late premoult (Stages D_2–D_4) was in most larvae relatively brief (< 12 to 24 h).

Survival decreased during development at an increasing rate, since the instantaneous mortality rate increased from stage to stage (Fig. 2). Most larvae died in the metamorphic moults from Zoea II to megalopa

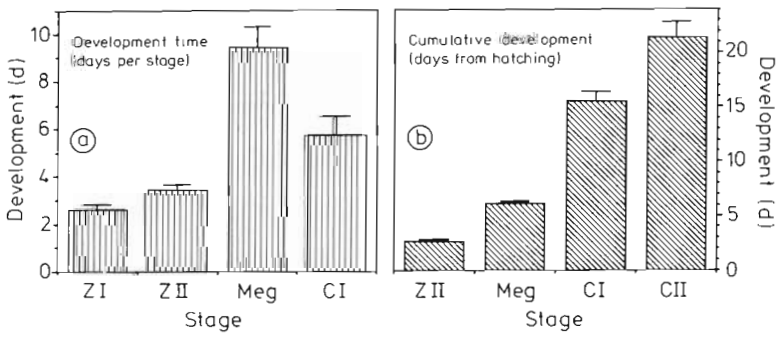

Fig. 1. *Libinia ferreirae*. (a) Development duration (d) in each larval stage (Zoea I, II, megalopa) and in the first juvenile (CI); (b) cumulative development (d) from hatching to the following postembryonic stages

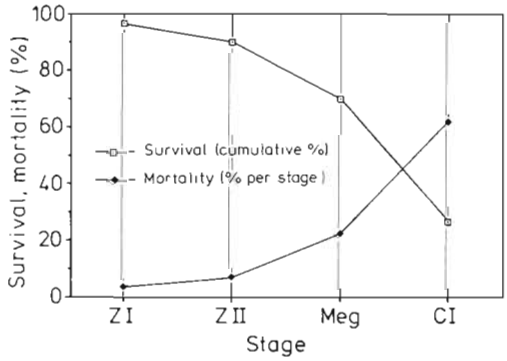

Fig. 2. *Libinia ferreirae*. Cumulative survival (% of initial number; $n = 30$) and mortality in each stage (% of individuals surviving to a given instar) during larval development

and from megalopa to first crab stage. However, high mortality continued also in the following juvenile instars, in most instances associated with moulting.

Rates of development and survival were not recorded in the second hatch; however, a clear delay was observed here in both zoeal moults, and mortality was in general considerably higher. The megalopa stage was reached by only a few individuals, and metamorphosis to the first juvenile did not occur in the second hatch.

Growth

The larvae of the first hatch showed a very steep increase in DW during their first day of development (Fig. 3a), rising from 47.5 to 70 µg per individual. About half of this initial gain, however, was due to a rapid uptake of inorganic materials, leading to a substantially increased ash content (Fig. 3a, b). During the rest of the moult cycle, there was little further increase in DW (to a maximum of 74 µg), and the absolute amount of ash remained fairly stable (12 to 15 µg). The amount of organic substance (AFDW), in contrast, showed a significant further increase, from 48 to 61 µg per larva (Fig. 3a).

The larvae of the second hatch also gained weight very rapidly during the first few hours after hatching, again largely due to a significantly increasing ash content (Fig. 4a, b). This brief growth phase followed a period of little growth, then another phase of increasing biomass, and eventually a weight loss, prior to moulting (Fig. 4a). These changes were caused mainly by variation in AFDW, whereas the absolute ash content remained rather stable (13 to 17 µg), and consequently, the percentage of ash showed a variation pattern inverse to that of AFDW (Fig. 4a, b).

Oscillations in instantaneous growth rates (expressed as µg AFDW ind.$^{-1}$ d^{-1}) are depicted in Fig. 5a, b. They show that the degree of variation in daily biomass

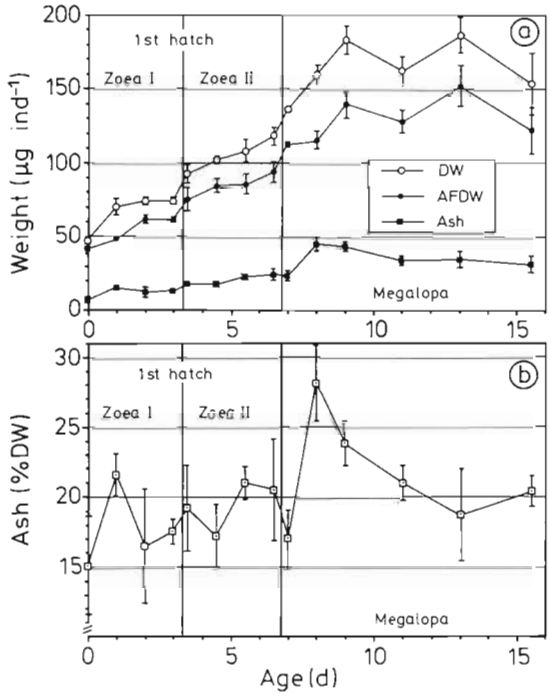

Fig. 3. *Libinia ferreirae*, first hatch. Growth during larval development. (a) Dry weight (DW), ash-free dry weight (AFDW), and ash content per individual; (b) weight-specific ash content (% of DW); x ± SD ($n = 5$)

accumulation rates was much higher in the second hatch. This applies to both the amplitude and the number of oscillations per moult cycle.

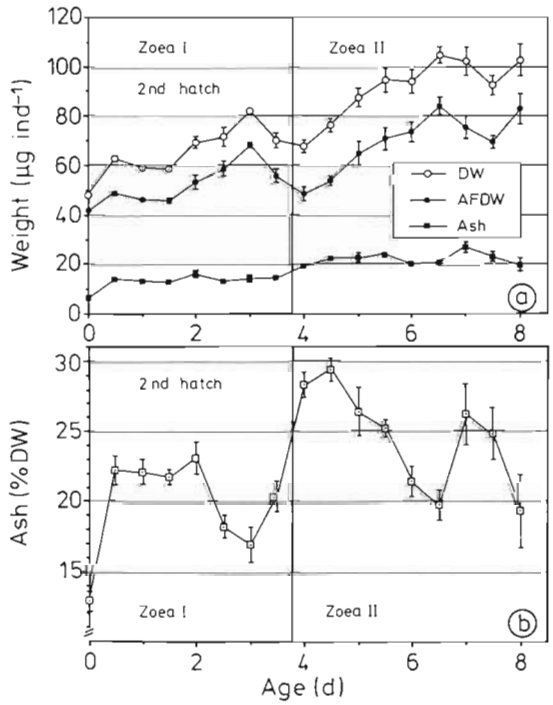

Fig. 4. *Libinia ferreirae*, second hatch. Growth during zoeal development. For explanation see Fig. 3

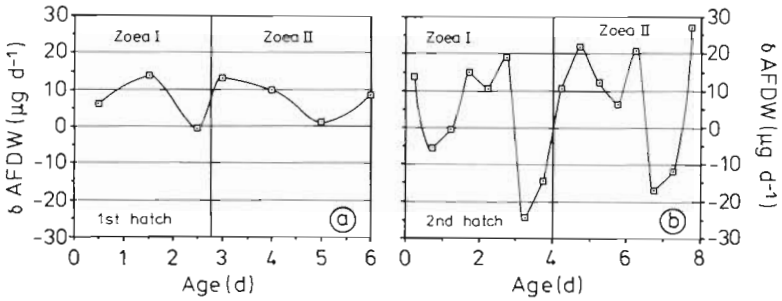

Fig. 5. *Libinia ferreirae*. Instantaneous growth rate (µg AFDW ind.$^{-1}$ d^{-1}) during zoeal development. (a) First, (b) second hatch

Freshly hatched Zoea I had an almost identical initial weight in the 2 hatches (47.5 vs 48.1 µg), but later the freshly moulted Zoea II was significantly heavier in the first hatch: 92 vs 68 µg. This difference in Zoea I growth was made up for by very fast growth in the Zoea II of the second hatch (Figs. 3a and 4a). However, near the end of the Zoea II moult cycle, the larvae of the second hatch again showed unusual variations of biomass, including a phase of loss in organic substance (Fig. 4a, b). Since only a few of them survived the moult to the megalopa, their subsequent growth could not be followed.

Both hatches showed a fairly stable ash content during Zoea II development, with slightly increasing values (ranging between 17 and 27 µg ind.$^{-1}$). Thus, variation in the percentage of ash reflected mainly variations in AFDW (Figs. 3b and 4b).

The growth pattern of the megalopa was not very clear, due to a relatively high variability in its biomass, in particular in AFDW (Fig. 3a). Ash content increased dramatically during the first day of its moult cycle, then decreased both in absolute (Fig. 3a) and relative (weight-specific; Fig. 3b) terms. The average level of weight-specific ash content reveals an increasing tendency from Zoea I to megalopa (Fig. 3b), indicating an increasing calcification.

Cumulative growth figures (differences between final and initial values) are shown in Fig. 6. In the first hatch, greatest gain in DW and AFDW occurred in the 2 zoeal stages, whereas the megalopa (although lasting much longer, cf. Fig. 1a) gained the least weight (Fig. 6a). This tendency is even more conspicuous in percentage growth (related to the initial values in each stage; Fig. 6c). The accumulation rate of inorganic substances (ash, in µg ind.$^{-1}$), in contrast, increased slightly from the first to the last larval stage (Fig. 6a). The percentage gain of ash, however, showed the opposite trend (Fig. 6c).

Zoea I larvae of the second hatch were stunted, but enhanced growth rates in the Zoea II (cf. Fig. 5) compensated for this delay (Fig. 6b). Much of the DW gained during Zoea I development was in this hatch inorganic material, whereas the following stage accumulated proportionally much more organic substances (Fig. 6b, d).

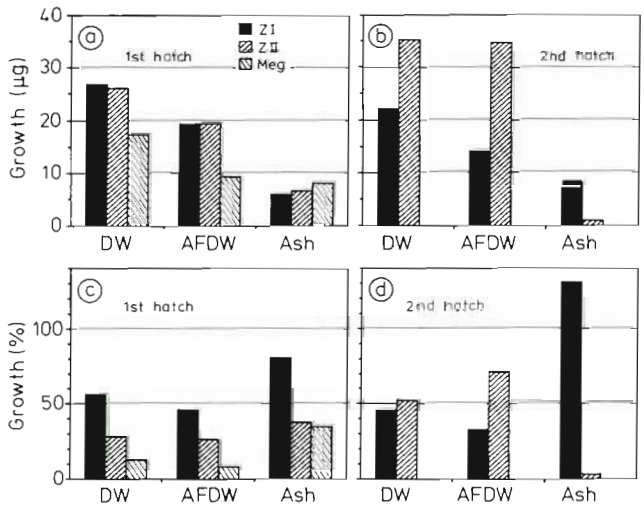

Fig. 6. *Libinia ferreirae*. Cumulative growth per larval stage. (a, b) absolute gain (µg DW, AFDW, ash, ind.$^{-1}$); (c, d) relative gain (% of initial values in each stage). (a, c) First, (b, d) second hatch

Respiration

Oxygen consumption (measured in the first hatch only) varied conspicuously during larval development (Fig. 7a). It was minimum in the middle of the Zoea I and maximum at the beginning (and again, in the middle) of the megalopa instar. Then, prior to metamorphosis, it decreased again.

Weight-specific respiration (QO_2) followed a somewhat different pattern (Fig. 7b). The highest value (9.5 µg O_2 mg^{-1} DW) was measured in freshly hatched Zoea I, the lowest in late megalopa larvae, shortly before metamorphosis (3.8 µg O_2 mg^{-1} DW). Between these 2 extreme values, there was a cyclic pattern, with high metabolic rates near ecdysis (except near metamorphosis), and low rates during the zoeal intermoult periods.

In the megalopa, QO_2 decreased from an initial maximum value during postmoult, then it increased again, reached a second maximum in the middle of the moult

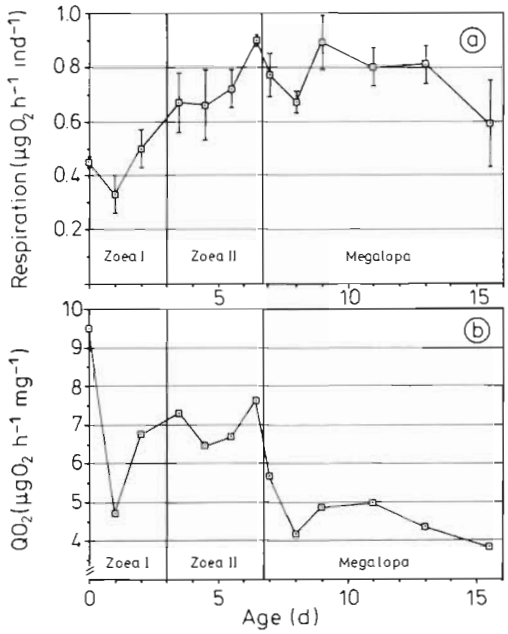

Fig. 7. *Libinia ferreirae*. Metabolism during larval development. (a) Respiration rate ind.$^{-1}$; (b) weight-specific respiration rate (QO_2; mg^{-1} DW)

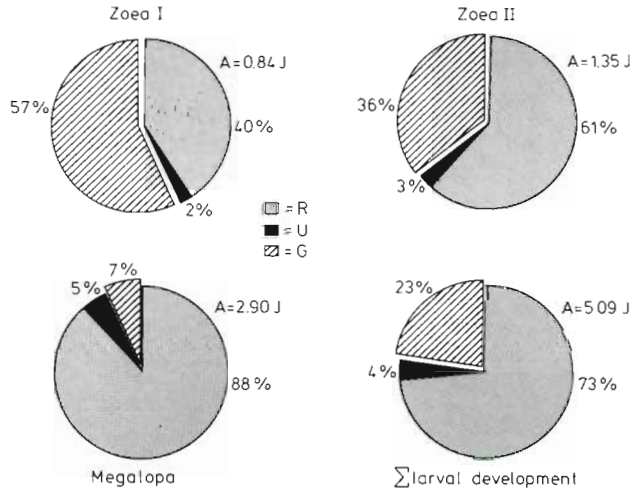

Fig. 8. *Libinia ferreirae*. Energy partitioning (% of assimilation, A, in Joules) in each of the larval stages, and integrated for complete larval development; respiratory losses (R), excretory losses (U), energy accumulated during growth (G). The percentage of G/A is identical with net growth efficiency, K_2. For energy conversion factors and methods of estimation see text

cycle (late intermoult or early premoult), and eventually decreased again during premoult.

Energy partitioning

Assimilation and partitioning of energy were not measured directly, but some estimates are possible from the present data. Assimilation (A) is represented by the sum:

$$A = G + R + U$$

where G = growth (including exuvia production); R = respiratory energy loss; U = energy loss via nitrogenous (ammonia) excretion. The accumulation of energy during body growth may be roughly estimated from total organic material, assuming an energy content of ca 24 Joules per mg AFDW in the zoeal stages, and 20 J mg^{-1} in the megalopa (Anger et al. 1983). Metabolic losses can be estimated from oxygen consumption, if one assumes an equivalent of 14.06 Joules per mg O_2 (Gnaiger 1983). Nitrogen excretion constituted only a minor part of the energy budget in other spider crab larvae (Anger 1988b). We adopted these values from *Hyas araneus* and assumed U to be 2, 3, and 5 % of total assimilation in the 3 larval instars, respectively. We further assume average development durations of 2.5, 3.5, and 9.5 d (Fig. 1), average respiration rates of 0.4, 0.7, and 0.8 µg O_2 h^{-1} ind.$^{-1}$ (Fig. 7), and cumulative growth rates of 20, 20, and 10 µg AFDW ind^{-1} (Fig. 6) in the consecutive larval stages. From these values, total assimilation, growth, and metabolic and excretory losses may be calculated (Fig. 8).

They show the following tendencies: the portion of assimilated energy that is channelled into growth (i.e. net growth efficiency, K_2) clearly decreases during larval development, with 57, 36, and 7 % in the Zoea I, Zoea II, and megalopa stages, respectively. The proportion of metabolism within the budget increases in the same order: 40, 61, and 88 % (Fig. 8). Cumulative figures of energy partitioning integrated for complete larval development from hatching to metamorphosis show an intermediate pattern, with an average K_2 of 23 %. Total assimilation and respiration values increase in an exponential way from instar to instar: A = 0.84, 1.35, 2.90 Joules; R = 0.34, 0.83, and 2.56 J ind.$^{-1}$, respectively.

DISCUSSION

The results of the present study can be compared with those obtained in a closely related species, *Libinia emarginata* (Schatzlein & Costlow 1978), and to some degree also with *Hyas* spp. (e.g. Anger & Jacobi 1985, Jacobi & Anger 1985a). Growth in *L. emarginata* larvae was unfortunately given only as wet weight, and measurements were made without defining the stage within the larval moult cycle, so that in this case there is only a limited comparability of data. Growth was measured also in the larvae of the spider crab *Inachus dorsettensis* (Anger 1988a), but here no respiration data are available.

Development duration of *Libinia ferreirae* larvae at 25 °C is very similar to that in *L. emarginata* reared at the same temperature (Bookhout & Costlow 1970, Johns & Lang 1977, Anger et al. 1981). *L. dubia* developed somewhat faster, but at a slightly higher temperature (Sandifer & van Engel 1971). Species with a boreal or antiboreal (*L. spinosa, Hyas* spp.), or a boreal-subtropical distribution *(Inachus dorsettensis)* cannot be reared at such high temperatures, and in their normal (lower) temperature range they develop much more slowly (Boschi & Scelzo 1968, Jacobi & Anger 1985b). Even so, development at 20 °C is in the tropical-subtropical species *L. emarginata* still considerably faster than in *L. spinosa* originating from temperate waters (cf. Boschi & Scelzo 1968, Bigford 1978). The relative durations of the moult cycle stages during Zoea I development were in *L. ferreirae* similar to those in *L. emarginata, Hyas araneus* and other decapod larvae (Anger 1983, 1987).

Survival figures in the first hatch (Fig. 2) suggest that our experimental conditions approximated the environmental and nutritional needs of the zoeae, but not of later developmental stages. Mortality was extremely high at metamorphosis, and it surprisingly continued in the juveniles, although these were maintained individually, with sand as a substrate. Since they fed very well on larger *Artemia* nauplii, it may be concluded that the cause of this continued mortality was inadequate food quality rather than insufficient food quantity. It may be speculated that a very particular substrate (possibly also serving as a food source) would be favourable for successful metamorphosis and juvenile development: namely, a jelly fish. Moreira (1961) reported an association between *Libinia ferreirae* and the scyphozoan *Mastigias scintillae.* Also the first author of the present paper observed, near Pontal do Sul, a live juvenile specimen of *L. ferreirae* on a stranded unidentified jelly fish, whereas small juveniles were not found by us in material dredged from the seafloor, where the adults live. This possible association should be further investigated both in the field and in the laboratory.

Libinia ferreirae larvae are heavier than those of *L. emarginata* (Schatzlein & Costlow 1978; if DW is assumed to average ca 80 % of wet weight in crab larvae: Anger & Dawirs 1982) and *Inachus dorsettensis* (Anger 1988a), but they are not as heavy as *Hyas* spp. larvae (Anger & Jacobi 1985, Jacobi & Anger 1985a). All these Majidae larvae are much heavier than those from other brachyuran families studied so far (see Lindley 1988 for review). Cumulative growth figures per larval stage (Fig. 6), however, appear to range among the lowest on record (cf. Anger 1984, 1988, Lindley 1988). Such comparisons must be treated with some caution, as experimental conditions vary among different investigations, and there are apparently significant differences between larvae from different hatches, even when these are treated, as far as possible, in the same way. More studies are needed that consider such variability. Also changes during individual moult cycles have still received too little attention.

The temporal resolution in our first experiment, in which the larvae developed successfully and in a regular manner, was not good enough to allow a detailed analysis and modelling of growth or respiration patterns during individual moult cycles. The growth curves shown in Fig. 3a are compatible with previous observations in brachyuran larvae (e.g. Anger & Dawirs 1982, Dawirs 1983, Anger & Jacobi 1985, Jacobi & Anger 1985a, Dawirs et al. 1986, Anger 1988a). It is particularly interesting to note that *Libinia ferreirae* corresponds to other species in that the megalopa appears to reveal a bell-shaped growth curve, suggesting that this might be a general pattern.

Instantaneous growth rates showed a cyclic pattern (Fig. 5), with higher amplitude and frequency of variation in the second (less viable) hatch. This low viability, if not purely genetic, might have been caused by some unknown stress exerted on the early larvae (possibly a day of over-feeding?), or even acting on the late embryos while they were still attached to their mother. Sanders & Costlow (1981) and Sanders et al. (1983, 1985) suggested a regulation mechanism in larval growth that would counteract stress and would lead to an oscillating growth pattern with transient overreactions. Stebbing (1981) observed such a response pattern, and termed it 'hormesis'. The present data could support this hypothesis, but more growth studies with high temporal resolution are necessary to establish and understand the significance of oscillating instantaneous growth rates in brachyuran larvae.

Respiration rates of *Libinia ferreirae* larvae were about 5 to 10 times higher than those measured by Schatzlein & Costlow (1978) in *L. emarginata* at the same temperature. Since this applies also to the weight-specific rates (QO_2; Fig. 7b), the discrepancy cannot be explained by the greater size of *L. ferreirae.* It was probably caused by methodological differences: Schatzlein & Costlow (1978) placed the crab larvae in respirometer flasks with only 0.2 cm^3 seawater, whereas in the present study the larvae had ca 60 cm^3 during the experiment, and each Winkler bottle contained up to 10 larvae. The great difference in respiration rates thus may be caused by swimming activity and, possibly, aggressive interaction (attempted cannibalism and avoidance reactions) vs enforced inactivity in small respirometers. Our values may be closer to active metabolism, whereas Schatzlein's & Costlow's may be closer to basal metabolism. On the other hand, experiment duration (in the absence of food) was

longer in our study, which should reduce larval respiration rates as compared to short-term measurements.

The weight-specific respiration rates (QO_2) of *Libinia ferreirae* larvae were in general also higher than in *Hyas* spp., even when the latter were studied near the upper end of their scale of temperature toleration (Jacobi & Anger 1985b). This difference, however, may be explained by the greater weight of *Hyas* spp. larvae causing lower weight-specific metabolic rates (Zeuthen 1947).

The peculiar variation pattern of QO_2 during the megalopa moult cycle (Fig. 7b) is interesting, because similar patterns have also been observed in *Hyas araneus* (Anger & Jacobi 1985) and *H. coarctatus* (Jacobi & Anger 1985a). The initial phase of decreasing weight-specific (and per individual) respiration rates corresponds to a period of rapid accumulation of both inorganic material (calcification of the relatively heavy megalopa cuticle; cf. Anger 1984) and of organic reserves, probably mainly metabolically inactive lipid deposits (Anger & Dawirs 1982). This period is followed by reconstruction of the larval epidermis (Anger 1983), accompanied by increased metabolism (Fig. 7b). During the premoult phase, the megalopa becomes increasingly inactive, so that internal activity (epidermal reconstruction) is counterbalanced by lack of swimming activity. The last period preceding metamorphosis is usually characterized by extremely sluggish behaviour and consequently, low respiration. The latter phase, however, was not as obvious in *Hyas* spp. as in *Libinia ferreirae*.

The partition of assimilated energy could be estimated only roughly, but some clear trends may be seen (Fig. 8). The amount of energy channelled into growth, i.e. net growth efficiency (K_2), decreases considerably during development, due to increasing amounts of metabolic loss. This loss is enhanced by increasing portions of growth that are lost as exuviae (Anger 1984, 1988b). A decline in K_2 during larval development has been found also in *Hyas* spp. (Anger & Jacobi 1985, Jacobi & Anger 1985a, Anger 1988b) as well as in some other decapod larvae (Reeve 1969, Dawirs 1983). In contrast, other authors found decreasing K_2 values in developing decapod larvae (see McConaugha 1985 for review), so that no general pattern can be seen at present.

More studies of bioenergetic and other physiological aspects of crustacean larval development will be necessary to show general traits and how these are modified by geographical distribution and associated genetic adaptations to different environmental conditions.

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