Laboratory experiments on the larval development of *Hyas araneus* (Decapoda, Majidae)

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ABSTRACT: Experiments have been carried out on the duration of larval development of the spider crab *Hyas araneus* L., in relation to temperature, food quality, and individual variation. A graphical model is presented which predicts larval occurrence and settlement in the field (Helgoland waters, North Sea). Preliminary observations are reported on predator-prey interactions with larvae of the spionid polychaete *Polydora ciliata*. Cannibalism and necrophagy during starvation experiments with zooplankton are considered: In larvae which are not kept in individual confinement, maximum survival time doubles due to feeding on living or dead sibling larvae. Analyses are presented revealing elemental and biochemical composition of starved and fed larvae as well as energy equivalents calculated from these data. During starvation, early larvae lose carbon, nitrogen, and hydrogen. Their main metabolic substrate is protein; lipid is utilized to a much lesser extent. Exoskeleton formation is, apparently, independent of nutrition: Zoea-1 larvae starved for 8 days contain the same amount of chitin as larvae fed well over this period of time. Energy calculations suggest an extremely low respiration rate and a very effective reconstruction of body material in starved larvae.

INTRODUCTION

Population dynamics in pelagic communities is a major source of variation in the production of economically important major predators such as fish or coelenterates (e.g. Hempel, 1974; Greve, 1977; Greve & Parsons, 1977; Landry, 1977). In order to tackle the difficult task of analyzing such processes in relation to environmental factors and biological properties of the organims involved, a joint project was started in 1977 at the Biologische Anstalt Helgoland (Biologische Anstalt Helgoland, Jahresbericht 1978). This programme comprises rearing and cultivation experiments with planktonic organisms typical for the ecosystem of the German Bight, experiments on intra- and interspecific interactions of different populations and, finally, the development of a simulation model describing and predicting changes in a simplified system. To approach the latter goal, among other principal information, basic data on autecological, reproductive, physiological, and biochemical details characterizing the components of this system must be provided.

The spider crab *Hyas araneus* is one of these components. It is very common, not only around the island of Helgoland in the North Sea, but over a wide geographic range (Christiansen, 1971). Each mature *H. araneus* female can release about 10 000 to 30 000 larvae per hatching season (Schriever, 1976). Thus, the meroplanktonic developmental stages are presumed to play a conspicuous role in the pelagic food web as predators, and probably also as prey for young fish, natant decapods, and other predatory or decomposer organisms during late winter and spring, when they are liberated.

Nevertheless, very little is known about these larvae. Their morphology was first described in detail by Christiansen (1973). Rearing of all larval stages was performed first by Christiansen (1971) and Schriever (1976).

In the present study, the temperature range in rearing experiments was extended down to 2 °C and thus, for the first time, data have been obtained on early larval development at temperatures comparable to those prevailing in the natural environment during hatching. Using the development-temperature relations found in these experiments, and described in the above literature, a rough model has been derived to describe the presumptive time and duration of larval occurrence in the field.

Some preliminary observations on the influence of food quality and genetic variation on duration of development are reported. These factors constitute potential sources of error in estimations of the role of crab larvae within the system under consideration. A particular aspect of this role is the predation on spionid larvae which are a very frequent component in spring plankton. This was studied in preliminary experiments in order to produce the basic information necessary for further experimental design, and to ascertain the order of magnitude of the predation rate to be expected in later studies.

The energy gain due to feeding, the survival rate under starvation, and the energy transfer to predators are important ecological aspects in natural ecosystems and, consequently, in simulation models describing them. Such aspects were investigated in particular for the first free-swimming larval stage (Zoea 1), and some preliminary data are also given for the other stages.

MATERIALS AND METHODS

Obtaining and handling of larvae

Most of the egg-carrying *Hyas araneus* females were dredged from a deep channel southwest of Helgoland („Helgoländer Tiefe Rinne") from depths of ca. 30–50 m during December (1976, 1977) and January (1977, 1978). Some were trapped in lobster baskets in the shallower rocky subtidal region around the island.

According to daily plankton observations, hatching in *Hyas araneus* begins near Helgoland in early February, and lasts mainly from mid-February to mid-March. In the laboratory, hatching occurred during the same period, but was artificially prolonged by temperature manipulations. In aquaria, at 12 °C larval liberation started in mid-January, at 2 °C it lasted from early March to May. Hence, larvae could be made available for experiments over 4 months. Regarding the release of their zoeae, egg-carrying females maintained over more than one year in flow-through culture responded in the same

manner as those caught in nature just before natural offspring liberation. Larvae obtained under these conditions did not differ in survival rate, body weight or other criteria observed from those released under conditions of natural habitat temperature (4 °C) in February.

The larvae were reared in beakers of different sizes. Early stages were maintained in beakers ranging form 0.5 to 1 l in capacity, later developmental stages in beakers of 5 and 10 l capacity. Natural seawater from Helgoland (29–30°/₀₀ S) was used after removing particles > 0.25 μm with a Millipore membrane filter. Care was taken that larval densities did not exceed 50 individuals l⁻¹ (suggested by Schriever, 1976). Slight aeration was applied in order to provide oxygen, and to keep the larvae in suspension since these show only little swimming activity as compared to other decapod larvae. Antibiotics were not applied, neither in standard cultures nor in experiments. The water was normally changed three times per week, in some experiments exactly every 2 days.

Unless otherwise stated, a standard temperature of 12 °C and a standard food mixture of *Brachionus plicatilis* and *Artemia salina* (ratio ca. 10:1; ca. 50–100 food organisms ml⁻¹) were maintained throughout the experiments. The rotifers were taken from a mass culture fed with yeast suspension. Rotifers were concentrated by using a nylon gauze (63 μm), washed, and resuspended in an algal culture (*Dunaliella* sp., grown in F/2 medium); the rotifer-algal mixtures were incubated for one day before using them as larval food in order to enrich *B. plicatilis* with algal vitamins. After each water change, the rotifers were drained out and added into the beakers containing brachyuran larvae to a final concentration of approximately 50–100 individuals ml⁻¹. Freshly hatched *A. salina* nauplii and a small quantitiy of centrifuged *Dunaliella* sp. were also added. Food concentration was controlled only roughly by means of 1 ml samples taken with a graded pipette and checked under a dissecting microscope. The ration given was found to be much higher than could be consumed until the next water and food change, and hence its exact amount was considered to be of minor importance.

Experiments

During preliminary experiments designed to assess comparative nutritional values of different potential food organisms, excess rations were provided in order to exclude limitation in prey availability and to ensure food quality as crucial factor. The organisms tested were: the flagellatte *Oxyrrhis* sp., the ciliate *Fabraea salina*, the rotifer *Brachionus plicatilis* (without addition of *Artemia salina*), and larvae of the polychaete *Polydora ciliata*. The latter was isolated from natural plankton and maintained for 1–2 days in *Dunaliella* culture before being offered as prey. The two protozoans were cultured in the laboratory, and also fed on the same green flagellate. During this experiment, water changes and feeding were carried out regularly every 2 days.

The exact amount of food consumed was determined in preliminary experiments on the predator-prey interaction with larvae of *Polydora ciliata*. These experiments were conducted in order to obtain basic information on behaviour and food requirements of early larval stages of *Hyas araneus*. Beakers with 1 l capacity were used. In the first series of experiments prey concentration varied, in the second it was kept constant, while predator

density varied. Both zoeae and spionid larvae were counted again after 24 h, and feeding rates calculated from the differences observed in prey numbers.

In order to assess the potential importance of cannibalism among Zoea-1 larvae in laboratory cultures and mortality rates under starvation conditions, two further experiments were set up. In the first one, beakers of 1 l capacity each (triplicates) were filled with filtered seawater and 20 freshly hatched *Hyas araneus* larvae. They were aerated and maintained without food. Every other day the water was changed, and all living individuals were examined under a dissecting microscope, counted, and placed back into the beakers. Dead animals or parts thereof were removed. For the second experiment, 100 larvae were placed individually into small beakers of 30–50 ml capacity without aeration. Again, filtered seawater without food organisms was used; the water was changed every second day, and mortality was recorded.

The laborious technique of maintaining single individuals in small beakers was also applied for further starvation experiments performed in connection with biochemical and elemental analyses. To obtain sufficient quantity of material for these investigations, several thousand larvae had to be maintained.

All experiments were carried out in temperature-controlled rooms. The developmental time as a function of temperature was observed in triplicates at 2 °, 6 °, 10 °, and 12 °C. Comparison of different food organisms (in triplicates) were conducted at 10 °C, all other experiments at 12 °C.

Elemental and biochemical analyses

For determination of *wet weight*, individual larvae were sorted alive under a dissecting microscope, blotted for about 10 s on filter paper, and transferred to pre-weighed silver cartridges. Total weight was measured on an Autobalance AD–2 (Perkin-Elmer) to the nearest 0.1 μg.

In order to obtain *dry weight*, the larvae were deep-frozen and subsequently vacuum dried within the cartridges at $< 10^{-2}$ mbar in a GT 2 (Leybold-Heraeus) apparatus for about 3 h. Rinsing of larvae in water from an ion exchanger prior to drying was not applied in our analyses, because this procedure creates a risk of osmotic damage with consequent leaching of organic matter. In small samples, adherent salt is considered to be present in such small amounts that it has no significant influence on further analytical results; this could indeed be demonstrated in test series: A comparison of rinsed and untreated larvae revealed no significant differences in their dry weight, ash content, or elemental composition. It is confirmed to some extent by the results of Platt et al. (1969) and by the observations of Omori (1969), and Ikeda (1971, 1974). The latter author also did not rinse zooplankton before carrying out elemental analyses.

The minimum drying time was also determined in a test. After 2 h of drying, no further decrease in weight was observed. For standard procedures, drying time was therefore fixed to a minimum of 3 h. This is about three times less than observed in oven drying at 60 °C. Vacuum drying was preferred and used exclusively in this study, because it takes less time and, due to the much lower temperature, does not affect biochemical composition. Test measurements of dry weight and ash, however, did not differ significantly in these two methods.

Before analyses, the material was stored in a desiccator over silica gel in vacuum. *Carbon, nitrogen,* and *hydrogen* contents of larvae were determined by means of an Elemental Analyzer Model 1104 (Carlo Erba Science) using cyclohexane–2,4-dinitrophe-nyl-hydrazone as standard. The capacity of the analyzer for highest accuracy is 0.2 to 2 mg per sample. Thus, depending on developmental stage and individual dry weight, 1–10 larvae were analyzed in each sample; each analysis comprised 5, in some cases 10 replicates. The accuracy of the apparatus was tested by frequent controls repeating analyses of the standard substance. Standard variation proved to be less than $\pm$ 3 % of mean display.

Before biochemical analyses, vacuum dried material was thoroughly homogenized. Dilutions were made wherever found necessary, and values later computed. The analytical procedures for determination of *protein* (biuret), *carbohydrate* (phenol, sulphuric acid), *lipid* (choroform, methanol), *chitin* (sodium hydroxide), and *ash* contents (muffle furnace at 500 °C) followed the standard methods described by Raymont et al. (1964). The accuracy of these methods is estimated to be $\leq \pm$ 10 %. From the biochemical analyses performed, *energy equivalents* were calculated using the conversion factors given by Winberg (1971): 5.65 cal mg^{-1} for protein, 4.10 for carbohydrate, and 9.45 for lipid. These factors are very close to those already found by Rinke & Hertling (1937) for marine crustaceans. The lower factor for protein (5.10) given by Cummins & Wuycheck (1971) corresponds more to phytoplankton and seston (Hallegraef, 1978), while that of Winberg is better applicable to animal biomass. This value had to be corrected for biologically unavailable nitrogen oxidation calories according to Kersting (1972) by subtracting 5.9 cal (mg N)$^{-1}$. N contents were estimated as 16 % (by weight) for protein, and 6 % for chitin. Since chitin is a substance practically indigestible by predatory zooplankton and fish, energy equivalents disregarding it were also calculated. Carbon-based calculations of caloric values using the conversion factors of Platt et al. (1969), gave higher values than were obtained by considering biochemical composition. The N-corrected factor given by Salonen et al. (1976) seems to be more applicable, because the results are much closer to the estimates based on protein, carbohydrate, and lipid. All energy equivalents are expressed in Joule units (1 J $\triangleq$ 0.239 cal).

RESULTS AND DISCUSSION

Influence of temperature on larval development

Developmental rates of *Hyas araneus* larvae were observed in studies by Christiansen (1971), Schriever (1976), and in the present work over a total temperature range from 2 ° to 20 °C (Table 1). Christiansen had problems with disease and could only obtain results comparable to those of Schriever and us when antibiotics had been applied. At both extremely low and high temperatures development ceases before reaching the megalopa stage. At 2 °C the last Zoea-2 died 145 days after hatching. The optimum range for development is apparently 10 °–15 °C.

Mean duration of all larval stages and the total larval development were calculated from the values in Table 1 and are presented graphically (Fig. 1). Idealized curves were drawn to express approximately the development-temperature relationships: Zoeal stages 1

Table 1

Hyas araneus: Larval development in relation to temperature. Time range (days) and mean (in parentheses) from hatching as zoea 1 to reaching of later larval stages. Source n° : 1 = this paper; 2 = Christiansen (1971); 3 = Schriever (1976). — = stage not reached; * = stage reached only with antibiotics applied

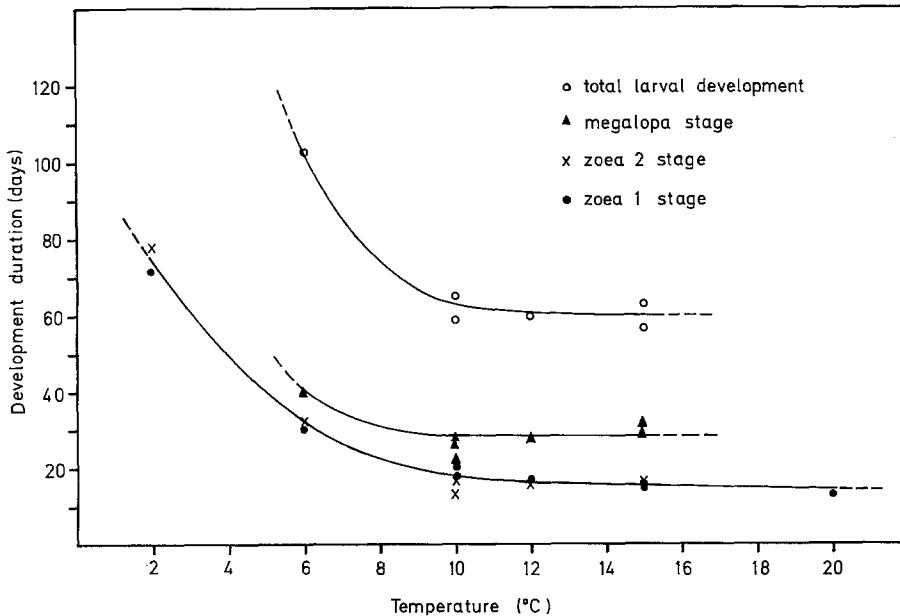| Temperature (°C)	Source	Zoea 2	Megalopa	Crab 1
2	1	65–81 (72)	–	–
6	1	28–40 (31)	61–68 (63)	100–107 (103)
10	1	19–24 (20)	27–39 (33)	49–65 (59)
10	2	23–40 (31)	–	–
10	2	15–29 (21)*	32–44 (38)*	65*
10	3	15–22 (18)	34–48 (40)	–
12	1	14–21 (17)	30–35 (33)	58–63 (60)
15	2	16–21 (18)	–	–
15	2	12–19 (15)*	24–31 (28)*	52–67 (57)*
15	3	13–19 (16)	29–36 (32)	60–74 (63)
20	3	10–16 (13)	–	–

Fig. 1: *Hyas araneus:* Duration of larval development in relation to temperature. Mean values calculated from Table 1

and 2 seemingly have almost identical durations at identical temperature, while the megalopa stage lasts for a significantly longer time. For all stages, and thus also for the total development, temperature effects are pronounced below 10 °C, but are very small above this level.

Since temperature is not constant in nature, the assumed relationships summarized in Figure 1 have been used to calculate approximate developmental durations in the field

(Fig. 2). Water temperature in Figure 2 is given as long-term average according to data by Weigel (1978). In the upper part of the graph, the estimated durations of larval stages are presented for a case were embryonic development is completed in mid-February and hatching of praezoeae takes place at this time. This very first larval stage is not considered here, because it lasts for only a few hours even at low temperature. The total development to the first crab stage in this case takes about 110 days, almost half of this period as Zoea 1, due to low temperatures at the beginning of larval life.
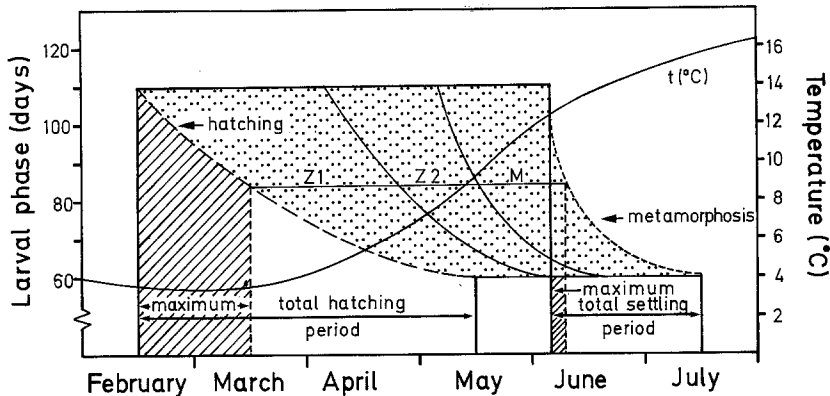

Fig. 2: *Hyas araneus:* Occurrence of larval stages in Helgoland waters during spring season: Graphical model based on experimental results as summarized in Figure 1. Z1, Z2: zoeal stages; M: megalopa stage

Such early hatching and consequently long duration of development is regarded as normal in the vicinity of Helgoland. In Norwegian water, however, Christiansen (1971, 1973) caught egg-carrying females as late as April and recorded hatching of early larvae even in mid-May. If such late larvae liberation is possible also near Helgoland, it would be rather an exception than the rule, and must be regarded as the absolute end of the hatching season. In the lower part of the graph (Fig. 2), the assumed development duration for the last larvae produced in the year is shown. Due to increasingly high temperature, intermoult periods are much shorter in these larvae. Thus the first crab stage is reached only 6 weeks later than in larvae which had hatched 3 months before.

This means that the pelagic phase in the development of *Hyas araneus* near Helgoland lasts a minimum period of ca. 2 months, and a maximum period of almost 4 months (Fig. 1). Figure 2 shows the presumed duration of all stages as well as the total larval development (left scale) in relation to hatching date (abszissa) and temperature (right scale). Since we regard a main hatching period from mid-February to mid-March as a rule for Helgoland waters, a „normal" duration of planktonic development of about 84–110 days is expected for this region. Our graphical model also predicts that the majoritiy of larvae which had been released during the first month (the principal) of the hatching season will metamorphose within a very short period, in early to mid-June.

Further analysis shows that only Zoea 1 is subject to high variation in intermoult duration; in Zoea 2 variation is much less, and the megalopa has an almost constant duration, because it occurs at temperatures of >10 °C, which are of little influence on
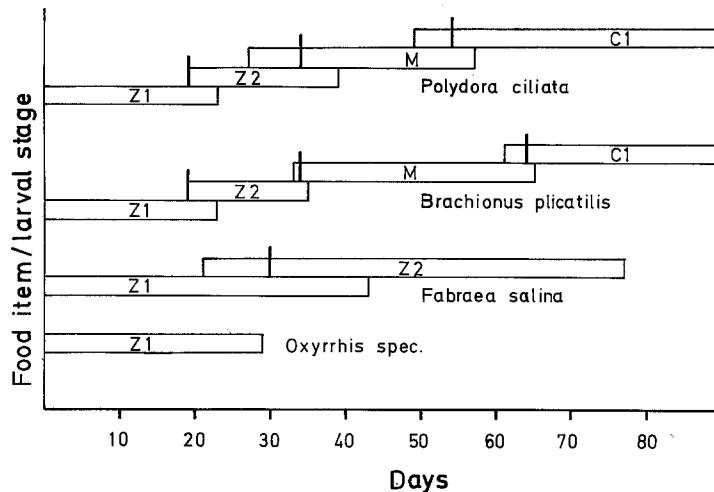
Fig. 3: *Hyas araneus:* Duration of larval development in relation to food organisms offered. Symbols for larval stages as in Figure 2; C1: first crab stage. Vertical lines: time at which 50 % of all survived individuals have reached a given stage

developmental rate (cf. Fig. 1) Extrapolation of these assumptions to other areas with similar temperature regimes seems to be possible as an approximation. For general considerations in plankton ecology these predictions mean an exclusive occurrence of Zoea 1 during February and March, and an increasing dominance of Zoea 2 from mid-April to mid-May, while the first stage disappears during that time. Subsequently, megalopae, become dominant until mid-June, when most of them leave the pelagic environment after metamorphosis to the first crab stage. According to this rough model, after this period, only very few recruits are expected and they should disappear at the latest in mid-July.

These predictions are based exclusively on the temperature factor. They can only be a reliable approximation to reality if nutrition exerts no significant influence or if natural nutrition is comparable in its effect to the food offered in the laboratory.

Influence of food on larval development

Individual variation

Food quality and quantity are key factors influencing not only the rate of survival and metamorphosis in meroplanktonic larvae, but also the duration of development (e.g. Brick, 1974; Sulkin, 1975; Christiansen & Yang, 1976; Sulkin & Norman, 1976). Rate of development seems to be a particularly sensitive indicator for the nutritional value of food organisms.

In Figure 3, the effect of food quality on larval development in *Hyas araneus* is shown and compared for some organisms. Two protozoan species and one rotifer, which can be easily reared in laboratory mass cultures, and one „natural" food organism (larvae of the spionid polychaete *Polydora ciliata*) were offered at high densities (ca. 1000 ind. l^{-1}) as prey in experiments.

The flagellate *Oxyrrhis* sp. apparently could not be consumed because of its small size: The second zoeal stage was never reached, and the survival time of early zoeae was almost identical with that observed in starved larvae (Fig. 6), if not maintained individually.

The larger-sized ciliate *Fabraea salina* is eaten, but has only low food value for *Hyas araneus* larvae: Survival time in the first zoea stage was significantly prolonged, and a few individuals also reached the second stage. The Zoea 2 stage also could last for a much longer time than in standard cultures (Table 1), but no further moulting occurred. Probably in this food organism predator-prey size relation is too unfavourable to allow sufficient energy gain in predation.

Brachionus plicatilis is a commonly used food organism in aquaculture and scientific research (for review see Kinne, 1977). Many authors (e.g. Christiansen & Yang, 1976; Schriever, 1976; Sulkin & Epifanio, 1975; Sulkin et al., 1976, and earlier investigators referred to in these papers regard it as suitable only for early developmental stages in decapods. Thus, it was mostly used only in the beginning of rearing experiments and later displaced by *Artemia salina* nauplii or (as done in our standard rearing) given in a mixture together with the brine shrimp. Figure 3, however, reveals that complete larval development of *H. araneus* is also possible when using exclusively the rotifer as food. Metamorphosis to the crab stage is only slightly delayed as compared to larvae feeding on spionid larvae or mixed food, and appears to be quite normal in regard to timing.

This experiment reveals that too small-sized prey is unsuitable as food even if offered at high densities, and that „natural" food organisms, which occur in high densities in the plankton together with its predator, are highly suitable for rearing decapod larvae.

Christiansen (1971, 1973) found variation in larval size of *Hyas araneus* which had been treated in the same way, and she attributes it to geographic, environmental, and
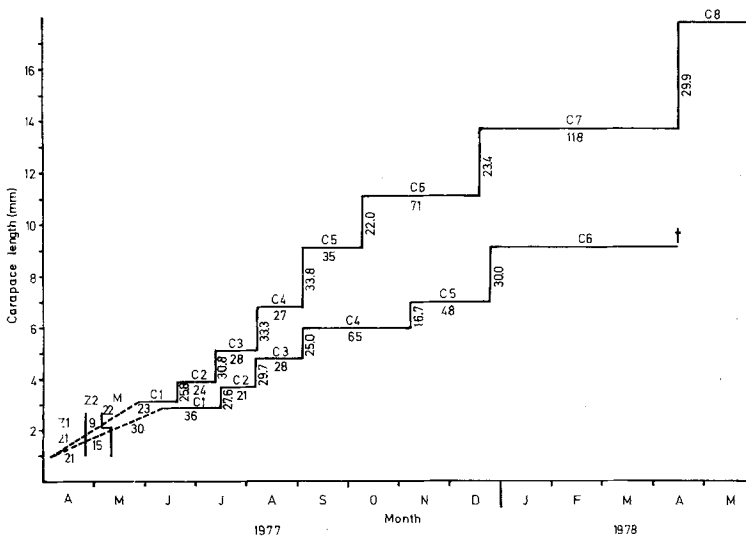

Fig. 4: *Hyas araneus:* Larval and postlarval development of two individuals. Symbols for the stages as in Figures 2 and 3. Numbers at vertical lines in the graph: percentage increments in carapace length; numbers at horizontal lines: intermoult durations (days)

genetic factors. This variation can also be recognized in terms of viability and developmental rate (e.g. the experimental results summarized in Table 1). It has been followed over a period of one year in postlarval growth of crabs reared in the experiments described above. They were maintained under identical conditions individually at 12 °C in 1 l beakers with gravel as substratum, slight aeration, feeding three times per week, and food consisting of mussel and shrimp meat.

In Figure 4, larval development (at 10 °C) and postlarval growth (at 12 °C) is shown for the two individuals which exhibited the fastest and slowest growth rates, respectively. The individual which required a longer time to metamorphose to the first bottom stage had mostly longer intermoult periods and smaller length increments also in its postlarval life. It died after one year without apparent cause.

No final conclusions can be drawn from this observation; however, it seems likely that growth rates and viability are not only functions of environmental factors, such as temperature and food supply, but also to a relatively high degree of genetic variation.

Predator-prey interactions between Zoea-1 stage larvae of *Hyas araneus* and larvae of *Polydora ciliata*

In spring plankton near Helgoland, both larvae of the spionid *Polydora ciliata* and of the spider crab *Hyas araneus* are common, the former ones often occurring in high numbers. Thus, predator-prey interactions between these two species are expected to occur frequently in this region.

By keeping constant predator density and varying the initial prey concentration (Fig. 5a), an increasing feeding rate can be observed in relation to absolute (spionids l^{-1}) and consequently also to relative prey density (spionids: zoeae). In this relationship, a saturation density must be assumed, which does not permit further increase in feeding rate if exceeded. Indeed, a tendency of approaching a plateau can be observed in Figure 5a; however, the exact value for this upper threshold has to be determined in further experiments.

The feeding rate decreased considerably with increasing predator density (Fig. 5b). This fact is presumably caused mainly by high predation rates at the beginning of the experiments and the resulting lower average densities in prey organisms during the entire experiment. In addition, a mutual interference between the crab larvae could have diminished predation rates. Since predator densities of 10 individuals l^{-1} or more certainly do not occur in nature, this effect should be regarded as an experimental artefact. Thus, further studies have to consider especially the range 1–10 zoeae l^{-1} in order to obtain natural maximum rates of predation.

This holds true also for further experiments with varying prey concentrations. They have to be carried out with a much lower zoeal density than in these pilot observations. According to these initial observations, plateau concentrations in spionid larvae with maximum predation rates must be expected near an order of magnitude of >1000 individuals l^{-1}, i.e. above the highest densities ever reported in the literature for *Polydora ciliata* (Daro & Polk, 1973). This finding, if confirmed, would mean that spionid larvae alone normally cannot sufficiently support crab larvae in nature. If other zoplankton of
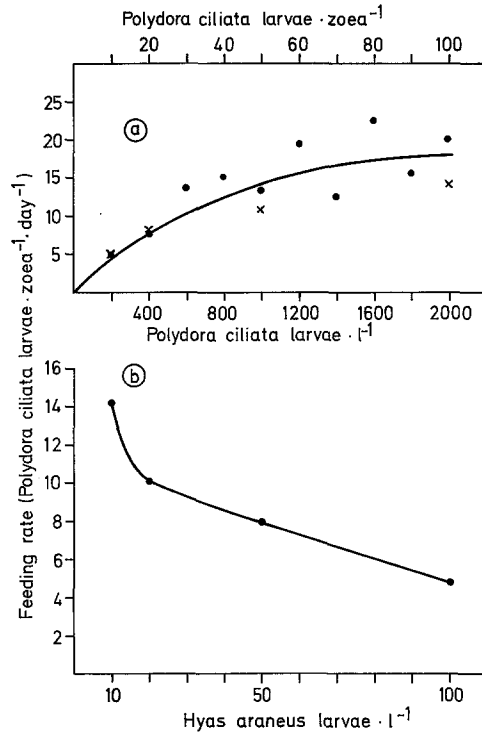
Fig. 5: *Hyas araneus:* Feeding rate of zoea-1 larvae on larvae of *Polydora ciliata* given as prey, (a) in relation to relative (prey predator^{-1}) and absolute (prey. l^{-1}) prey density, and (b) in relation to absolute predator density

suitable size and availability (only relatively slow swimmers can be caught by *Hyas araneus*) at high density is also missing, nutritional deficiency must be regarded as a major source of larval mortality in *H. araneus*.

Starvation and cannibalism

In boreal sea regions, variation in food production is high. Thus, suvival rates in starved zooplankton are generally regarded as an ecologically important factor (for recent discussion see Ikeda, 1971, 1974, 1977; Conover, 1978). However, in starvation experiments with zooplankton, many individuals have usually been kept together in the same beaker or bottle (e.g. Ikeda, loc. cit.; Mayzaud, 1973, 1976), so that cannibalism or feeding upon dead individuals could not be excluded. Hence, results obtained in this way do not really apply to starvation but rather to insufficient nutrition only.

In Figure 6, cumulative percentage-mortality rates observed by means of this method are compared with those of individually kept zoeae (Z 1). Although dead individuals were removed every other day, maximum suvival time doubled where cannibalism or necrophagy occurred. This indicates a well-developed ability for utilizing food sources of minor

quality (such as carrion) in periods of poor prey availability (see also *Fabrea salina* in Fig. 3). Hence for experiments on biochemical changes under starvation, we applied exclusively the elaborate but reliable method of maintaining each individual separately.

Carbon, nitrogen, and hydrogen contents in fed and starved larvae

Many data on elemental and biochemical composition or caloric equivalents of planktonic organisms have been published in the last decades (e.g. Vinogradov, 1953; Beers, 1966; Omori, 1969; Cummins & Wuycheck, 1971; Thayer et al., 1972; Childress & Nygaard, 1974; Ikeda, 1974), but hardly any data on decapod larvae. This fact is a consequence of low natural densities of decapod larvae in plankton communities. Hence, rearing of larvae is necessary to obtain sufficient material for chemical analyses. However, rearing experiments have usually been carried out with different aims. Rearing of mero-planktonic larvae for biochemical analyses during growth and starvation is surprisingly rare in the field of nutritional ecology of plankton.

Table 2 summarizes the values measured for individual body weight and elemental composition in larvae of *Hyas araneus* (as far as determined; starved animals not included). The percentages of carbon (C), nitrogen (N), and hydrogen (H) do not vary much within and between different stages, in contrast to the absolute amounts (μg per individual), which increase considerably during the larval development. Since only relatively few analyses on Zoea 2 and megalopa have been performed, our values do not cover the whole range observable in these stages, but rather the order of magnitude only.

For Zoea 1, the full range can be seen in Table 2. Gain in total body weight and principal elements amounts to more than 100 % within one intermoult. Thus, if estimating those items for a given stage found in a sample, at least the dry weight should be determined. Even then there is considerable variation not only in relation to age, but also to the past nutrition of the larvae as well. The percentage values for C, N, and H, as well as

Table 2

Hyas araneus: Range of values for fresh weight (FW), dry weight (DW), carbon (C), nitrogen (N), hydrogen (H), C/N ratio, and energy equivalents (Joule) per individual found in larval stages. Percentage values related to dry weight

	Praezoea	Zoea 1	Zoea 2	Megalopa
FW (μg)	252–390	381–860	866–1022	1828–2241
DW (μg)	46–67	55–148	186–352	303–506
C (%)		29.5–38.7	33.0–39.3	30.9–32.4
C (μg)		21–50	61–91	140–154
N (%)	not	6.4–9.2	6.2–9.0	7.1–7.4
N (μg)	determined	5–12	14–19	32–35
H (%)		4.4–6.0	4.5–6.0	4.7–4.9
H (μg)		3–7	9–12	21–22
C/N		4.0–4.9	4.4–4.8	4.3–4.5
Joule	0.68–0.99	0.87–2.07	2.52–3.77	5.80–6.38

the C/N ratios are comparable to data found in many other zooplankton groups (see e.g. the reviews by Vinogradov, 1953; Omori, 1969; Ikeda, 1974), though great variation occurs.

The effect of starvation on the composition of Zoea 1 larvae was followed over 12 days (Table 3), i.e. to a time already lethal for about 80 % of the larvae (Fig. 6). Two days after the beginning of the experiment, the surprising fact was observed that no change in dry weight had occurred, but a reduction in C, N, and H, regardless of feeding or starving conditions. It is possible that, except for uptake of prezoeal exoskeleton material immediately after moulting, hardly any food was ingested during this time, while parts of the body had to be reconstructed in the build-up of the new exoskeleton. Thereafter, all body constituents observed and the total body weight increased in fed individuals until the 8th day. At this time, the maximum dry weight of this stage (in that particular case about 126 µg per individual) was reached. The maximum weight as well as the initial weight of a given stage apparently depend much on genetic factors: Mean initial dry weights of Zoea 1 varied in different broods between 60 and 72 (total range in single determinations 55–75) µg per individual, their mean maximum weights between 125 and 140 (total range 122–148) µg per individual. Variation within a brood is very low (standard deviation mostly $\leq \pm$ 3 µg).

Both relative and absolute amounts of C, N, and H also increase after attaining the maximum dry weight. Starved zoeae, however, lose about 14 % of their initial dry weight, and 43–47 % of the elements considered here within 12 days. This loss in organic material is significantly higher than the general upper limit estimated by Ikeda (1974). He assumed 20 % loss as being lethal for starved zooplankton. During the same period, fed larvae gain 75 % in dry weight, and 91–95 % in the elements C, N and H. Four days later, in up to 2 day-old Zoea 2 a striking increase in organic matter and total dry weight can again be observed. This applies only to the total amounts, not the percentage values, which decrease after moulting, The further development could not be followed due to lack of material.

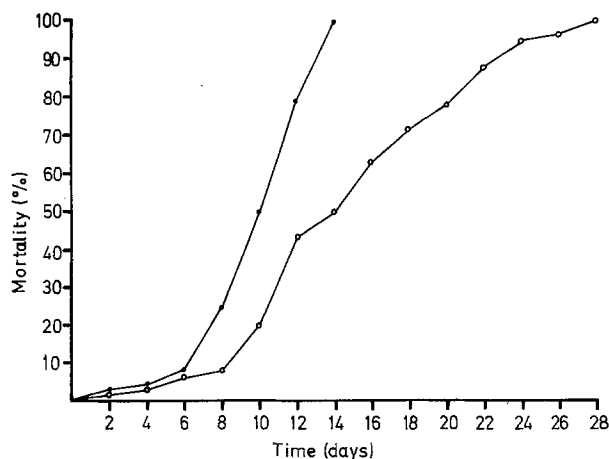Calculating energy equivalents by means of the N-corrected formula of Salonen et al.

Fig. 6: *Hyas araneus:* Cumulative mortality rate in starved zoea-1 larvae, allowing (open circles) and excluding (closed circles) cannibalism and necrophagy

Table 3

Hyas araneus: Variation in body weight and chemical constituents (symbols as in Table 2) under starvation (s) and feeding (f) conditions. Mean ($\bar{x}$) ± standard deviation. % H_2O related to fresh weight, all other percentage values related to dry weight

		0 (s)	0 (f)	2 (s)	2 (f)	Days after moulting to zoea-1 stage (Z 1) 4 (f)	6 (f)	8 (f)	10 (f)	12 (s)	12 (f)	Z 2 16 (f)
FW (μg)	$\bar{x}$	447	423	476	434	471	507	501	528	458	746	893
	±	36	11	22	25	28	23	25	20	46	79	21
DW (μg)	$\bar{x}$	71	72	71	70	92	105	125	125	60	126	205
	±	4	2	4	5	8	11	5	8	7	3	2
H_2O	(%)	84.1	83.0	85.1	83.9	80.5	79.2	75.0	76.3	87.5	83.1	77.1
C (%)	$\bar{x}$	33.8	34.6	27.9	30.3	30.6	34.9	35.2	36.6	22.8	37.6	33.9
	±	1.5	0.5	1.2	1.1	0.5	1.2	0.5	1.4	1.9	0.9	2.5
C (μg)	$\bar{x}$	24.1	24.9	19.8	21.3	28.1	36.8	44.2	45.8	13.7	47.5	69.3
	±	1.0	0.3	0.9	0.8	0.5	1.4	0.7	1.7	1.1	1.1	5.2
N (%)	$\bar{x}$	8.3	8.2	6.5	7.2	6.7	7.7	7.4	8.1	5.1	9.0	7.4
	±	0.4	0.1	0.5	0.2	0.2	0.2	0.1	0.2	0.3	0.1	0.7
N (μg)	$\bar{x}$	5.9	5.9	4.6	5.0	6.1	7.7	9.3	10.1	3.1	11.3	15.1
	±	0.2	0.1	0.3	0.1	0.2	0.2	0.1	0.2	0.2	0.2	1.4
H (%)	$\bar{x}$	5.1	5.2	4.1	4.5	4.3	5.0	5.3	5.4	3.4	5.7	5.1
	±	0.2	0.1	0.1	0.2	0.2	0.2	0.1	0.3	0.3	0.2	0.5
H (μg)	$\bar{x}$	3.6	3.7	2.9	3.2	4.0	5.3	6.7	6.8	2.0	7.2	10.4
	±	0.2	0.1	0.1	0.1	0.1	0.2	0.1	0.4	0.2	0.2	1.0
C/N	$\bar{x}$	4.1	4.2	4.3	4.2	4.6	4.8	4.8	4.5	4.5	4.2	4.6
	±	0.03	0.18	0.10	0.05	0.09	0.07	0.01	0.08	0.19	0.05	0.20

(1976), values of 12.6 to 15.6 J mg^{-1} (i.e. 0.88 to 1.97 J per individual) are obtained in fed Zoea 1 and 9.5 J mg^{-1} (0.57J per individual) in starved ones after 12 days. These estimations are based upon carbon contents, and thus do not necessarily express physiological values, since inorganic and chitin carbon are potential sources of error. However, as will be shown in the following section, C-based and biochemical based calculations of energy equivalents correspond rather closely, if N and chitin corrections are made.

Starvation effects on biochemical composition of early stages

Biochemical composition and energy equivalents of early larvae are given in Table 4 and in Figure 7. Differences in protein, carbohydrate, lipid, and ash contents of praezoeae and freshly moulted Zoea 1 (Z1 Od) do not exceed the confidence limits of the analytical methods. More surprising is the relatively high amount of chitin in Z1 larvae found shortly (maximum within 6 h) after moulting. This observation can only be explained by very fast chitin synthesis and uptake of praezoeal exoskeletons or parts of them. Also the C-H-N

Table 4

Hyas araneus: Biochemical composition and energy equivalents in early larval stages under starvation (s) and feeding (f) conditions. Od, 8d = time (days) from hatching as zoea-1 stage (Z1). Mean (x̄) ± standard deviation. Percentage values related to dry weight

|		Praezoea	Z1 Od	Z1 8d(s)	Z1 8d(f)
FW (μg)	x̄	338.0	420.6	514.7	517.6
	±	14.6	19.9	48.3	18.3
DW (μg)	x̄	54.3	60.4	72.7	134.4
	Y	1.7	2.2	0.9	3.4
H_2O (%)	x̄	83.9	85.6	85.9	74.0
	±	1.2	1.2	1.7	1.6
Protein	(μg)	24.4	27.3	13.1	41.5
	(%)	45.0	45.2	18.0	30.9
Carbohydrate	(μg)	2.0	1.8	1.9	4.7
	(%)	3.6	3.0	2.6	3.5
Lipid	(μg)	7.2	7.8	6.6	12.0
	(%)	13.3	13.0	9.2	8.9
Ash	(μg)	12.4	12.1	14.5	16.7
	(%)	22.9	20.0	20.0	12.4
Chitin	(μg)	4.5	6.8	30.7	29.6
	(%)	8.3	11.2	42.2	22.0
Protein: lipid		3.4	3.5	2.0	3.5
Energy	(J mg^{-1})	16.02	16.28	14.22	13.64
equivalents	(J ind^{-1})	0.88	0.96	1.05	1.84
incl./excl.	(J mg^{-1})	14.77	14.52	7.62	10.21
chitin	(J ind^{-1})	0.79	0.88	0.54	1.38
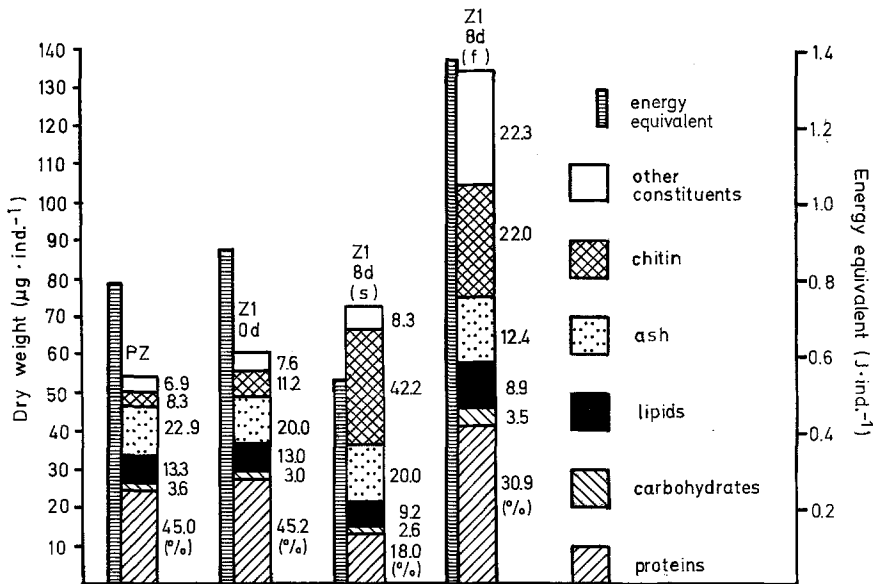
Fig. 7: *Hyas araneus:* Variation in dry weight, biochemical composition, and energy equivalents in early larval stages. PZ: praezoea stage; all other symbols as in Table 4. Biochemical constituents given in µg individual $^{-1}$ (left scale) and in % dry weight (numbers besides bars)

analyses (see above) indicated a relatively high metabolism in fed larvae during the first two days which could, in part, be caused by reconstruction processes in the larval body.

Eight days later (Z1 8d), much has changed in biochemical composition: starved zoeae (s) have lost 52.0 % of their initial protein, and 15.4 % of their lipid, while carbohydrates remain unchanged, and ash has increased by 19.8 %. The most striking alterations are found in the building-up of chitin and the catabolism of protein. Surprisingly, the amount of chitin is almost identical in fed and starved larvae after 8 days. Its fraction (22 % of dry weight in fed zoeae) is much higher than previously recorded data on planktonic crustaceans (e.g. Raymont et al., 1969, 1971; Childress & Nygaard, 1974). Thus, the formation of the exoskeleton seems to be completely independent of nutrition. The main metabolic substrate is protein. In the same period, fed larvae (f) have gained 52 % protein, 53.8 % lipid, 161.1 % carbohydrates, and 38.0 % ash; as in starved zoeae, chitin has increased by more than 300 % of the initial amount.

Due to the relatively lower building-up of lipid and protein as compared to chitin, energetic values of larval bodies, expressed as J mg^{-1}, are lower after 8 days feeding than in the beginning of larval development. Energy equivalents per individual, however, have considerably increased. Thus, if using those decapod larvae as food organisms, e.g. for fish or larger crustaceans, very early stages would be much more suitable than later ones, not only because of lower rearing costs, but also because each milligramme of available organic matter contains about 1.4 times more physiological energy than in later zoeae.

The average energy loss in starved zoeae (disregarding chitin) is about – 0.4 J per individual day^{-1}, but almost – 0.9 J mg^{-1} day^{-1}, while the gain in fed larvae is ca. + 0.6 J per individual day^{-1}. If chitin is included, no energy loss can be measured in starved larvae over

8 days. This surprising fact indicates an extremely low respiration rate under starvation conditions (c. f. Ikeda, 1977). Apparently, almost all available energy has been transformed to chitin without measurable loss.

The finding that protein can be utilized as main energy source during starvation corresponds to some observations in zooplankton physiology (e.g. Ikeda, 1971, 1974; Mayzaud, 1976). Generally, lipid is the major metabolic substrate (Lawrence, 1976), but predatory plankton organisms often do not have enough reserves of it, and thus have to use protein catabolism as energy producing process (Ikeda, 1974). Also, under good feeding conditions, metabolism of protein is much higher than that of lipid (Table 4; cf. Ikeda, 1977). Carbohydrates cannot be utilized to a noteworthy degree, since they constitute only a very small fraction in most planktonic animals.

Concluding remarks

Larvae of the spider crab *Hyas araneus* occur frequently in the plankton of the German Bight over a period of more than 4 months during late winter and spring (Fig. 2). If the populations of this decapod are fairly stable, larval mortality rate must be very high in nature. According to our laboratory observations, mortality is highest in zoeal stages, much lower in megalopae, and very low in benthic juveniles. That means that the most voracious stages in terms of large-particle feeding probably occur only in low numbers in the plankton. Thus it is likely that total energy input into the pelagic system by early larval stages of *H. araneus* is higher than the output due to plankton feeding by all larval stages. However, comparing the values in Tables 2 to 4 with those found for other plankton organisms in the biochemical literature cited above, crab larvae certainly do not constitute a major energy source as do, for example, copepods or other holoplankters. On the other hand, larvae of *H. araneus* are relatively large, slow swimmers. This fact might not only influence their own nutrition and distribution in the water column, but also the reponses of higher predators, which in part may depend on such kind of prey.

Further experiments on interspecific interaction – considering also behavioural traits, starvation ability, and biochemical composition comprising all larval stages – must be carried out in order to obtain a more reliable estimate of the role which these larvae play within the pelagic system of the German Bight and of comparable sea regions.

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