# ELEMENTAL COMPOSITION (C,N,H) AND ENERGY IN GROWING AND STARVING LARVAE OF *HYAS ARANEUS* (DECAPODA, MAJIDAE)

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## ABSTRACT

Laboratory-reared larvae of the spider crab, *Hyas araneus* L., were studied with regard to their fresh weight (FW), dry weight (DW), carbon (C), nitrogen (N), hydrogen (H), and energy content (J; estimated from C). FW remains fairly constant in each larval stage, regardless of feeding or starving conditions. This is due to regular changes in water content as opposed to those in organic constitutents. FW therefore is not a good measure for living biomass. Growth in fed zoeal stages, if expressed by gain in any parameter but FW, can be described by power functions of time. There is a considerable gain (by a factor of 2 to 3) within each of these two instars. In the magalopa also a high amount of C, N, H, and energy is accumulated, but most of this gain is lost again during the last third of its stage duration. This finding suggests that there is no more food uptake during this last period preceding metamorphosis to the crab. In all larval stages, weight-specific energy (J/mg DW) follows rather a cyclic pattern with decreases before and after molts, and increases during intermolt periods. It shows a decreasing trend during larval development. The loss in cast exoskeletons is <10% of premolt organic matter in the zoeal stages, but >30% in the megalopa. During starvation, biomass declines in an exponential pattern. Larvae of all stages die, when ca. 40 to 60% of their living substance and energy is lost. The C:N ratio suggests that protein serves as the main source of energy; in the final phase, presumbaly, lipids are also catabolized. Weight-specific energy and probably also metabolism decrease in a hyperbola-shaped curve.

Advanced rearing techniques developed in the last three decades have greatly increased our knowledge of autecology and physiology of meroplanktonic marine larvae. However, there is little quantitative information on growth, energetic needs, and reserves.

Within the literature on decapod larvae, there are numerous data on size increments from one developmental stage to the next (Rice 1968), but few on biomass production. Since size is fairly constant in each particular instar, this information represents only a rough measure of actual growth patterns.

A number of authors have investigated biochemical or energetic aspects of larval development in decapod crustaceans: Reeve (1969), Mootz and Epifanio (1974), Frank et al. (1975), Sulkin et al. (1975), Logan and Epifanio (1978), Morgan et al. (1978), Anger and Nair (1979), Capuzzo and Lancaster (1979), Omori (1979), Dawirs (1980), Stephenson and Knight (1980). These studies, however, mainly concentrated on gross differences among larval stages rather than on changes within single instars. Thus, biomass was either considered practically constant in each stage, or it was interpolated by means of (mostly exponential) regression equations describing growth from the first to the last larval instar. The present paper attempts to analyze actual growth patterns within stages of the spider crab, *Hyas araneus*.

Growth achieved in the laboratory under optimal food conditions (as in this paper) probably represents only one end of the scope in which development is possible, rather than a typical expression of it. The other end is characterized by the poorest food level still allowing minimal growth. Anger and Dawirs (1981) discussed the potential ecological role of starvation in a variable environment. They showed that larvae of *Hyas araneus* are well adapted to this condition.

In the present study diminution and growth rates were estimated from frequent samples of starved and fed larvae. They constitute a further step toward a better understanding of larval ecology and energetics in North Sea species as required in a joint research project (Anger and

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Manuscript accepted December 1981.
FISHERY BULLETIN: VOL. 80, NO. 3, 1982.

Nair 1979; Dawirs 1979, 1980; Anger and Dawirs 1981).

## MATERIALS AND METHODS

Ovigerous *Hyas araneus* were dredged from a deep channel near the island of Helgoland (North Sea) during early winter in 1978-79 and 1979-80. After hatching, the zoeae were isolated in vials and maintained individually at 12°C. Food (a mixture of freshly hatched Australian *Artemia* sp. nauplii and the rotifer *Brachionus plicatilis*) and filtered seawater were changed every second day. The methods of obtaining and rearing the larvae have been described in detail by Anger and Dawirs (1981).

For determination of wet weight, larvae were caught individually with pen-steel forceps, briefly rinsed in water from an ion exchanger, blotted for about 10 s on filter paper, and transferred to preweighed silver cartridges. All weight measurements were carried out on an Autobalance AD-2 (Perkin-Elmer)[3] to the nearest 0.1 $\mu$g. The techniques and equipment used for obtaining dry weight (DW), carbon (C), nitrogen (N), and hydrogen (H) content of larvae and young crabs were the same as described by Anger and Nair (1979) and Dawirs (1980): deep freezing, vacuum drying, weighing, and combustion in a C-H-N analyzer (Model 1106, Carlo Erba Science). Only rinsing of the material (see above) was added as an initial step. This standard procedure was adopted to remove possible adherent salt and thus to increase the accuracy of the measurements. Comparison of test measurements, however, did not show significant differences (Anger and Nair 1979).

Energy estimates (J) were obtained from carbon values by applying the N-corrected regression equation given by Salonen et al. (1976). Statistical procedures were the same as referred to in detail by Anger and Dawirs (1981). In regression equations, intercept ($b$) and slope ($m$) are given; in addition, correlation coefficients ($r$) and their level of significance ($P$) for deviation from zero are provided. For logarithmic transformations, ln (= $\log_e$) was applied. All statistical tests were two-tailed.

In May 1979, a first series of 46 analyses comprising 123 individually reared zoea-1 larvae (Z-1) of *Hyas araneus* was carried out to compare their growth patterns with those previously observed by Anger and Nair (1979) in commonly reared zoeae. This set of data showed unsatisfactorily high variation, and high mortality prevented a larger number of analyses. For this reason, in February 1980 another set of 92 analyses comprising 110 prezoeae, 274 Z-1, and 30 early Z-2 was obtained (Table 1). The data for later stages given in Table 2 had been obtained in March and April 1979 (112 samples, 149 individuals).

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

## RESULTS

### Larval Growth

Fresh weight (FW) values fluctuated around constant levels in all larval stages without clear increase in a single stage (Tables 1, 2). This steplike growth pattern did not allow any analysis of actual body growth during larval instars.

The gain in total live weight (FW) from the prezoea to the freshly metamorphosed crab was ca. 770%. It was 640% in DW, and only ca. 470% in C, N, and H. The absolute increase during larval development is shown in Figure 1. During the extremely short, nonfeeding prezoea stage there was no gain in C, N, H, and energy. Molting to the Z-1 resulted in a minor loss of organic constituents (cast cuticle) and in some uptake of water and salt (Table 1; Fig. 1). During the following instars there was an appreciably absolute increase in all parameters considered. It was generally strongest in the second zoeal stage and, surprisingly, weakest in the megalopa.

The values shown in Figure 1 for Z-1, Z-2, and magalopa form a straight line when arranged in a semilogarithmic scale. This indicates that growth from stage to stage followed an exponential pattern during this period.

The different growth patterns in wet weight (steplike) and DW (gradual) were caused by a combination of these two patterns in the water content of the larvae; during each molt, it suddenly increased, and then it gradually decreased during the molt cycle. This decrease could be expressed as a power function in all larval instars: $\ln (\% H_2O) = b + m \ln (t+1)$, where $b$ is approximately the logarithm of the initial water content, $m$ is the slope, and $t$ is the time (days from the beginning of a particular stage). All $r$'s for these fitted curves were significantly different from zero ($P<0.001$). The rate of de-

TABLE 1.—*Hyas araneus* larval growth. Fresh weight (FW), dry weight (DW), water content ($H_2O$), carbon (C), nitrogen (N), hydrogen (H), C:N ratio (C/N, by weight), energy content (Joule, J), number of analyses ($n$), and number of individuals analyzed ($N$). Mean values ±95% confidence intervals.

| | | | Prezoea | Zoea 1 | | | | | | | | | | | | | | Zoea 2 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Time (d): | | 0 | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 0 | 1 |
| FW | | $\bar{x}$ | 338 | 493 | 537 | 536 | 558 | 563 | 575 | 560 | 583 | 604 | 607 | 618 | 594 | 595 | 606 | 1,008 | 1,076 |
| | (μg) | ± | 9 | 10 | 22 | 28 | 10 | 22 | 26 | 27 | 12 | 10 | 21 | 42 | 26 | 17 | — | 48 | 131 |
| DW | | $\bar{x}$ | 57 | 65 | 95 | 108 | 122 | 134 | 142 | 141 | 155 | 153 | 166 | 166 | 174 | 167 | 170 | 168 | 189 |
| | (μg) | ± | 3 | 1 | 4 | 5 | 5 | 4 | 5 | 7 | 2 | 3 | 6 | 6 | 6 | 6 | — | 6 | 10 |
| $H_2O$ | (%) | | 85.6 | 86.8 | 82.4 | 79.8 | 78.1 | 76.1 | 75.2 | 74.8 | 73.5 | 74.7 | 72.8 | 73.2 | 70.7 | 71.9 | 71.9 | 83.3 | 82.4 |
| C | (%) | $\bar{x}$ | 41.9 | 35.1 | 32.2 | 32.0 | 33.2 | 34.0 | 35.8 | 36.7 | 36.7 | 39.3 | 39.0 | 40.4 | 40.5 | 40.4 | 40.0 | 38.7 | 36.1 |
| | | ± | 0.5 | 0.3 | 0.5 | 0.2 | 0.5 | 0.3 | 0.6 | 0.5 | 0.6 | 0.5 | 0.4 | 0.5 | 0.6 | 0.8 | — | 0.8 | 1.0 |
| | (μg) | $\bar{x}$ | 23.9 | 22.9 | 30.5 | 34.6 | 40.6 | 45.9 | 50.9 | 51.8 | 56.8 | 60.1 | 64.6 | 67.1 | 70.5 | 67.5 | 68.1 | 65.1 | 68.1 |
| | | ± | 1.3 | 0.3 | 1.9 | 1.6 | 1.4 | 1.2 | 2.8 | 2.8 | 1.2 | 1.3 | 3.0 | 2.3 | 3.4 | 3.6 | — | 1.2 | 3.6 |
| N | (%) | $\bar{x}$ | 10.6 | 8.1 | 6.7 | 6.4 | 6.5 | 6.4 | 6.7 | 7.0 | 7.2 | 7.6 | 7.6 | 8.1 | 8.3 | 8.3 | 8.3 | 8.3 | 7.6 |
| | | ± | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.2 | 0.1 | 0.1 | 0.3 | 0.2 | 0.2 | 0.1 | 0.1 | 0.2 | — | 0.1 | 0.2 |
| | (μg) | $\bar{x}$ | 6.0 | 5.3 | 6.4 | 6.9 | 8.0 | 8.7 | 9.5 | 9.9 | 11.0 | 11.6 | 12.7 | 13.4 | 14.0 | 14.0 | 14.2 | 13.9 | 14.3 |
| | | ± | 0.3 | 0.1 | 0.4 | 0.3 | 0.2 | 0.3 | 0.4 | 0.4 | 0.5 | 0.1 | 0.6 | 0.6 | 0.5 | 0.7 | — | 0.2 | 0.6 |
| H | (%) | $\bar{x}$ | 6.6 | 5.0 | 4.8 | 4.7 | 4.9 | 5.1 | 5.2 | 5.6 | 5.6 | 5.9 | 5.8 | 6.1 | 6.3 | 6.2 | 6.0 | 6.1 | 5.6 |
| | | ± | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.2 | 0.1 | 0.1 | 0.1 | 0.1 | 0.2 | — | 0.1 | 0.2 |
| | (μg) | $\bar{x}$ | 3.8 | 3.3 | 4.5 | 5.1 | 6.0 | 6.9 | 7.4 | 7.9 | 8.6 | 9.0 | 9.7 | 10.1 | 10.9 | 10.4 | 10.6 | 10.3 | 10.6 |
| | | ± | 0.2 | 0.1 | 0.4 | 0.2 | 0.2 | 0.1 | 0.4 | 0.5 | 0.3 | 0.3 | 0.5 | 0.3 | 0.6 | 0.7 | — | 0.2 | 0.6 |
| C/N | | $\bar{x}$ | 3.9 | 4.3 | 4.8 | 5.0 | 5.1 | 5.3 | 5.3 | 5.2 | 5.2 | 5.2 | 5.1 | 5.0 | 5.0 | 4.9 | 4.8 | 4.7 | 4.8 |
| | | ± | 0.1 | 0.03 | 0.04 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.2 | 0.1 | 0.1 | 0.1 | 0.1 | 0.05 | — | 0.1 | 0.1 |
| J/ind. | | $\bar{x}$ | 0.89 | 0.79 | 1.01 | 1.15 | 1.37 | 1.56 | 1.77 | 1.82 | 1.99 | 2.17 | 2.33 | 2.46 | 2.59 | 2.48 | 2.49 | 2.34 | 2.37 |
| | | ± | 0.05 | 0.01 | 0.06 | 0.05 | 0.05 | 0.04 | 0.11 | 0.10 | 0.05 | 0.05 | 0.12 | 0.08 | 0.11 | 0.15 | — | 0.03 | 0.14 |
| J/mg DW | | $\bar{x}$ | 15.6 | 12.1 | 10.7 | 10.6 | 11.2 | 11.5 | 12.4 | 12.8 | 12.9 | 14.1 | 14.0 | 14.8 | 14.9 | 14.8 | 14.6 | 13.9 | 12.6 |
| | | ± | 0.9 | 0.2 | 0.2 | 0.1 | 0.3 | 0.2 | 0.3 | 0.2 | 0.3 | 0.3 | 0.2 | 0.03 | 0.4 | 0.4 | — | 0.4 | 0.5 |
| $n$ (analyses) | | | 11 | 10 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 1 | 5 | 5 |
| $N$ (individuals) | | | 110 | 50 | 25 | 25 | 25 | 25 | 15 | 15 | 15 | 15 | 15 | 15 | 15 | 15 | 4 | 15 | 15 |

TABLE 2.—*Hyas araneus* larval growth. For explanation of abbreviations see Table 1.

| | | Zoea 2 | | | | | Megalopa | | | | | | | Crab 1 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Time (d): | | 0 | 1 | 4 | 8 | 11 | 0 | 4 | 8 | 12 | 16 | 20 | 24 | 0 | 1 | 2 |
| FW | $\bar{x}$ | 994 | 1,150 | 1,206 | 1,011 | 1,094 | 2,289 | 1,861 | 1,961 | 2,163 | 2,496 | 2,187 | 1,872 | 2,926 | 3,597 | 4,065 |
| (μg) | ± | 36 | 308 | 236 | 108 | 31 | 236 | 97 | 180 | 461 | 395 | 297 | 153 | 330 | 238 | 577 |
| DW | $\bar{x}$ | 144 | 172 | 253 | 280 | 291 | 333 | 428 | 517 | 576 | 656 | 576 | 450 | 424 | 622 | 902 |
| (μg) | ± | 7 | 27 | 25 | 25 | 11 | 55 | 88 | 92 | 170 | 57 | 125 | 62 | 87 | 51 | 135 |
| $H_2O$ (%) | | 87.3 | 86.9 | 82.7 | 78.3 | 79.0 | 87.3 | 81.3 | 79.2 | 79.0 | 79.2 | 79.2 | 80.6 | 87.3 | 85.2 | 77.8 |
| C (%) | $\bar{x}$ | 32.2 | 37.5 | 35.5 | 36.8 | 38.5 | 35.6 | 30.4 | 32.6 | 31.4 | 33.2 | 33.6 | 31.1 | 33.5 | 32.4 | 29.3 |
| | ± | 1.2 | 2.7 | 1.8 | 1.2 | 0.6 | 2.0 | 0.9 | 1.8 | 3.1 | 2.2 | 2.2 | 2.0 | 1.7 | 0.7 | 3.5 |
| (μg) | $\bar{x}$ | 46.3 | 62.8 | 89.7 | 103.3 | 111.9 | 118.9 | 130.5 | 169.8 | 183.6 | 218.3 | 195.0 | 141.2 | 137.3 | 201.1 | 264.5 |
| | ± | 2.1 | 11.2 | 12.3 | 12.1 | 5.5 | 21.9 | 29.9 | 36.5 | 70.8 | 28.9 | 56.1 | 28.5 | 26.4 | 16.1 | 47.7 |
| N (%) | $\bar{x}$ | 8.0 | 8.4 | 7.6 | 8.2 | 8.5 | 8.2 | 6.2 | 7.0 | 7.1 | 7.9 | 7.8 | 7.0 | 8.3 | 7.8 | 6.4 |
| | ± | 0.3 | 0.2 | 0.3 | 0.2 | 0.2 | 0.5 | 0.1 | 0.4 | 0.5 | 0.2 | 0.5 | 0.3 | 0.6 | 0.3 | 1.1 |
| (μg) | $\bar{x}$ | 11.6 | 14.4 | 19.2 | 23.0 | 24.6 | 27.1 | 26.5 | 36.5 | 41.6 | 51.9 | 45.1 | 31.6 | 34.9 | 48.2 | 57.7 |
| | ± | 0.2 | 2.0 | 2.1 | 2.3 | 1.2 | 4.2 | 5.6 | 7.9 | 14.3 | 5.5 | 13.0 | 5.7 | 5.5 | 3.4 | 11.3 |
| H (%) | $\bar{x}$ | 4.8 | 5.7 | 5.2 | 5.5 | 5.7 | 5.3 | 4.6 | 5.0 | 4.8 | 5.2 | 5.2 | 4.9 | 4.9 | 4.9 | 4.3 |
| | ± | 0.2 | 0.2 | 0.3 | 0.2 | 0.1 | 0.4 | 0.1 | 0.4 | 0.5 | 0.2 | 0.4 | 0.4 | 0.3 | 0.2 | 0.6 |
| (μg) | $\bar{x}$ | 6.9 | 9.8 | 13.2 | 15.5 | 16.7 | 17.8 | 19.9 | 26.0 | 28.0 | 34.0 | 30.4 | 22.1 | 20.8 | 30.2 | 39.1 |
| | ± | 0.4 | 1.5 | 1.9 | 2.1 | 1.0 | 3.4 | 4.6 | 6.3 | 10.6 | 4.2 | 8.9 | 4.5 | 4.0 | 2.3 | 7.3 |
| C/N | $\bar{x}$ | 4.0 | 4.4 | 4.6 | 4.5 | 4.5 | 4.4 | 4.9 | 4.6 | 4.4 | 4.2 | 4.3 | 4.4 | 3.9 | 4.2 | 4.6 |
| | ± | 0.1 | 0.2 | 0.1 | 0.2 | 0.1 | 0.2 | 0.2 | 0.2 | 0.2 | 0.2 | 0.1 | 0.1 | 0.2 | 0.1 | 0.3 |
| J/ind. | $\bar{x}$ | 1.54 | 2.20 | 3.11 | 3.64 | 4.02 | 4.14 | 4.25 | 5.70 | 6.09 | 7.37 | 6.63 | 4.66 | 4.58 | 6.71 | 8.49 |
| | ± | 0.08 | 0.42 | 0.47 | 0.48 | 0.22 | 0.81 | 1.02 | 1.31 | 2.58 | 1.15 | 2.10 | 1.06 | 0.88 | 0.54 | 1.77 |
| J/mg DW | $\bar{x}$ | 10.7 | 12.8 | 12.1 | 13.0 | 13.8 | 12.4 | 9.9 | 10.9 | 10.4 | 11.2 | 11.4 | 10.3 | 10.9 | 10.8 | 9.4 |
| | ± | 0.6 | 1.5 | 0.8 | 0.6 | 0.3 | 1.0 | 0.4 | 0.8 | 1.5 | 1.1 | 1.1 | 0.9 | 0.7 | 0.4 | 1.6 |
| *n* (analyses) | | 10 | 3 | 11 | 8 | 14 | 9 | 5 | 7 | 5 | 5 | 5 | 7 | 6 | 13 | 4 |
| *N* (individuals) | | 41 | 9 | 11 | 8 | 14 | 9 | 5 | 7 | 5 | 5 | 5 | 7 | 6 | 13 | 4 |

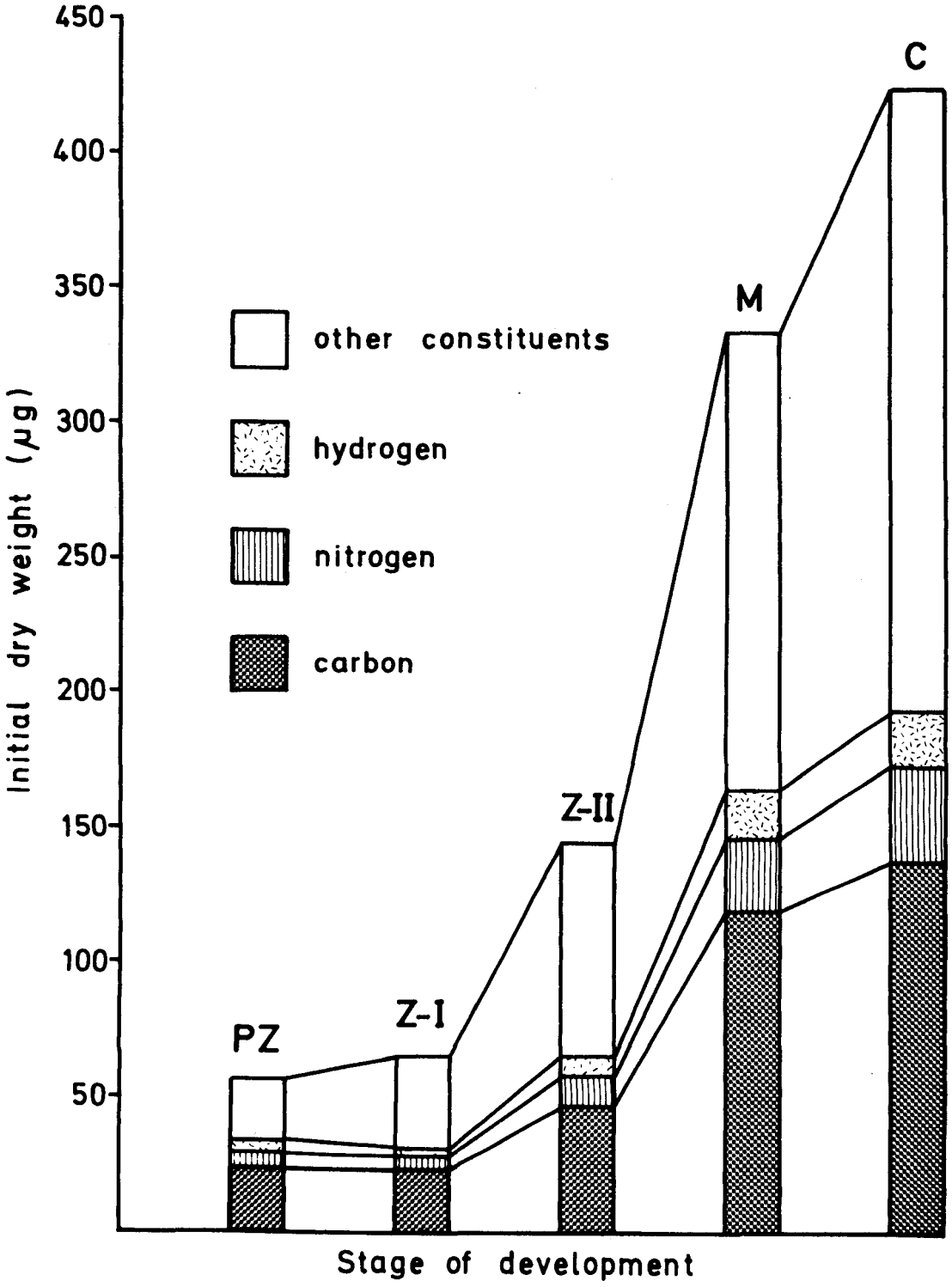


FIGURE 1.—*Hyas araneus*. Initial dry weight, carbon, nitrogen, and hydrogen content in the prezoea (PZ), zoeal stages (Z-I, Z-II), megalopa (M), and first crab stage (C).

crease gradually declined during larval development (Tables 1, 2). This trend was reflected by decreasing $m$ of fitted regression curves: −0.074 in the Z-1, −0.045 in the Z-2, and −0.031 in the megalopa. In Figure 2 only the first regression (Z-1) is shown as the most accurately measured example (the curve for starved zoeae given in the same graph will be discussed below).

Growth in zoeal stages can also be described as a power function of $t$: $\ln y = b + m \ln (t+1)$, where $y$ is any measure of biomass except FW (DW, C, N, H, J). The $b$ values were almost identical with the logarithms of the initial biomass measure under consideration, the $m$ values varied between 0.29 and 0.48 (Table 3).

The fitted curves describe the actual growth patterns until late premolt was reached. In this very advanced period in the Z-1 stage (days 12 and 13), growth ceased or even switched to a slight loss. These last values were not included in the Z-1 regressions. The fitted growth curves were converted to percentage values of early postmolt levels, so that direct comparison of relative increase rates became possible (Fig. 3; Z-1 curves for 1980 values only).

In zoeae the individual energy content (J) revealed the strongest increment, DW the weakest. The rate of increase in N was similar to that in DW, whereas C and H increased at a higher rate during individual growth (Table 3). A comparison of the biomass values in first zoeae obtained in two different seasons and years shows that the 1979 larvae were not only less viable (see above), but also showed lower initial biomass (reflected by lower $b$ values in all regression equations describing growth) and lower growth rates (reflected by $m$ values), especially in C, H, and J.

TABLE 3.—Parameters of regression equations for individual growth in larval stages of *Hyas araneus*: $\ln y = b + m \cdot \ln (t+1)$. $t$ = time (d); $r$ = correlation coefficient; df = degrees of freedom; dry weight (DW), carbon (C), nitrogen (N), hydrogen (H) in μg, and energy contents (J).

| Stage | $y$ | $b$ | $m$ | $r$ | df |
|---|---|---|---|---|---|
| Zoea I[1] | DW | 4.164 | 0.300 | 0.924 | 44 |
| Zoea I | DW | 4.228 | 0.385 | 0.989 | 64 |
| Zoea I[1] | C | 2.918 | 0.370 | 0.873 | 44 |
| Zoea I | C | 3.107 | 0.451 | 0.994 | 64 |
| Zoea I[1] | N | 1.495 | 0.331 | 0.839 | 44 |
| Zoea I | N | 1.604 | 0.384 | 0.979 | 60 |
| Zoea I[1] | H | 1.016 | 0.354 | 0.833 | 44 |
| Zoea I | H | 1.164 | 0.475 | 0.994 | 62 |
| Zoea I[1] | J | −0.511 | 0.377 | 0.870 | 44 |
| Zoea I | J | −0.292 | 0.479 | 0.990 | 64 |
| Zoea II | DW | 4.986 | 0.290 | 0.938 | 44 |
| Zoea II | C | 3.858 | 0.354 | 0.934 | 44 |
| Zoea II | N | 2.449 | 0.305 | 0.938 | 44 |
| Zoea II | H | 1.961 | 0.350 | 0.925 | 44 |
| Zoea II | J | 0.457 | 0.381 | 0.927 | 44 |

[1]1979 observation (all others from 1980).

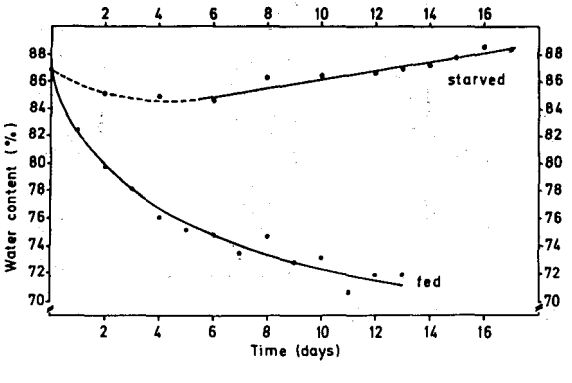


FIGURE 2.—*Hyas araneus*. Water content (% fresh weight) in Z-1 larvae fed and starved for different lengths of time.

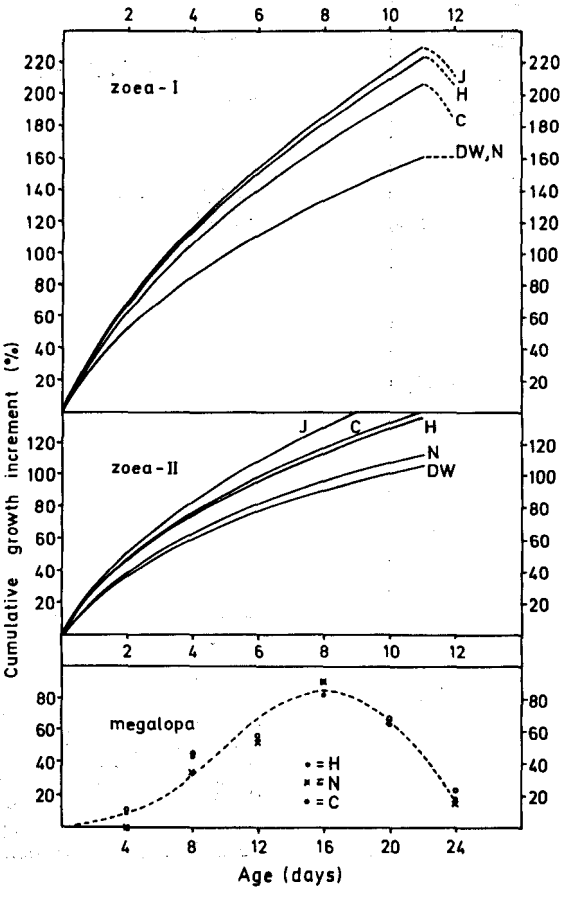


FIGURE 3.—*Hyas araneus*. Growth patterns [dry weight (DW), energy contents (J), carbon (C), nitrogen (N), and hydrogen (H) per individual] in all larval stages expressed as percentage of early postmolt levels. Solid curves: fitted by equations (see text); dotted curves: fitted by eye.

However, due to high variation among the 1979 samples, these differences were not statistically significant.

In May 1979, eight Z-2 of *H. araneus* were isolated from a plankton sample and analyzed for comparison. The results (Table 4) compared favorably with those of late laboratory-reared Z-2 larvae (Table 2), although C and H values were slightly higher in the field-caught larvae.

It becomes obvious from Figure 3 (lower graph) that growth in the megalopa was quite different from that in the zoeal stages. Since variation among analyses (see Table 2) was rather high, calculation of fitted growth curves was not considered useful and, therefore, only the assumed pattern was displayed in the diagram as an eye-fitted curve. A surprising decrease in all parameters was found during the last third of the megalopa stage. As a result, young crabs contained only little more organic substances than young megalopae (Fig. 1).

From the above results, approximate average daily energy gains per individual (J/d per ind.) can be calculated. In the 1979 Z-1 larvae a value of 0.08 was estimated. This compares favorably with the data reported by Anger and Nair (1979). They found 0.06 (their figures −0.4 and 0.6 on page 51 are erroneous; they should read −0.04 and 0.06), based on C contents, and 0.07 to 0.11, based on biochemical composition (excluding and including chitin, respectively). Since the 1980 larvae grew better (see above), their daily energy gain was higher: 0.16 J/d per ind. In the second zoeal stage a value of 0.22 was found (Fig. 1). In the megalopa it was similar (0.20) until day 16, when it dropped to −0.34 until metamorphosis; on the average, a weak gain (0.02 J/d per ind.) resulted.

TABLE 4.—Ranges and arithmetic means ($\bar{x}$) for *Hyas araneus* zoea-2 from Helgoland plankton in May 1979. Four analyses comprising eight individuals. For explanation of abbreviations see Table 1.

| | | Range | $\bar{x}$ |
|---|---|---|---|
| FW | (µg) | 1,162-1,292 | 1,220 |
| DW | (µg) | 304-346 | 322 |
| $H_2O$ | (%) | 72.6-74.4 | 73.6 |
| C | (%) | 35.0-36.9 | 35.7 |
| | (µg) | 106.7-127.4 | 115.2 |
| N | (%) | 7.60-7.73 | 7.67 |
| | (µg) | 23.1-26.7 | 24.7 |
| H | (%) | 5.23-5.51 | 5.36 |
| | (µg) | 15.9-19.0 | 17.3 |
| C/N | | 4.53-4.77 | 4.66 |
| J/ind. | | 3.67-4.49 | 4.00 |
| J/mg DW | | 12.1-13.0 | 12.4 |

The weight-specific energy content (J/mg DW) followed a cyclic pattern (Fig. 4). Due to salt uptake, it decreased during molt, and then it increased again during growth. From instar to instar there was a conspicuous decreasing trend. It was related to a decrease in the percentage of organic substances, expressed as maximum sum of the C, N, and H portions (upper part of Fig. 4).

The ratio between single elements can be used as an index for biochemical composition. Changes in the C:N ratio mainly indicate shifts in the relative amounts of lipids (plus carbohydrates) and proteins (plus free amino acids) (Fig. 5). There were no major differences found during the molt cycles. In all larval stages there was an initial increase, followed by a decline.

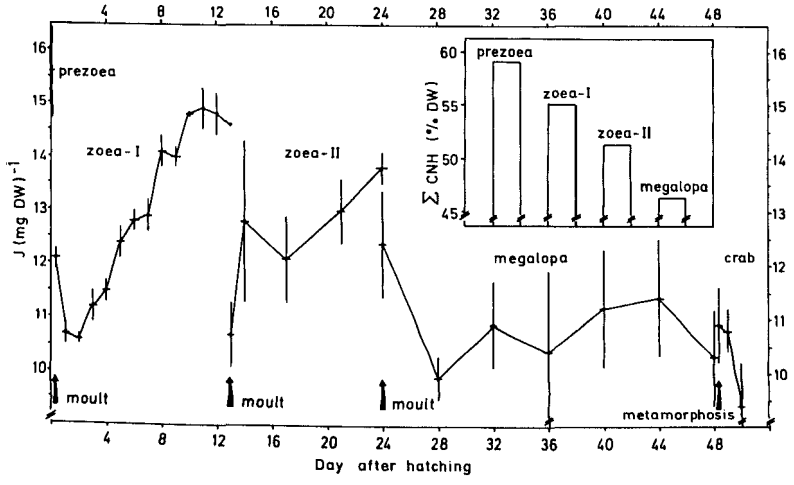


FIGURE 4.—*Hyas araneus*. Changes in weight-specific energy during larval development; vertical lines: 95% confidence intervals of the means. Upper right: Maximum sum of carbon (C), nitrogen (N), and hydrogen (H) in all larval stages.

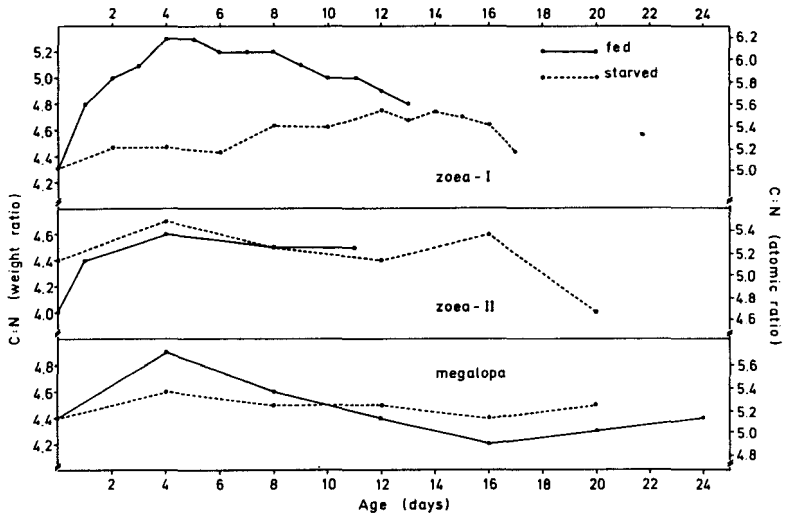


FIGURE 5.—*Hyas araneus*. C:N (carbon:nitrogen) ratio in larvae fed and starved for different lengths of time.

Certainly the buildup of the chitin cuticle, and perhaps also the disproportionately strong storage of lipids, contributed to the increase. The subsequent decrease in the C:N ratio suggests that more proteins than other organic constituents were accumlated later. This trend was best visible in the Z-1 and megalopa stages; in the latter it was followed by a new increase beginning on day 16. This period was identical with that of decreasing biomass (Fig. 3). The curves given in Figure 5 for starved larvae will be discussed below.

The C:H ratio remained fairly constant within stages, and it did not differ much among larval instars. The mean values and 95% confidence intervals (weight-based) were 6.67±0.08 in the Z-1 (1980), 6.64±0.26 in the Z-2, and 6.49±0.11 in the megalopa. In field-caught Z-2 larvae and in young crabs mean ratios of 6.66 and 6.67 were found. The ratios in the Z-1 and megalopa stages were statistically different from each other ($P<0.01$). There was also a significant difference ($P = 0.002$) between the figures in the Z-1 from 1979 (6.86±0.09) and from 1980 (see above).

The growth patterns described in Figure 3 do not consider losses due to shedding of exuviae. In order to determine the approximate amount of organic substances cast during molts, occasional analyses of exuviae were carried out (Table 5). Wet weight and DW measurements did not provide useful results, because the amount of water and salt inside the cast could not be accurately determined. The composition of the exuviae corresponded closely to that of its main component, chitin. Deviations from the theoretical atomic ratio C:N:H = 9:1:14 can partly be explained by analytical inaccuracies (see 95% confidence limits in the megalopa), partly by other biochemical components of exuviae, or by slight chemical changes before sampling and analyzing the casts (partial decomposition).

The amount of organic matter lost during zoeal molts was far lower than during metamorphosis to the crab: 4 to 5% versus 19% in N, 6 to 9% versus 29% in both C and H (Table 5). Assuming an energy content of ca. 18 J/mg dry organic exuvial matter (after Winberg 1971, somewhat corrected for protein compounds) and a C content of ca. 45% (according to the molecular formula of chitin), then the energy losses should be ca. 0.23 J in the Z-1, 0.29 in the Z-2, and 1.61 in the megalopa. These estimates correspond to ca. 9, 7, and 34% of total body energy levels in late premolt in these stages. Compared with average daily energy fixation rates (see above), these figures mean losses of ca. 1.3 to 1.4 d in the zoeal stages, and ca. 8 d in the megalopa.

Preliminary experiments were carried out to

TABLE 5.—Composition [carbon (C), nitrogen (N), hydrogen (H)] of larval exuviae of *Hyas araneus* and percentage of premolt matter cast at ecdysis. $n$ = number of analyses, $N$ = number of exuviae analyzed.

| | C (µg) | N (µg) | H (µg) | Weight ratio | Atomic ratio | $n$ | $N$ |
|---|---|---|---|---|---|---|---|
| Zoea-I | 5.85 | 0.67 | 0.92 | 8.7:1:1.4 | 10:1:19 | 1 | 15 |
| % cast | 9 | 5 | 9 | | | | |
| Zoea-II | 7.20 | 1.10 | 1.10 | 6.6:1:1 | 8:1:14 | 1 | 10 |
| % cast | 6 | 4 | 7 | | | | |
| Megalopa $\bar{x}$ | 40.56 | 5.46 | 6.39 | 7.5:1:1.2 | 9:1:16 | 7 | 7 |
| ± | 4.07 | 0.62 | 0.56 | | | | |
| % cast | 29 | 17 | 29 | | | | |

determine food consumption in the Z-1 stage using *Artemia salina* nauplii as prey. The average values found were near 20 μg C/d per ind. or 0.8 to 0.9 J/d. Gross growth efficiency therefore should be about 10 to 20%. The amount taken up by the larvae (3 d old) corresponded to ca. 55% of their own body C and to ca. 36% of their own DW. In light of the experimental conditions, we consider this near the maximum level.

## Loss of Biomass During Starvation

FW of starving larvae did not show significant changes (Tables 6 to 8). Also water content could not always be measured with sufficient accuracy to detect clear trends. In the Z-1 and in the megalopa, first a slight decrease and later a conspicuous increase of water content occurred. The latter trend was linear in the Z-1 (Fig. 2); it could

TABLE 6.—*Hyas araneus* losses in starved Z-1 larvae. For explanation of abbreviations see Table 1.

| Time (d): | | 0 | 2 | 4 | 6 | 8 | 10 | 12 | 13 | 14 | 15 | 16 | 17 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| FW | $\bar{x}$ | 493 | 538 | 522 | 501 | 534 | 533 | 532 | 557 | 547 | 577 | 584 | 589 |
| (μg) | ± | 10 | 16 | 27 | 20 | 16 | 29 | 38 | 14 | 28 | 52 | 35 | 39 |
| DW | $\bar{x}$ | 65 | 80 | 79 | 77 | 74 | 73 | 71 | 73 | 70 | 70 | 66 | 68 |
| (μg) | ± | 1 | 2 | 3 | 3 | 3 | 2 | 2 | 3 | 1 | 2 | 1 | 4 |
| $H_2O$ (%) | | 86.8 | 85.1 | 84.9 | 84.6 | 86.2 | 86.4 | 86.6 | 86.9 | 87.2 | 87.8 | 88.6 | 88.4 |
| C (%) | $\bar{x}$ | 35.1 | 27.5 | 25.8 | 24.7 | 24.6 | 23.2 | 22.8 | 22.0 | 22.2 | 21.7 | 22.1 | 21.4 |
| | ± | 0.3 | 0.4 | 0.3 | 0.2 | 0.3 | 0.4 | 0.6 | 0.3 | 0.3 | 0.4 | 0.3 | 1.0 |
| (μg) | $\bar{x}$ | 22.9 | 21.9 | 20.4 | 19.0 | 18.2 | 16.8 | 16.2 | 16.1 | 15.6 | 15.3 | 14.6 | 14.6 |
| | ± | 0.3 | 0.2 | 0.7 | 0.7 | 0.8 | 0.5 | 0.8 | 0.8 | 0.2 | 0.5 | 0.4 | 0.7 |
| N (%) | $\bar{x}$ | 8.1 | 6.2 | 5.8 | 5.57 | 5.3 | 5.0 | 4.8 | 4.72 | 4.7 | 4.6 | 4.8 | 4.8 |
| | ± | 0.1 | 0.1 | 0.1 | 0.04 | 0.2 | 0.2 | 0.2 | 0.05 | 0.1 | 0.1 | 0.1 | 0.2 |
| (μg) | $\bar{x}$ | 5.3 | 4.91 | 4.6 | 4.3 | 3.9 | 3.6 | 3.4 | 3.4 | 3.30 | 3.26 | 3.16 | 3.3 |
| | ± | 0.1 | 0.04 | 0.1 | 0.2 | 0.2 | 0.1 | 0.2 | 0.1 | 0.06 | 0.07 | 0.03 | 0.1 |
| H (%) | $\bar{x}$ | 5.0 | 3.82 | 3.55 | 3.60 | 3.33 | 3.27 | 3.15 | 3.11 | 3.17 | 3.3 | 3.2 | 3.0 |
| | ± | 0.1 | 0.05 | 0.05 | 0.04 | 0.04 | 0.07 | 0.11 | 0.06 | 0.02 | 0.3 | 0.1 | 0.4 |
| (μg) | $\bar{x}$ | 3.3 | 3.05 | 2.8 | 2.8 | 2.5 | 2.4 | 2.2 | 2.3 | 2.23 | 2.2 | 2.1 | 2.1 |
| | ± | 0.1 | 0.02 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.02 | 0.1 | 0.1 | 0.1 |
| C/N | $\bar{x}$ | 4.31 | 4.47 | 4.47 | 4.43 | 4.63 | 4.62 | 4.75 | 4.67 | 4.74 | 4.70 | 4.64 | 4.43 |
| | ± | 0.03 | 0.04 | 0.04 | 0.06 | 0.12 | 0.10 | 0.11 | 0.09 | 0.07 | 0.05 | 0.11 | 0.05 |
| J/ind. | $\bar{x}$ | 0.79 | 0.69 | 0.62 | 0.57 | 0.55 | 0.50 | 0.48 | 0.47 | 0.45 | 0.44 | 0.42 | 0.42 |
| | ± | 0.01 | 0.01 | 0.02 | 0.02 | 0.02 | 0.01 | 0.02 | 0.02 | 0.01 | 0.02 | 0.01 | 0.02 |
| J/mg DW | $\bar{x}$ | 12.1 | 8.6 | 7.9 | 7.4 | 7.4 | 6.8 | 6.7 | 6.4 | 6.5 | 6.3 | 6.4 | 6.1 |
| | ± | 0.2 | 0.3 | 0.1 | 0.1 | 0.1 | 0.2 | 0.2 | 0.1 | 0.1 | 0.1 | 0.1 | 0.4 |
| *n* (analyses) | | 10 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 3 |
| *N* (individuals) | | 50 | 25 | 25 | 25 | 25 | 25 | 25 | 25 | 25 | 25 | 25 | 13 |

TABLE 7.—*Hyas araneus* losses in starved Z-2 larvae. For explanation of abbrevations see Table 1.

| Time (d): | | 0 | 4 | [1]4 | 8 | [1]8 | 12 | [1]12 | 16 | 20 |
|---|---|---|---|---|---|---|---|---|---|---|
| FW | $\bar{x}$ | 1,150 | 2,422 | 1,219 | 1,184 | 1,176 | 1,034 | 1,022 | 929 | 1,240 |
| (μg) | ± | 308 | 349 | 68 | 102 | 67 | 144 | — | 263 | 474 |
| DW | $\bar{x}$ | 172 | 174 | 195 | 145 | 170 | 154 | 172 | 153 | 131 |
| (μg) | ± | 28 | 14 | 15 | 17 | 24 | 12 | — | 17 | 14 |
| $H_2O$ (%) | | 85.0 | 92.8 | 84.0 | 87.8 | 85.5 | 85.1 | 83.2 | 83.5 | 89.4 |
| C (%) | $\bar{x}$ | 36.5 | 29.9 | 30.4 | 28.2 | 27.2 | 26.7 | 26.6 | 25.5 | 22.2 |
| | ± | 2.7 | 1.2 | 1.9 | 1.4 | 1.7 | 2.2 | — | 1.4 | 2.1 |
| (μg) | $\bar{x}$ | 62.8 | 52.1 | 59.6 | 40.8 | 46.5 | 41.1 | 45.6 | 39.0 | 29.0 |
| | ± | 11.2 | 6.0 | 8.1 | 5.6 | 9.0 | 5.6 | — | 5.9 | 5.4 |
| N (%) | $\bar{x}$ | 8.4 | 6.4 | 7.0 | 6.3 | 6.4 | 6.1 | 6.3 | 5.6 | 5.5 |
| | ± | 0.3 | 0.3 | 0.7 | 0.8 | 0.3 | 0.1 | — | 0.3 | 0.4 |
| (μg) | $\bar{x}$ | 14.4 | 11.1 | 13.5 | 9.1 | 10.9 | 9.7 | 10.9 | 8.6 | 7.2 |
| | ± | 1.9 | 1.3 | 2.2 | 1.9 | 1.9 | 0.9 | — | 0.9 | 1.3 |
| H (%) | $\bar{x}$ | 5.7 | 4.3 | 4.2 | 3.9 | 3.7 | 3.8 | 3.8 | 3.7 | 3.1 |
| | ± | 0.3 | 0.2 | 0.4 | 0.4 | 0.3 | 0.4 | — | 0.2 | 0.4 |
| (μg) | $\bar{x}$ | 9.8 | 7.5 | 8.2 | 5.6 | 6.3 | 6.2 | 6.5 | 5.6 | 4.1 |
| | ± | 1.6 | 0.8 | 1.3 | 1.0 | 1.3 | 0.8 | — | 0.8 | 0.9 |
| C/N | $\bar{x}$ | 4.4 | 4.7 | 4.4 | 4.5 | 4.3 | 4.4 | 4.2 | 4.6 | 4.0 |
| | ± | 0.3 | 0.1 | 0.3 | 0.5 | 0.3 | 0.4 | — | 0.3 | 0.1 |
| J/ind. | $\bar{x}$ | 2.2 | 1.7 | 1.9 | 1.3 | 1.4 | 1.3 | 1.4 | 1.2 | 0.8 |
| | ± | 0.4 | 0.2 | 0.3 | 0.2 | 0.3 | 0.2 | — | 0.2 | 0.2 |
| J/mg DW | $\bar{x}$ | 12.8 | 9.6 | 9.9 | 8.9 | 8.5 | 8.2 | 8.2 | 7.8 | 6.4 |
| | ± | 1.0 | 0.6 | 0.9 | 0.6 | 0.7 | 1.0 | — | 0.6 | 0.8 |
| *n* (analyses) | | 3 | 5 | 5 | 5 | 5 | 5 | 2 | 5 | 5 |

[1]Analyses of group maintained larvae.

TABLE 8.—*Hyas araneus* losses in starved megalopa larvae. For explanation of abbreviations see Table 1.

| | Time (d): | | 0 | 4 | 8 | 12 | 16 | 20 |
|---|---|---|---|---|---|---|---|---|
| FW | | $\bar{x}$ | 2,289 | 2,131 | 1,963 | 2,200 | 2,275 | 2,370 |
| | (μg) | ± | 236 | 192 | 268 | 280 | 158 | 406 |
| DW | | $\bar{x}$ | 333 | 327 | 309 | 358 | 304 | 281 |
| | (μg) | ± | 55 | 55 | 74 | 103 | 96 | 106 |
| $H_2O$ | (%) | | 85.4 | 84.7 | 84.3 | 83.7 | 86.6 | 88.2 |
| C | (%) | $\bar{x}$ | 35.6 | 25.8 | 23.3 | 23.1 | 23.0 | 22.8 |
| | | ± | 2.0 | 0.6 | 1.0 | 1.2 | 1.6 | 1.1 |
| | (μg) | $\bar{x}$ | 118.9 | 84.7 | 72.2 | 83.1 | 70.5 | 64.0 |
| | | ± | 21.9 | 16.3 | 17.9 | 27.7 | 26.8 | 26.7 |
| N | (%) | $\bar{x}$ | 8.2 | 5.6 | 5.1 | 5.1 | 5.2 | 5.1 |
| | | ± | 0.5 | 0.3 | 0.3 | 0.1 | 0.3 | 0.3 |
| | (μg) | $\bar{x}$ | 27.1 | 18.4 | 15.9 | 18.4 | 15.9 | 14.2 |
| | | ± | 4.2 | 3.6 | 3.8 | 5.6 | 5.2 | 4.6 |
| H | (%) | $x$ | 5.3 | 3.7 | 3.4 | 3.5 | 3.3 | 3.5 |
| | | ± | 0.4 | 0.2 | 0.2 | 0.3 | 0.2 | 0.3 |
| | (μg) | $\bar{x}$ | 17.8 | 12.0 | 10.5 | 12.6 | 10.2 | 9.8 |
| | | ± | 3.4 | 2.5 | 2.7 | 4.5 | 3.7 | 4.7 |
| C/N | | $\bar{x}$ | 4.4 | 4.6 | 4.5 | 4.5 | 4.4 | 4.5 |
| | | ± | 0.2 | 0.2 | 0.1 | 0.2 | 0.3 | 0.5 |
| J/ind. | | $\bar{x}$ | 4.1 | 2.6 | 2.1 | 2.4 | 2.1 | 1.9 |
| | | ± | 0.8 | 0.5 | 0.5 | 0.9 | 0.8 | 0.8 |
| J/mg DW | | $\bar{x}$ | 12.4 | 7.9 | 6.9 | 6.8 | 6.8 | 6.7 |
| | | ± | 1.0 | 0.3 | 0.4 | 0.5 | 0.6 | 0.4 |
| *n* (analyses) | | | 9 | 5 | 5 | 5 | 5 | 3 |

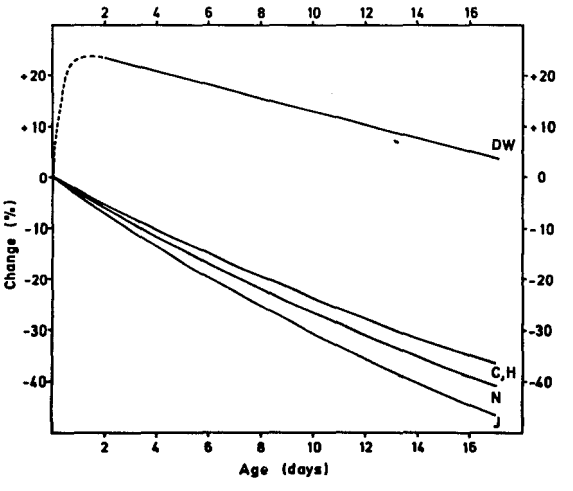


FIGURE 6.—*Hyas araneus*. Loss patterns [dry weight (DW), energy content (J), carbon (C), nitrogen (N), and hydrogen (H) per individual] in starved Z-1 larvae. Solid lines: fitted by equations (see text); dotted curve: fitted by eye.

be expressed by the statistically significant regression equation: $\%H_2O = 83 + 0.32\ t$ ($r = 0.959$; $P<10^{-4}$), where $t$ = time (days from hatching). This effect was visible by eye: larvae, which had starved for a long time, acquired an increasingly bloated appearance like those exposed to a hypotonic medium.

DW tended to decrease during starvation, but due mostly to high variation among parallel determinations, only in the Z-1 stage could a statistically significant trend be found between days 2 and 17 (Fig. 6): DW (μg) $= 82 - 0.85\ t$ ($r = 0.966$; $P<10^{-5}$).

The decreases in C, N, H, and J during $t$ followed an exponential pattern: $\ln y = b + mt$, where $y$ is any measure for biomass (C, N, H in μg) or energy (J). To allow direct comparison, fitted curves were again converted to percentage values and shown in Figure 6 (only Z-1 stage as an example). For the other stages similar curves were obtained (Table 9). The slope parameters (= regression coefficients, $m$, in the log-transformed equations) were not statistically significantly different from each other. The $b$ values were very close to the logarithms of the initial figures for biomass.

In all three larval instars the energy content (J/ind.) dropped more drastically than C, N, and H contents (Table 9). In the Z-1 there was also a slightly stronger decline in N as compared with C and H (Fig. 6). The maximal losses observed shortly before starvation death of the larvae

TABLE 9.—Parameters of regression equations for loss of individual biomass in starved larval stages of *Hyas araneus*: $\ln y = b + mt$; $t$ = time (d). For further explanation see Table 3.

| Stage | *y* | *b* | *m* | *r* | df |
|---|---|---|---|---|---|
| Zoea I | C | 3.127 | −0.028 | −0.986 | 61 |
| Zoea I | N | 1.653 | −0.032 | −0.984 | 61 |
| Zoea I | H | 1.167 | −0.027 | −0.972 | 61 |
| Zoea I | J | −0.285 | −0.037 | −0.981 | 61 |
| Zoea II | C | 4.082 | −0.033 | −0.868 | 25 |
| Zoea II | N | 2.548 | −0.029 | −0.836 | 25 |
| Zoea II | H | 2.166 | −0.036 | −0.843 | 25 |
| Zoea II | J | 0.698 | −0.041 | −0.886 | 25 |
| Megalopa | C | 4.663 | −0.028 | −0.634 | 32 |
| Megalopa | N | 3.181 | −0.030 | −0.673 | 32 |
| Megalopa | H | 2.748 | −0.029 | −0.608 | 32 |
| Megalopa | J | 1.268 | −0.038 | −0.698 | 32 |

were ca. 36 to 46% in the Z-1, 45 to 58% in the Z-2, and 43 to 51% in the megalopa.

The average daily energy loss per individual increased from the first to the last larval stage. If converted to weight-specific figures, a weak opposite trend became visible. This means that increasing reserves became available during the progress of development, and weight-specific metabolism tended to decrease somewhat. However, the above average values are only rough estimates, since the loss patterns are nonlinear (see above), but they do reflect general differences among stages (Table 10).

The decrease pattern in weight-specific energy contents of starved larvae (within stages) followed a hyperbola: $\ln$ J/mg DW $= b + m \ln(t + 1)$, where $t$ = time (days), $b$ is close to the logarithm of the initial value, and $m$ is the slope.

TABLE 10.—Average daily energy loss in starved larval stages of *Hyas araneus* (estimated from carbon-hydrogen-nitrogen values). J = energy contents; DW = dry weight.

| Stage | J/d per ind. | J/d per mg DW |
|---|---|---|
| Zoea I | 0.02 | 0.35 |
| Zoea II | 0.07 | 0.32 |
| Megalopa | 0.11 | 0.28 |

The *b* values of the fitted curves were ca. 2.5, the *m*'s were −0.20 (Z-2) to −0.23 (Z-1); and the *r*'s varied between −0.964 ($P<0.002$; Z-2) and −0.992 ($P<10^{-10}$; Z-1).

Using the conversion factor 20.19 J/ml $O_2$ given by Brody (1945), approximate figures for oxygen consumption could be estimated from the energy values in Tables 6 to 8. In all stages there was apparently a drastic reduction in respiration rate during the first few days of starvation (Table 11). For comparison of the stages, again average values were computed (from values in Table 10). Corresponding to the weight-specific energy values (see above), from which they were derived, a weak decreasing trend became apparent (Table 11).

The C:N ratio (Fig. 5) did not follow a uniform pattern in starved larvae. In the Z-1 stage a long period of gradual increase was followed by a short period of rapid decrease. This suggests that protein was catabolized at a higher rate than other constituents during most of the starvation period; only in the premortal phase, were N-poor substances (most probably lipids) apparently used as the main energy source. In the Z-2 and in the megalopa variation was too high to discern clear trends. In the former instar the C:N ratio also showed a drop at the end suggesting some similarity with the Z-1, whereas in the latter stage apparently it did not change at all.

The C:H ratio was practically constant in all larval instars. It was in most cases significantly lower in fed than in starved larvae. The mean values and 95% confidence intervals (by weight) were 6.67±0.08 versus 7.07±0.012 in the Z-1 ($P<10^{-5}$), 6.64±0.26 versus 6.98±0.30 in the Z-2 (not significant), and 6.49±0.11 versus 6.80±0.28 in the megalopa ($P=0.014$). There was a similar statistically significant difference ($P = 0.002$) between the C:H ratios found in Z-1 larvae in May 1979 (6.86±0.09) and in February 1980 (6.67±0.08).

TABLE 11.—Weight-specific respiration rates (µl $O_2$/h per mg dry weight) in relation to the time of starvation of *Hyas araneus*.

| Stage | Days of starvation | | | | |
|---|---|---|---|---|---|
| | 2 | 4 | 8 | >8 | $\bar{x}$[1] |
| Zoea I | 3.6 | 0.7 | 0.3 | | 0.73 |
| Zoea II | | 1.6 | 0.4 | | 0.66 |
| Megalopa | | 2.3 | 0.5 | 0.2 | 0.59 |

[1]Computed from Table 10 data.

## DISCUSSION

Larval growth has been measured and described in a number of different ways. Increments in zoeal body size obey the general rules summarized by Rice (1968), who calculated an average growth factor of 1.29 for brachyurans. From the figures given by Christiansen (1973) for *H. araneus*, factors of 1.26 to 1.30 can be derived, depending on the distance measured. A factor of 1.3 is also obtained, if size is assumed to be proportional to the cube root of DW. As pointed out by Rice (1968), the megalopa can hardly be included in those considerations because of its different shape.

It is generally accepted that FW is a poor measure of actual biomass. Its determination is inaccurate and thus yields highly variable results. Moreover, it does not change in an orderly manner during the molt cycle and therefore, it must be regarded as insensitive to changes in organic matter. This is caused by changes in the water content. It is difficult to understand why a number of authors described biochemical and physiological changes in developing crustacean larvae on a wet weight basis, and so severely reduced the value of their information. We suggest that FW or Formalin wet weight never be used as a reference base in such studies, but only as a source of additional information (e.g., for water content of tissues).

DW is a far better measure of biomass, although it is influenced by inorganic salts. Unfortunately, different drying methods (temperatures and times) are used by different investigators. Ash-free DW should improve the accuracy in physiological studies, if used as a basic unit. However, again drying and combustion temperatures and times are not uniformly applied.

Elemental composition, especially C content, can be used as a reliable expression of living organic substance. Inorganic C does not play a signficant role in marine planktonic organisms (Curl 1962) and therefore C is also a measure of energy equivalents (Salonen et al. 1976). C-based energy estimations apparently tend to be somewhat lower than those calculated from bio-

chemical composition (Anger and Nair 1979); comparison of both methods with direct calorimetry in identical material should be worthwhile. However, the J values given in this paper compare favorably with those reported elsewhere for decapod larvae (e.g., Cummins and Wuycheck 1971; Mootz and Epifanio 1974; Logan and Epifanio 1978; Capuzzo and Lancaster 1979; Dawirs 1980; Stephenson and Knight 1980).

The interpretation of changes in the relative chemical composition of larvae (C:N, C:H) leads to interesting assumptions about physiological processes, but there is a need for complementary biochemical investigations. Such analyses are planned for future studies as an extension of the present results. So far, our figures compare favorably with those given in the literature (Childress and Nygaard 1974; Ikeda 1974; Omori 1979; Dawirs 1980). Ikeda (1974) investigated a large number of zooplankton species, and he found that C:N (by weight) is in most cases 3 to 5, whereas C:H is mostly 6 to 7.

Growth (any measure except size and FW) during larval development in decapod crustacea usually follows—at least for some period—an exponential pattern, if gain from stage to stage is considered (Reeve 1969; Mootz and Epifanio 1974; Logan and Epifanio 1978; Johns and Pechenik 1980; Stephenson and Knight 1980). This also holds true for the zoeal stages of *Hyas araneus*. Interpolation of biomass values within single stages from such exponential curves yields poor correspondence of predicted and observed data, because growth within stages follows different patterns. In both zoeae it could be described most accurately by power functions, whereas exponential regressions do not fit as well. At the end of the molt cycle, however, such parabola-shaped fitted growth curves lose their applicability. This final period probably corresponds to the stages $D_2$ to $D_4$, during which molt is prepared by separating the epidermis from the old cuticle (Freeman and Costlow 1980). Possibly, there is no more significant food uptake during this phase of body reconstruction (Anger and Dawirs 1981).

In the megalopa, another growth pattern was found. The period of body reconstruction and of presumed inability to take up food preceding metamorphosis appears to be much longer in this stage. The daily energy loss per individual was three times higher during this time as opposed to megalopae starved from the beginning. This contrast suggests that a final fasting period is a normal part of the development program, not considered starvation, and thus not counterbalanced by reduced metabolism. This assumption is supported by a number of observations in other decapod megalopae (Mootz and Epifanio 1974; Schatzlein and Costlow 1978; Dawirs 1980; for recent review see Anger and Dawirs 1981).

The duration of the megalopa stage is much more variable than the zoeal instars. This fact may be related to the ecological role of the megalopa which is to select a biotope suitable for adult life. The capacity to delay selection should be related to the amount of reserve accumulated prior to the change in energy balance. This strategy is in contrast to that observed by Pechenik (1980) in gastropod larvae. These do not cease to grow with the onset of metamorphic competence, and their capability to delay metamorphosis appears to be related to the preceding growth rate. More detailed investigations on the nutritional and ecological needs of the megalopa stage are necessary for a better understanding of this critical phase in benthic recruitment.

All these complicated changes of biomass as well as their extent (two- to threefold increases within single stages) suggest that the use of "characteristic" values for particular instars applied in energy budgets and other energetic considerations must lead to very rough figures.

Another complicating factor is annual or seasonal variation in initial biomass of hatching larvae and in their growth rate. Since viability also appears to be related to this kind of variation, future studies will have to examine its degree and significance. The same holds true for possible systematic differences between laboratory-reared larvae and those obtained from wild plankton. Several authors (Knight 1970 and earlier papers; Rice and Provenzano 1970; Ingle and Rice 1971) observed higher growth rates in naturally grown developmental stages of different decapod species.

Only a small part of the organic matter accumulated during the zoeal stages is lost in exuviae. This is much different in the megalopa. More than three times more matter and energy was found in its cast exoskeleton than in both zoeae combined. These and other striking dissimilarities between zoea and megalopa larvae underline their different roles. The former accumulate energy-rich substances taken from the pelagic food web, and they are responsible for dispersal of the species. The latter stage, which

often crawls on the bottom, presumably will test suitable benthic habitats, before it goes through metamorphosis at a selected site. It appears that a rigid exoskeleton is advantageous as a protective means in the evolution of benthic crustaceans, whereas in pelagic species and stages it is probably disadvantageous for energetic reasons (increasing swimming energy).

The preliminary determinations of feeding rates on *Artemia sp.* nauplii yielded almost the same values (in C per day) as observed by Anger and Nair (1979) using *Polydora ciliata* larvae as prey. This confirms that the amounts in the above data are correct, but further studies considering the whole molt cycle in each larval stage will be necessary for comparisons with the growth measurements of the present investigation. The feeding rates observed in the Z-1 of *H. araneus* as well as larval DW are similar to those found by Mootz and Epifanio (1974) in the Z-4 stage of *Menippe mercenaria.*

Measuring the loss of organic matter and energy during starvation bears the same technical problems as measuring growth. FW, apart from its inaccuracy, is practically constant even during long-term starvation. This masking of changes in organic constituents is again caused by changes in water content. We assume that the underlying mechanism is some kind of starvation edema. Due to degradation of amino acids, the osmotic pressure in the hemolymph must decrease, and consequently water may passively enter body tissues. The water lost in the hemolymph might be replaced by seawater. This assumption would explain the observed net increase in body volume, water, and ash contents of starving larvae (Ikeda 1971, 1974; Mayzaud 1976). Instrusion of inorganic salts replacing degraded organic ions presumably is responsible not only for increasing ash portions, but also for the low degree of loss in DW. The latter observation means that DW can also be used in energetic studies of starving zooplankton to a limited degree, because it does not reflect actual losses in organic matter and energy.

Losses in C, N, H, and individual J's followed an exponential pattern with a weak curvature. The maximum possible losses until death amounted to ca. 40 to 60% of initial values, depending on the parameter and larval stage under consideration. These observations correspond to those by Anger and Nair (1979) and Dawirs (unpubl. data) on starved larvae of *H. araneus* and *Carcinus maenas*, respectively. Ikeda (1974) reported reductions in biomass of other zooplankton down to 20%. Our figures also become higher if chitin is excluded from these calculations.

Anger and Dawirs (1981) found that feeding after initial starvation in Z-1 larvae of *H. araneus* is successful only if a certain time (point-of-no-return, PNR) is not exceeded. Comparing this time span with the above biomass data, the actual limits of starvation resistance are already reached when 25 to 30% of organic matter (C,N,H) or 30 to 35% of individual energy are lost. Beyond this PNR another ca. 10% loss in all these parameters is possible, before the larva dies, regardless of eventual food availability. Fifty percent of the larvae already reach this limit ($PNR_{50}$) when only ca. 20% of the organic substance or ca. 25% of energy is lost. The PNR values for the other stages have not yet been determined.

Another finding reported by Anger and Dawirs (1981) is that relatively short initial feeding periods suffice for zoeae of *H. araneus* to successfully reach the next stage (Z-2 or megalopa), regardless of further food availability. Converting these time spans to biomass data, a surprising agreement in both zoeal stages is found: 50% of the larvae reach this "point-of-reserve-saturation" ($PRS_{50}$), when they have gained ca. 70% N, 90% C and H each, and ca. 95% energy (related to early postmolt levels). If food is continually available, considerable further accumulation of organic matter and energy will take place (see above), but this additional reserve will not be needed before the next stage is reached. If no prey is available during this period (presumably premolt) the next stage will be significantly prolonged, thus revealing a certain dependence on reserves accumulated during the preceding zoeal stage. Anger and Dawirs (1981) suggested that sterols (precursors of the molting hormone, ecdysterone) may play a crucial role in this phenomenon.

It is doubtful that energetics alone can explain the early appearance of the PNR, since the actual losses in organic body substance are rather low at that time. We assume that an irreversible damage in some hormonal or enzymatic system is involved in ecdysis.

The weight-specific metabolic rate is a major factor deciding the maximal survival time under starvation (Ikeda 1974). It is far lower in starved as compared with fed zooplankton (see, e.g., Ikeda 1977 and earlier papers cited therein;

Mayzaud 1976; Logan and Epifanio 1978; Capuzzo and Lancaster 1979). The hyperbola-shaped decrease pattern in weight-specific energy (see above) is in accordance with that described by Mayzaud (1976) for respiration rates in starved zooplankton. There is an initial acclimation period with strongly decreasing metabolic rate, followed by more or less constant values. Our estimates for oxygen consumption follow this pattern, and their amounts compare favorably with literature data, if starvation and relatively low temperature (12°C) are taken into account (for review see Schatzlein and Costlow 1978).

In a low temperature range, high $Q_{10}$ values are to be expected. This assumption is confirmed by extremely long survival times observed by Anger and Dawirs (1981). These figures of starvation resistance as well as our calculations of weight-specific respiration rates fit the quantitative relationship between these two parameters described by Ikeda (1974).

The metabolism of starved *H. araneus* larvae is mainly based on protein degradation (Anger and Nair 1979). According to the literature, this is a general feature in crustaceans (e.g., Mayzaud 1976; Ikeda 1977 and earlier papers; Capuzzo and Lancaster 1979). Our observations on changes in the C:N ratio suggest that during the final (premortal) period of long-term starvation, lipids also become important as a last reserve. However, at this time the larva is already doomed to die, regardless of eventual food availability, since the PNR has been exceeded (Anger and Dawirs 1981).

The amount of reserve and proportions of metabolic pathways apparently are also subject to annual and seasonal variation, possibly even to differences among different parts of one brood (e.g., Regnault 1969; Pandian and Schumann 1967; Pandian 1970; Pandian and Katre 1972; Anger and Dawirs 1981). Those changes may also explain differences between daily energy losses in starved zoeae estimated by Anger and Nair (1979) and in the present study. Future investigations will have to examine the amount and significance of such natural variation superimposed on the response patterns of decapod larvae in different feeding conditons.

## ACKNOWLEDGMENTS

This paper is a contribution to research project "Experimentelle Ökosystemanalyse" sponsored by Bundesministerium für Forschung and Technologie, Bonn, West Germany (Grant No. MFU-0328/1). We are grateful to our colleagues W. Greve, M. Janke, F. Schorn, and E. Wahl for providing food organisms. J. Ufer operated the C-H-N analyzer, and B. Lämmel made the drawings. Our thanks are also due to J. Markham for correcting the manuscript. The second author is indebted to Studienstiftung des Deutschen Volkes, Bonn - Bad Godesberg, for financial support.

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