HELGOLÄNDER MEERESUNTERSUCHUNGEN
Helgoländer Meeresunters. 36, 285–302 (1983)

Moult cycle and morphogenesis in *Hyas araneus* larvae (Decapoda, Majidae), reared in the laboratory

K. Anger

Biologische Anstalt Helgoland (Meeresstation);
D-2192 Helgoland,
Federal Republic of Germany

ABSTRACT: Moult cycle and morphogenesis in larval instars (zoea I, zoea II, megalopa) of the spider crab *Hyas araneus* (L.) were studied in the laboratory. Changes in the epidermis and cuticle were documented photographically at daily intervals to characterize the stages of the moult cycle. Stage A (early postmoult) is a very short period during which the larva takes up water. During late postmoult (B) and intermoult (C) the endocuticle is secreted, and there is conspicuous epidermal tissue condensation and growth. The onset of early premoult (D_0) is characterized by epidermal apolysis, occurring first at the bases of the setae in the telson of zoeal instars or in the rostrum of the megalopa, respectively. Intermediate premoult (D_1) is the main period of morphogenesis, in particular of setogenesis: in the setae of the zoeal telson and carapace there is invagination or (in the zoea II) degeneration of epidermal tissues. Formation of new setae in the interior of epidermal tubules was observed in zoeal maxillipeds and in the antennae of the zoea II and megalopa instars. During late premoult (Stages D_{2-4}) part of the new cuticle is secreted, and the results of morphogenesis become clearly visible. For technical reasons (rigid exoskeleton) only a preliminary account of the moult cycle in the megalopa can be given. A time schedule is suggested for the stages of the moult cycle. It is estimated that postmoult (A–B) takes ca 9 to 15 % of total instar duration, intermoult (C) ca 22 to 37 %, and premoult (D) ca 48 to 69 %. There is an increasing trend of relative portions of time (% of total instar duration) from instar to instar in Stages A–C (mainly in the latter) and a decreasing trend in Stage D (mainly in D_0 and D_{2-4}).

INTRODUCTION

Postembryonic development and growth of crustaceans is dependent on the repeated process of moulting. Shortly after each ecdysis, a new cycle of morphological changes begins in the epidermal and cuticular structure. These progressive moult preparations, which are termed "moult cycle", can be classified in decapods according to the system proposed by Drach (1939) and extended by Tchernigovtzeff (1965) and Drach & Tchernigovtzeff (1967).

Moult cycles or parts thereof have been investigated in many adult crustaceans (Herp & Bellon-Humbert, 1978; Dexter, 1981; Buchholz, 1982), but only in few larvae: Broad & Hubschmann (1963) noted some gross morphological details in shrimp larvae *(Palaemonetes kadiakensis)* and Rao et al. (1973) briefly described changes from intermoult to early premoult in lobster larvae *(Homarus americanus).* Herp & Bellon-Humbert (1978) gave a detailed account of the moult cycle in *Astacus leptodactylus* larvae. McNamara et al. (1980) studied morphological and physiological changes during the first larval stage of *Macrobrachium olfersii.* These larvae are well comparable to the

juveniles of penaeid prawns *(Penaeus californiensis* and *P. stylirostris)* investigated by Huner & Colvin (1979). Only Freeman & Costlow (1980) and McConaugha (1982) described morphogenesis and moult cycle in brachyuran larvae *(Rhithropanopeus harrisii).*

Besides these at least in part morphological studies there are a number of others referring to the hormonal and biochemical changes related to the moult cycle (Freeman & Costlow, 1979, 1980; McConaugha & Costlow, 1981; McConaugha, 1982).

The present investigation attempts to describe morphological changes in the epidermis and cuticle of larval spider crabs, *Hyas araneus* (Brachyura), and to provide a time scale for these events. Knowledge of the relative durations of the moult cycle stages is of utmost importance for the understanding of changes in larval food requirements (Anger & Dawirs, 1981; Anger et al., 1981), growth patterns, and biochemical processes (Anger & Dawirs, 1982; Anger et al., 1983; Dawirs, 1983). The external morphology of *H. araneus* larval instars has been described in detail by Christiansen (1973).

MATERIAL AND METHODS

Larvae of *Hyas araneus* were obtained from ovigerous females collected near Helgoland (North Sea), reared individually at constant 12 °C, and fed *Artemia* spec. nauplii and *Brachionus plicatilis* as described in detail by Anger & Dawirs (1981).

Samples of live larvae (3 to 5 individuals) were taken from culture vials at 24 h intervals and pipetted into a compression chamber as designed by Uhlig & Heimberg (1981). They were examined by means of an inverted transmitted light microscope "Axiomat IDC" (Zeiss, W. Germany), applying differential interference contrast (Nomarski). After having been pressed between the coverslips the larvae died. Therefore, new individuals had to be taken every day for microscopical examination. Fotos were taken with a built-in 35 mm camera (Zeiss) using Agfapan Professional ASA 25 (Agfa Gevaert, W. Germany) film and automatic exposure control.

Changes in the internal structures (epidermis and cuticle) were studied and documented at daily intervals during the entire larval development, which took ca 2 months.

The study concentrated on the following parts of the larval body: in the zoeal instars mainly the telson was examined, additionally the dorsal and rostral carapace spines, the antennae, and the maxillipeds. Of the telson the median part was examined thoroughly (Fig. 1), including (a) the bases of the three inner setae on each side, (b) the region around the lateral spine, and (c) the outer margin of the telson adjacent to the lateral

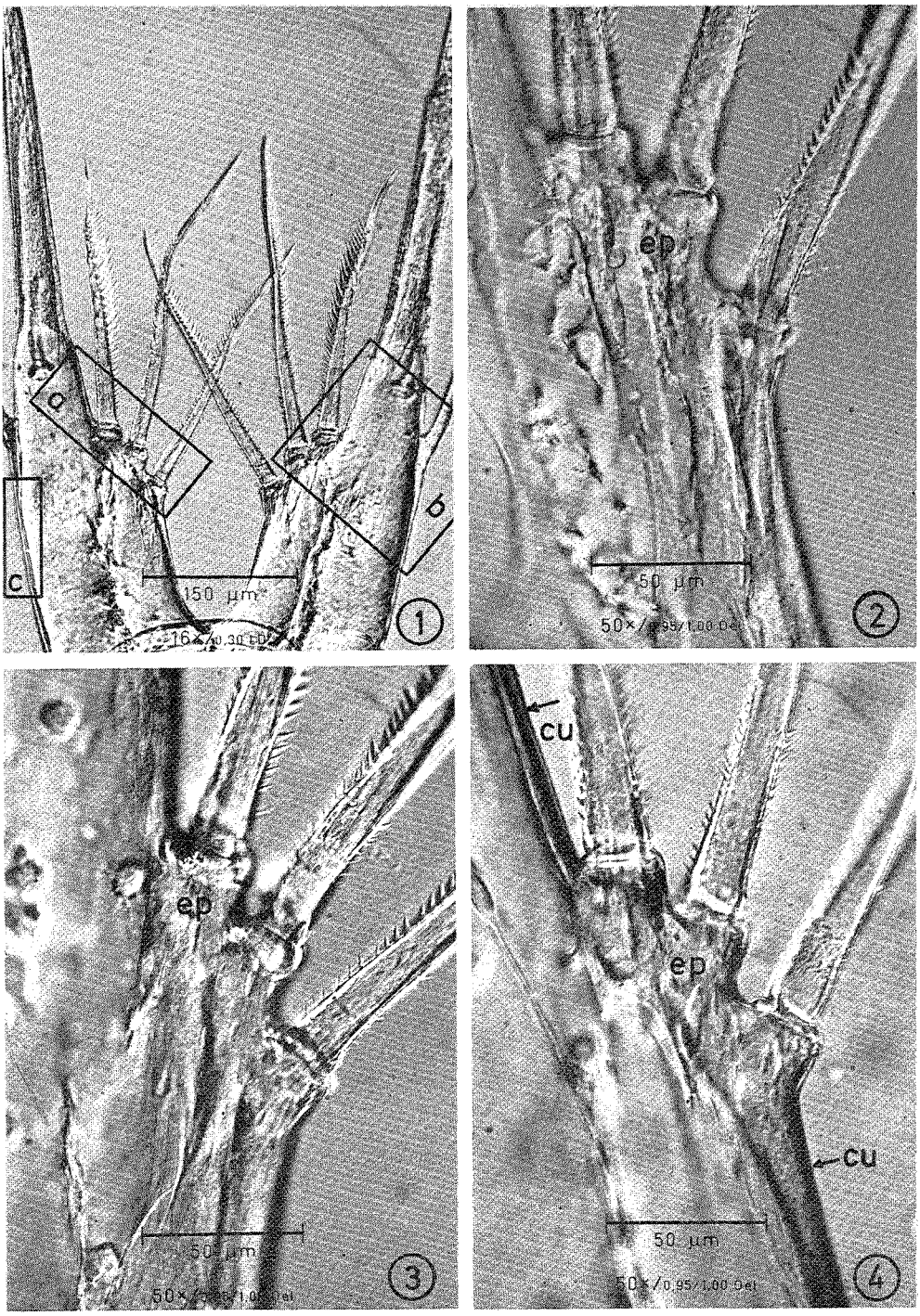
---

Fig. 1. *Hyas araneus,* zoea I: telson with areas of reference. a = bases of inner setae; b = region of the lateral spine; c = outer margin

Fig. 2. *Hyas araneus,* zoea I: telson (region a in Fig. 1) with spongy epidermis (ep). Stage A (immediately after hatching)

Fig. 3. *Hyas araneus,* zoea I: telson (region a in Fig. 1) with condensing epidermis (ep). Stage B (less than 1 day after hatching)

Fig. 4. *Hyas araneus,* zoea I: telson (region a in Fig. 1); with condensed epidermis (ep) and reenforced cuticle (cu). Stage C (2 days after hatching)


a
b
c
150 µm
1
ep
50 µm
2
ep
50 µm
3
cu
ep
cu
50 µm
4

spine. At the latter site, the cuticle thickness was measured. In the second instar, the limb buds were considered as well.

In general, carapace spines are less suitable for use in stage-classifying than the zoeal telson, because in the latter it is much easier to find exactly the same spot in different individuals. In the megalopa, observation of internal structures was difficult because of the much more rigid exoskeleton and the lack of long, transparent spines. In this instar, mainly the rostrum and the antennae were examined. The thickness of the cuticle was measured, in this case at the margin of the rostrum and in the fourth segment of the antennal flagellum.

To prevent confusion of the stages of larval development with those of the moult cycle, the term "stage" will be used to designate a unit of the moult cycle, using Drach's nomenclature, whereas the instars of larval development will be referred to by their name (zoea I, zoea II, megalopa) or in general by the term "instar". The very first instar, the praezoea, lasts only a brief period of a few minutes to maximally a few hours. It is not considered in this investigation. The term "hatching" therefore refers here to the moult from the prezoeal to the first zoeal instar.

RESULTS

Zoea I

Stage A (early postmoult)

Immediately after moulting, the exoskeleton is very thin, the larval body is completely soft. This can be ascertained by probing with forceps. The epidermal tissues have a spongy structure (Fig. 2). The thickness of the cuticle at the outer margin of the telson is ca 1.3 (1.2 to 1.4) µm.

Stage A is a very brief period (less than one hour) in which the larva takes up water until the cuticle is fully extended and the body with all its spines and appendages has gained the final shape characteristic of the instar.

Stage B (late postmoult)

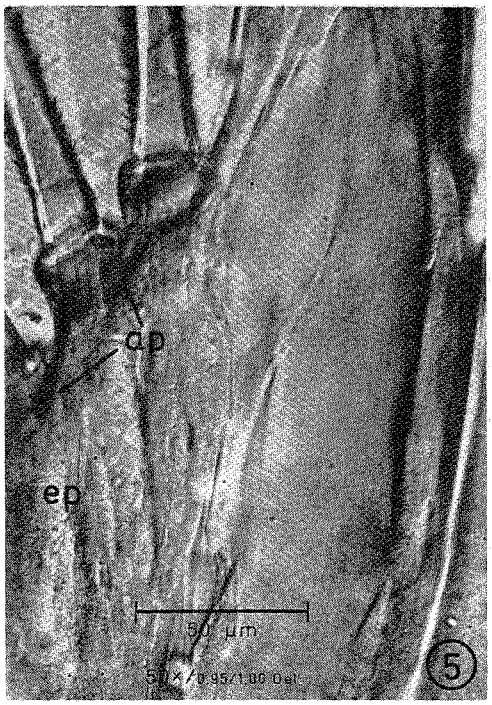
Most of the endocuticle is secreted during this stage. Thus, the exoskeleton becomes elastic and increasingly rigid. The epidermal tissues begin to concentrate along the cuticle surface, and they become denser compared to those of early postmoult (Fig. 3).

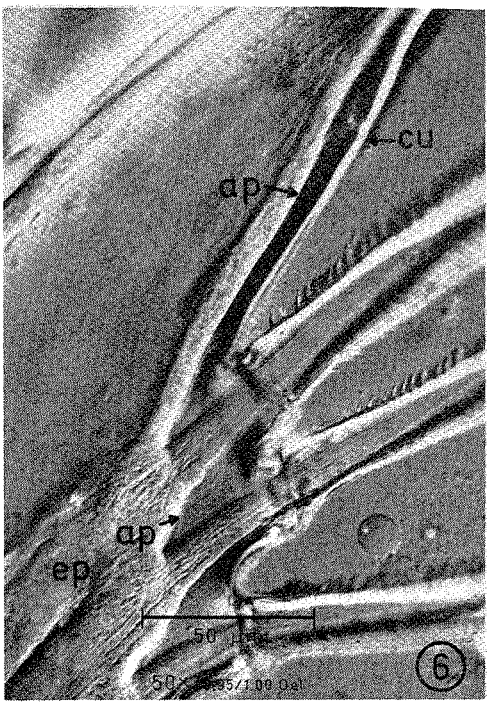
Fig. 5. *Hyas araneus*, zoea I: telson (regions a and b in Fig. 1) with growing epidermis (ep); apolysis (ap) at setal bases. Stage D_0 (4 days after hatching)

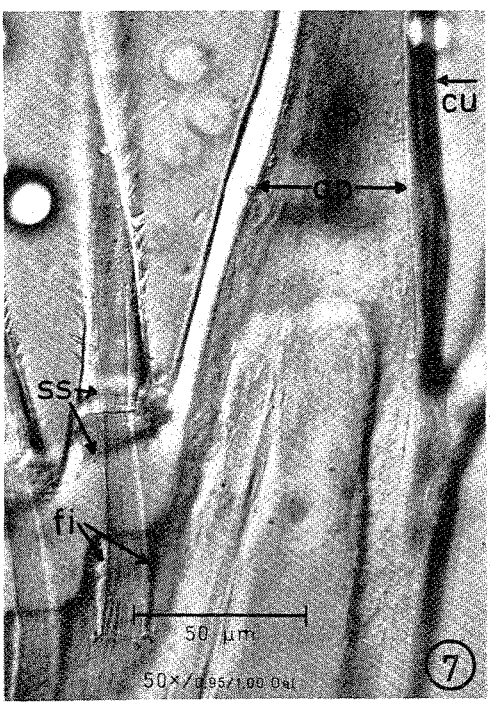
Fig. 6. *Hyas araneus*, zoea I: telson (region a in Fig. 1); epidermis (ep) with advanced apolysis (ap) at setal bases and in the outer ramus; cu = cuticle. Stage D_o, early premoult, (advanced; 6 days after hatching)

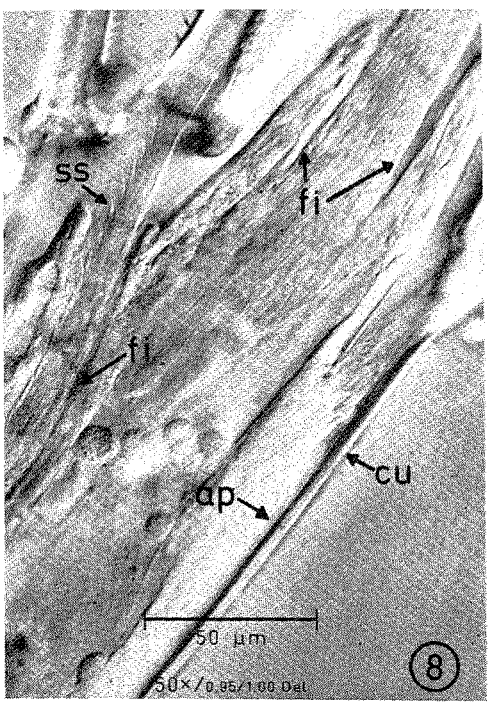
Fig. 7. *Hyas araneus*, zoea I: telson (regions a and b in Fig. 1); outer ramus filled with epidermal tissue (ep), showing advanced apolysis (ap); fold of invagination (fi) at setal bases; secondary spinules (ss) on new setae; cu = cuticle. Stage D_1 (early; 7 days after hatching)

Fig. 8. *Hyas araneus*, zoea I: telson (regions a, b and c in Fig. 1); deep folds of invagination (fi) at setal bases and in the proximal part of the inner ramus; new setae with secondary spinules (ss); outer margin with old cuticle (cu) and epidermal apolysis (ap). End of Stage D_1 / beginning of D_2 (8.5 days after hatching)


ap
ep
50 µm
50×/0.95/1.00 Oel
5


cu
ap
ap
ep
50 µm
6


cu
ap
ss
fi
50 µm
50×/0.95/1.00 Oel
7


ss
fi
fi
cu
ap
50 µm
50×/0.95/1.00 Oel
8

Postmoult Stages A and B combined last for ca 1 day at 12 °C. The cuticle at the outer margin of the telson reaches ca 3.5 (3.4 to 3.7) µm, when intermoult (Stage C) is approached.

Stage C (intermoult)

Condensation of the epidermal tissues continues (Fig. 4), accompanied by increasing tissue growth toward the end of this stage (cf. Fig. 5). The endocuticle is still being reinforced, but the rate of secretion decreases and finally ceases during intermoult. At the outer margin of the telson, the cuticle thickness finally reaches ca 4.8 (4.6 to 5.0) µm.

The mean duration of Stage C is ca 2.5 days at 12 °C. It is characterized by a lack of drastic morphological changes, by the completion of the endocuticle, and by an apparent accumulation of living biomass (tissue growth) in the entire larval body.

Stage D_0 (early premoult)

Epidermal tissues have further increased in both volume and density (Fig. 5). Separation of the epidermal matrix from the cuticle (apolysis) can be observed first under the articulation of the inner setae of the telson, ca 3.5 days after hatching of the zoea I (Fig. 5). During the following ca 3 days of development, the epidermis attains an increasingly fibrous structure, and apolysis proceeds in the rami of the bifurcated telson (Fig. 6), in the carapace spines, and in the appendages. Due to continuing epidermal cell growth, the distal parts of larger spines and of the telson rami become solidly filled with dense tissue (cf. Fig. 7). At the end of this stage of the moult cycle, the first secondary spinules already begin to appear on the new setae, i.e. before the first signs of invagination can be observed.

Stage D_1 (intermediate premoult)

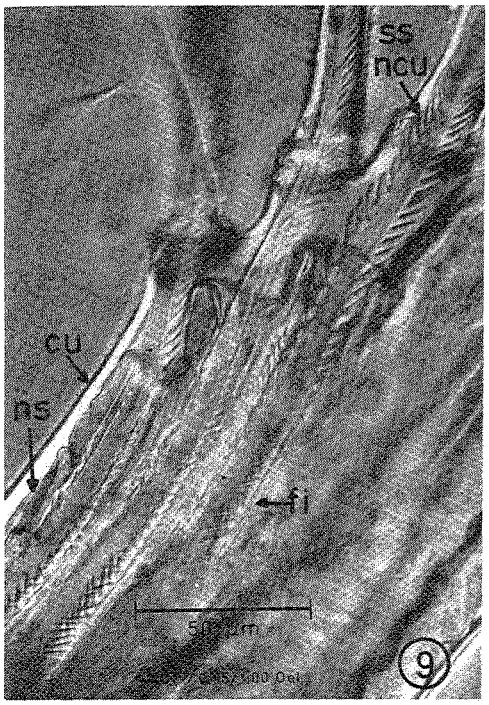
Seven days after hatching, invagination has already started with the articulation of the inner telson setae, and the secondary spinules are now clearly visible (Fig. 7). Retraction of the new spines, antennae, and telson branches from the sheaths of old cuticle continues during Stage D_1, which lasts for ca 2 days. In the second half of this phase, invagination and formation of secondary spinules also take place there. Figure 8 shows the beginning of invagination in a ramus of the telson and contemporarily advanced morphogenesis in an inner seta. Apolysis now starts in the maxillipeds.

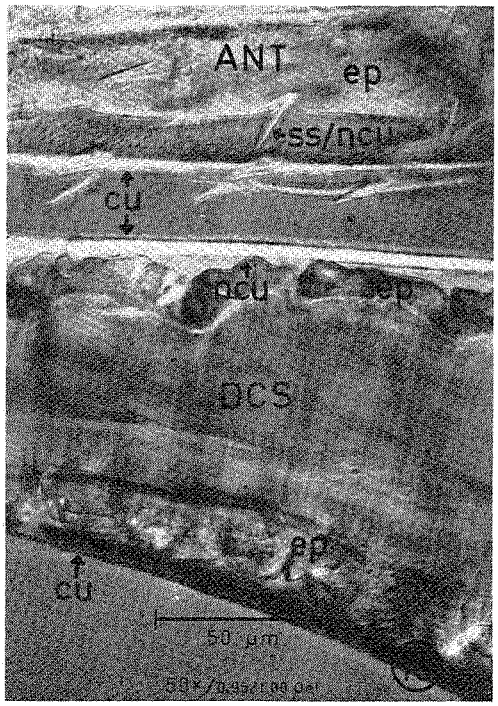
Fig. 9. *Hyas araneus*, zoea I: telson (region a in Fig. 1); new inner lateral seta (ns) of the zoea II instar; maximum invagination (fi); new cuticle (ncu) conspicuous on secondary spinules (ss); cu = old cuticle. Stage D_{2-4} (10 days after hatching)

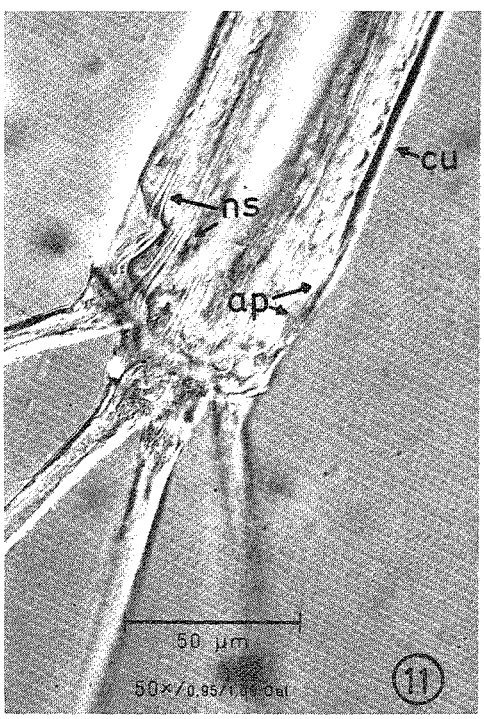
Fig. 10. *Hyas araneus*, zoea I: dorsal carapace spine (DCS) and antenna (ANT); detached epidermis (ep), in the antenna with secondary spinules and new cuticula (ss/ncu), pleated in the dorsal spine; cu = old cuticle. Stage D_{2-4} (10 days after hatching)

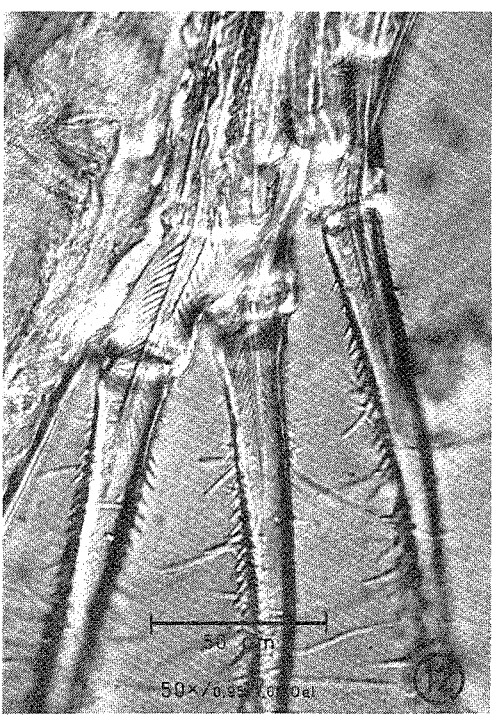
Fig. 11. *Hyas araneus*, zoea I: exopodite of maxilliped with old cuticle (cu), advanced apolysis (ap), reduced epidermis in the natatory setae; new setae (ns) formed inside epidermal tubules. Stage D_{2-4} (9 days after hatching)

Fig. 12. *Hyas araneus*, zoea I: telson (region a in Fig. 1); new setae withdrawing from old setal sheaths. Stage D_{3-4} (11 days after hatching; immediately before moulting)


ss
ncu
cu
ns
fi
50 µm
9


ANT
ep
ss/ncu
cu
ncu
ep
DCS
ep
cu
50 µm


cu
ns
ap
50 µm
11


50 µm

In the distal region of the old setae and spines, a long filament appears, which separates the old and new processes. The epidermis in the proximal parts of the new antennae and long spines acquires a pleated appearance, whereas in the distal regions it remains unfolded with clearly visible spinules developing on its surface (cf. Fig. 10).

The epidermal tissues in the natatory setae on the maxilliped exopodites detach from the cuticle during Stage D_1 and begin to degenerate. Stage D_1 may be defined as the time when morphogenesis of new epidermal structures mainly takes place. At the end of this stage, ca 8.5 days after hatching of the larva, the fold of invagination has reached its farthest point in all setae, and it is highly advanced in the branches of the telson as well as in spines and antennae. Completely new setae and appendages (e.g. two additional setae on the inner margin of the telson; Fig. 9) are formed during this stage. The epidermis still lacks a new cuticle.

Stages D_{2-4} (late premoult)

It would be very difficult and arbitrary to discern the temporal sequence of premoult Stages D_2 to D_4 in *H. araneus* larvae. Therefore, in accordance with Freeman & Costlow (1980), they are considered as combined in this study.

The beginning of Stage D_2 is characterized by the appearance of new cuticle. This is first visible on the setae and secondary spinules of the telson (Fig. 9), then on all other surfaces of the epidermis, which has meanwhile completely retracted from the exoskeleton along the spines, antennae, and other appendages (Fig. 10).

Morphogenesis taking place in the distal segment of the maxilliped exopodites becomes clearly visible in Stage D_2, when the new cuticle is secreted: new natatory setae (6 instead of 4) are formed in deep tubules within the epidermis of this segment, while the epidermis in the old setae is resorbed (Fig. 11).

Shortly before moulting (D_{3-4}), the epidermis reaches its greatest retraction from the old cuticle, and new setae withdraw from their old sheaths (Fig. 12). No microscopical evidence has been found that there is significant degeneration in the old larval exoskeleton: the thickness of the cuticle at the margin of the telson was not found to decrease during the final period of the moult cycle. When probing with forceps, however, the larvae appeared to have a softer carapace cuticle than that of earlier premoult and intermoult.

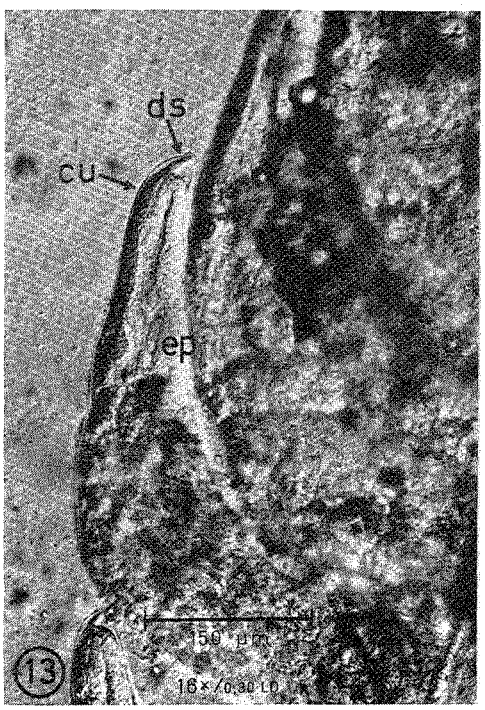
Observations suggest that Stage D_2 takes up most of the time of late premoult, which altogether lasts for ca 3 days. Moulting (Stage E) is a very brief process. As frequently observed in the laboratory, it takes only a few minutes. There is no coordination of moulting with the daily light cycle.

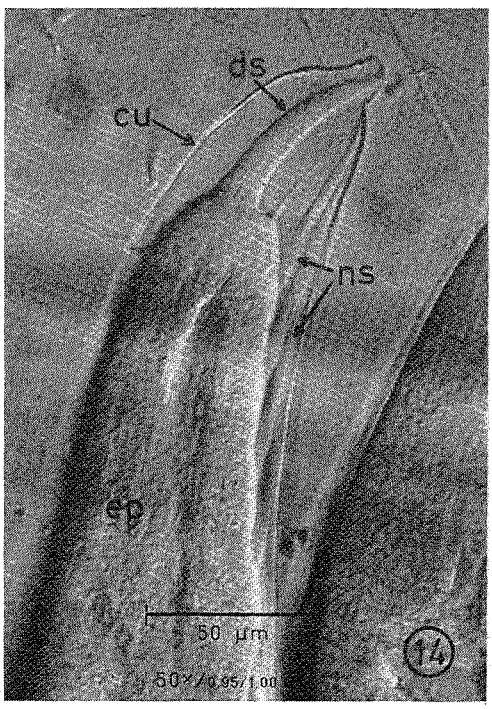
Fig. 13. *Hyas araneus*, zoea II: pereiopod buds with cuticle sheath (cu) and dactyl spine formation (ds); ep = epidermis. Stage C (5 days after moulting)

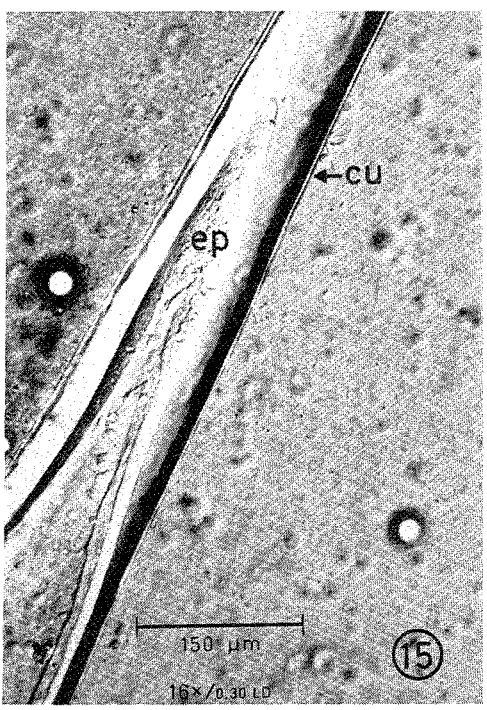
Fig. 14. *Hyas araneus*, zoea II: pereiopod bud with advanced dactyl spine formation (ds) and developing new setae (ns); ep = epidermis; cu = cuticle sheath. Stage D_0 (7 days after moulting)

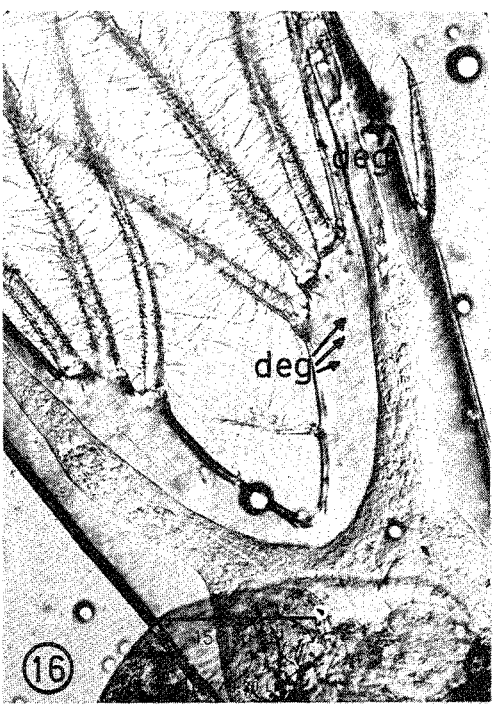
Fig. 15. *Hyas araneus*, zoea II: megalopal rostrum developing within the cuticle sheath (cu) of the rostral spine; ep = epidermis. Stage D_1 (11 days after moulting)

Fig. 16. *Hyas araneus*, zoea II: telson with degenerating epidermis (deg) in the rami, setae, and spines. Stage D_1 (9 days after moulting)


ds
cu
ep
50 µm
13
16×/0.30 LD


ds
cu
ns
ep
50 µm
14
50×/0.95/1.00


cu
ep
150 µm
15
16×/0.30 LD


deg
deg
16

Zoea II

Stages A and B

Postmoult appears as in the zoea I (Figs 2 and 3). Shortly after moulting, the thickness of the cuticle at the outer margin of the telson is ca 2.8 (2.6 to 3) µm. This is about double the value found in the zoea I. It increases within 2 days to ca 4.7 (4.6 to 4.8) µm.

As in the zoea I, the concentration of epidermal tissue can be clearly observed in the telson, the carapace spines, the antennae, and in the megalopal limb buds. There is no clear transition between Stages B and C.

Stage C

Most characters are as in the zoea I (cf. Fig. 4). The final cuticle thickness (see above) reaches ca 7.7 (7.5 to 8.0) µm 6 days after moulting. It is again about double the thickness measured in the zoea I.

Unlike the situation in the zoea I, some morphogenesis already occurs during intermoult: there is evident dactyl spine formation in the thoracic appendages (limb buds) (Fig. 13).

Stage D_0

The first gaps between retracting epidermis and cuticle are observed 6 days after moulting. Apparent detachment begins at both the inner and outer margins of the telson in the region of the outer and dorsal spines. Epidermis retraction is similar to that in the zoea I instar (Figs 5 and 6).

Already on day 7 of zoea II development there is far advanced apolysis in the telson, in the carapace spines, and in the antennae. Retraction of setae and spines from their sheaths begins earlier in Stage D_0 than in the zoea I instar. By day 8 apolysis is complete, and retraction of setae and spines is much advanced.

Morphogenesis of the limb buds proceeds fast during this stage: in the chelipeds myomere formation begins, and the differentiation of the dactyl spine and of setae in the posterior pereiopods is advanced (Fig. 14).

Stage D_1

In contrast to the zoea I, the intermediate phase of premoult is characterized more by epidermal degeneration than by invagination. The tissues of carapace spines are

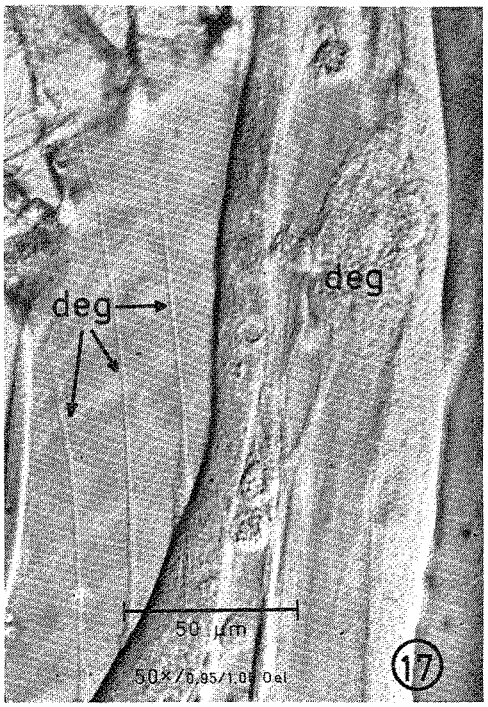
---

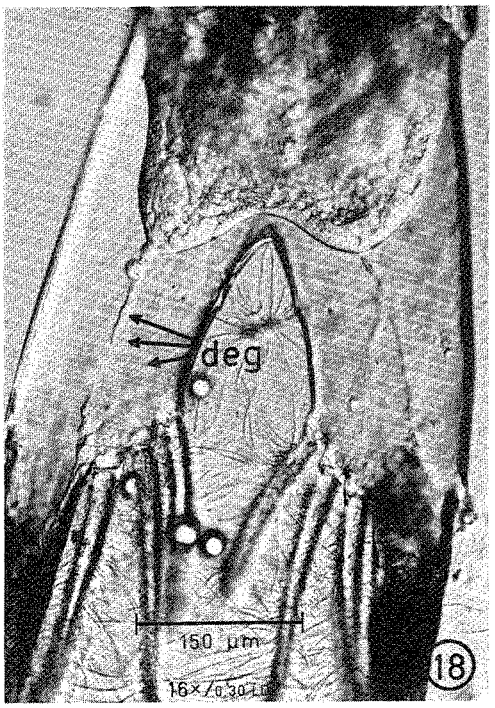
Fig. 17. *Hyas araneus*, zoea II: telson with degenerating epidermis (deg) in the outer ramus and the inner setae. Stage D_1 (9 days after moulting)

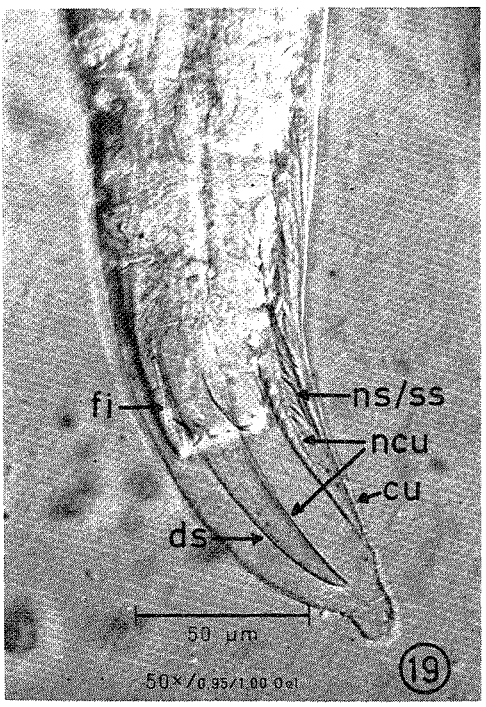
Fig. 18. *Hyas araneus*, zoea II: telson with advanced degeneration (deg) of epidermis; shape of megalopal telson already formed. Stage D_{2-4} (12 days after moulting)

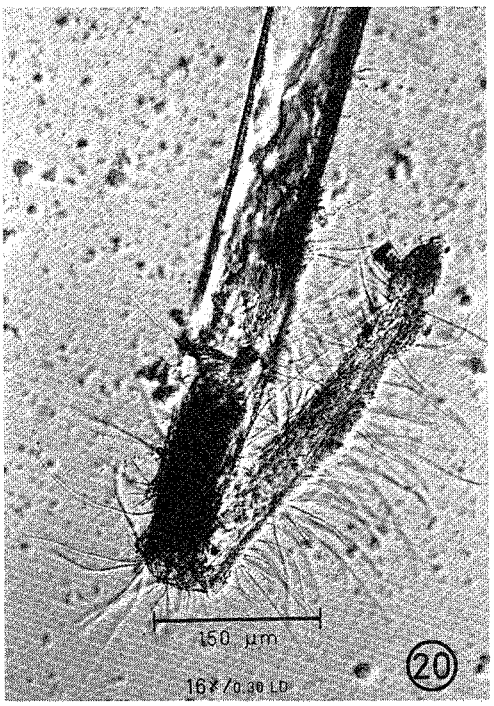
Fig. 19. *Hyas araneus*, zoea II: megalopal pereiopod inside the cuticle sheath (cu) of the limb bud; dactyl spine (ds) with fold of invagination (fi), new setae (ns), secondary spinules (ss), and new cuticle (ncu). Stage D_{2-4} (11 days after moulting)

Fig. 20. *Hyas araneus*, zoea II: dorsal spine with signs of degenerating cuticle and fungal filaments. Stage D_{2-4} (13 days after moulting)


deg
deg
50 µm
17


deg
150 µm
18


fi
ns/ss
ncu
cu
ds
50 µm
19


150 µm
20

resorbed, beginning from the tips and proceeding proximally. In addition, the megalopal rostrum is now formed within the sheath of the rostral spine (Fig. 15) by epidermal retraction and shrinking.

The branches of the telson with all spines and setae degenerate (Fig. 16, cf. Fig. 18). The inner setae remain as thin filaments (Figs 17 and 18) until late premoult. As in the zoea I, those structures are found on the tips of all retracted processes such as spines and setae.

Morphogenesis of appendages is quite apparent during premoult in the zoea II, as the morphological changes toward the megalopa are much greater than between the zoeal instars. From the beginning of Stage D_1 (ca 8.5 days after moult) there is invagination in the proximal parts of the dactyl spines in the pereiopods (cf. Fig. 19), and myomere formation is completed during the ca 2 days this stage lasts. Morphogenesis of new structures can also be observed in the maxillipeds, the pleopods, and the antennae.

At the end of Stage D_1, somewhat less than 11 days after moulting, degeneration processes are more or less completed. The new telson has already attained the shape it will have in the megalopa instar (Fig. 18). This is much different from morphogenesis in the zoea I telson (cf. Fig. 9).

Stages D_{2-4}

Stage D_2 begins with the appearance of the new cuticle, ca 11 days after moulting. It can clearly be seen in the dactyl spine, the setae, and the secondary spinules of the pereiopods (Fig. 19), which had been completed in their final morphology during Stage D_1.

In late premoult there are some microscopical indications of partial exoskeleton degeneration in the distal parts of the carapace spines and of the telson: in those regions the cuticle appears thin, and it often turns dark and tends to break away (Figs 18 and 20). Close examination suggests, however, that chitin is, to a great extent, not resorbed there by the larval body, but rather by fungi settling preferably on "hollow" parts of the exoskeleton (Fig. 20). Probing of the exoskeleton reveals that at least in the carapace region there must be some resorption of the old cuticle by the larval body.

Megalopa

Stages A–C

As in the previous stages. The cuticle thickness was measured (1) at the margin of the rostrum in the region where it narrows, near the border of the third and fourth segments of the antennal flagellum; (2) in the middle of the fourth segment of the antennal flagellum. Shortly before moulting (still in the sheath of the rostral spine of the zoea II [cf. Fig. 15]) and shortly after it (Fig. 21a), the rostral cuticle thickness is ca 2.6 (2.4–2.8) µm. Four days after moulting it has grown to ca 5.9 (5.7–6.2) µm, the approximate final thickness. In the antennal flagellum, the cuticle is reenforced from initially ca 1.5 (1.3–1.6) µm to ca 2.7 (2.5–2.8) µm during the same time span.

Three to four days after moulting the epidermal tissues have condensed considerably, and most of the endocuticle has been secreted (Fig. 21). This may be defined as the approximate border between Stages B and C in the megalopa instar.

As in the zoeal instars, intermoult does not reveal drastic morphological changes. Stage C is mainly characterized by apparent tissue growth, i.e. accumulation of living biomass.

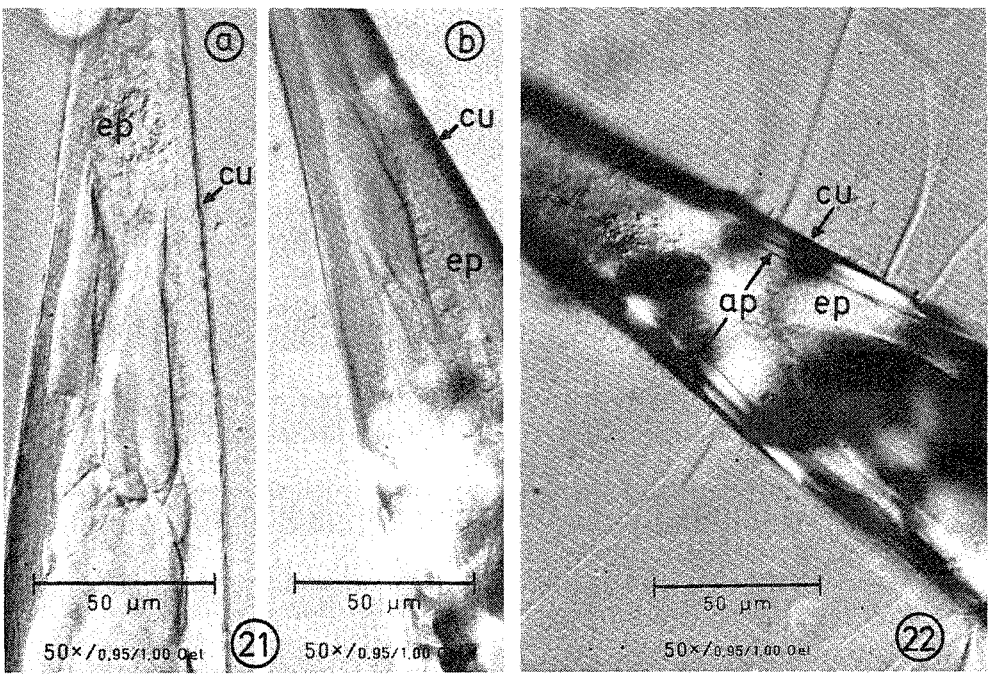


Fig. 21. *Hyas araneus*, megalopa: rostrum, (a) immediately after moulting (Stage A), and (b) one day later (Stage B). ep = epidermis; cu = cuticle

Fig. 22. *Hyas araneus*, megalopa: rostrum with detaching epidermis (ep), gap of apolysis (ap), cuticle (cu). Stage D_0 (14 days after moulting)

Stages D_{0-4}

The beginning of Stage D_0 can be clearly seen in the rostrum, when the epidermis detaches from the cuticle 14 days after moulting (Fig. 22). In the antennae, pereiopods, pleopods, and other appendages, apolysis does not appear until day 15 to 17.

18 days after moulting, separation of the epidermis from the cuticle is practically complete. Simultaneously, there ist evident morphogenesis of new setae and myomeres in the antennae. The rostral epidermis has been reduced to the approximate size and shape of the crab rostrum. This may be considered the beginning of Stage D_1. Advanced morphogenesis, accompanied by new cuticle formation (Stage D_2), becomes apparent ca 22 days after moulting.

The duration of premoult is highly variable. Metamorphosis in the megalopae used in this study occurred 23 to 32 days after moulting from the zoea II instar. The approximate mean duration of the premoult Stages D_0, D_1, and D_{2-4} may be estimated as 4, 4, and 5 days, respectively. These figures, however, must be considered preliminary,

as the simple microscopical methods applied in this study do not allow a reliable subdivision of the premoult stages in the megalopa because of its rigid and opaque exoskeleton. Further information will be gained employing histological techniques.

Absolute and relative durations of the moult cycle stages

An approximate time scale for the moult cycle stages in all larval instars is given in Figure 23.

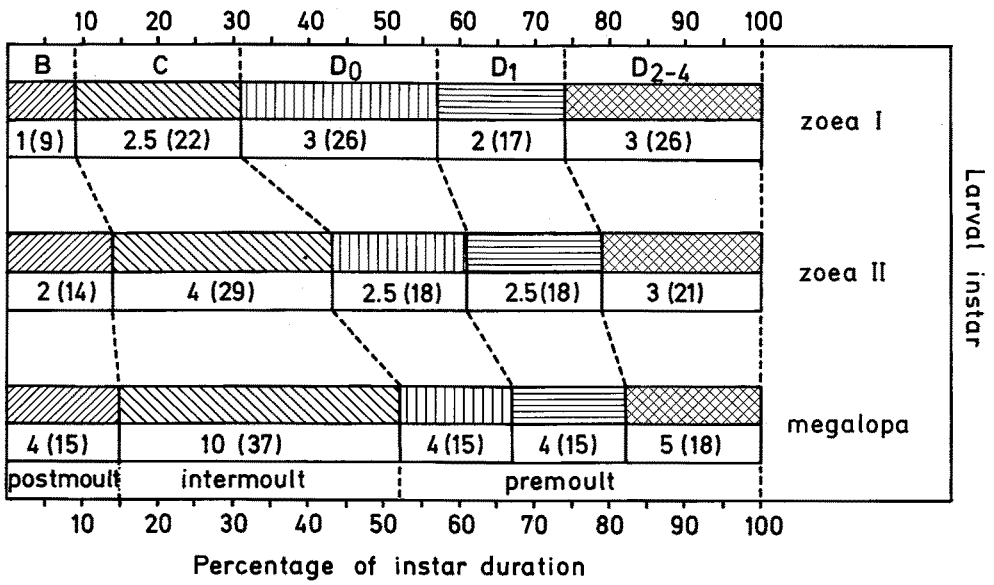


Fig. 23. *Hyas araneus:* time schedule for the moult cycle in all larval instars at 12 °C. Duration of the single stages given in days and as percentage of instar duration (the latter in parentheses)

The length of early postmoult (A) is negligible in comparison to the rest of the moult cycle in all larval instars of *H. araneus.* Therefore, it is omitted in Figure 23. Late postmoult (B) appears to increase slightly both in terms of absolute and relative figures from ca 1 day (9 % of instar duration) to ca 4 days (15 %) with larval development (Fig. 23). Since the transition between postmoult and intermoult is not very clear, this trend might be insignificant in percentage figures.

The intermoult period (C) increases conspicuously both in absolute and relative terms (Fig. 23). It amounts to circa one fifth to one fourth of zoea I duration, and more than one third of the megalopa. As a consequence, the relative time of premoult as a whole becomes shorter from instar to instar. The shortening of premoult takes place mainly in D_0 and, somewhat less, in D_{2-4}. D_1 appears rather constant in duration when relative figures are considered (15–18 %). Since total instar duration increases during larval development, this means increasing absolute time spans for intermediate premoult (D_1).

DISCUSSION

Classifying the stages of the moult cycle in decapod larvae bears a number of problems to be considered before attempting to compare our own observations with literature data: besides individual variation in the speed of development there is a lack of synchrony within different parts of the larval body. This is particularly obvious in events such as apolysis or invagination which can first be observed near the setal bases in the telson, and only later in larger spines or appendages. Similar variation was also observed by van Herp & Bellon-Humbert (1978) and Dexter (1981). Freeman & Costlow (1980) stated that "epidermal events occur at approximately the same rate in all regions of the integument"; however, they considered only the dorsal spines and antennae in *Rhithropanopeus harrisii* larvae. Since in *Hyas araneus* the moult cycle events are somewhat delayed in these parts of the larval body as compared to the telson, a similar pattern might be expected in *R. harrisii* too. In the present investigation the earliest occurrence of epidermal events was used to design a time schedule.

Individual variation in the occurrence of moult cycle events was found to be generally low in *H. araneus* zoeae. Preliminary observations suggest that individual variation in development time as found particularly in the megalopa instar may mainly be explained by variation in the late premoult period (D_{2-4}). This is probably in contrast to externally imposed variation due to starvation (Anger & Dawirs, 1981) or hormonal manipulations (Freeman & Costlow, 1980), which appear to affect mainly the intermoult period (C).

The technique of preparation is also of primary importance: as observed in preliminary experiments and also by Buchholz (1982), preservation of planktonic crustaceans in alcohol or formaldehyde results in artificially changed epidermal structures. Such artifacts may explain why Dexter (1981) found "apolysis" during intermoult. Therefore, the examination of live material certainly yields more reliable results than the study of preserved animals. The dissection of appendages as carried out e.g. by Herp & Bellon-Humbert (1978) and Buchholz (1982) can also change structures to be studied: when haemolymph pressure suddenly drops, the epidermis is often dislocated, and it can partially separate from the cuticle. For this reason, the compression chamber described by Uhlig & Heimberg (1981) was found to be suitable for the study of small crustaceans such as brachyuran larvae. Similar problems might be expected in other arthropods.

Drach's stage-classifying system (Drach & Tchernigovtzeff, 1967) appears to be generally applicable for decapod larvae also; however, modifications and extensions will be necessary, when more information on larval moult cycles is available. So far, the following characterizations may be suggested: there are no sharp transitions between early and late postmoult, and between the latter period and intermoult. During Stage A the larva actively takes up water and minerals, thus considerably increasing in both wet and dry weight (Anger & Dawirs, 1982). During that time, the epidermis appears heterogeneous (McNamara et al., 1980), granular and unstructured (Buchholz, 1982), or spongy (cf. section "Results").

During late postmoult (B) and intermoult (C), the epidermis in *H. araneus* larvae was found to condense and to grow (cf. Freeman & Costlow, 1980). "Stripe patterns" (Buchholz, 1982) or "setal tracks" (Dexter, 1981) were not observed in the present study. Condensation of tissues is accompanied by steep increase in biomass (dry weight,

carbon, nitrogen) and an equally steep decrease in the water content (Anger & Dawirs, 1982).

Anger & Dawirs (1981) suggested that premoult is started only after unknown essential substances (presumably sterols) have been taken up with food. When the amount of "reserves" exceeds a certain level, further development from D_0 through moulting runs automatically, independent of presence or absence of food. The time schedule given in Figure 23, together with the experimental results by Anger & Dawirs (1981) suggest again that in zoeal instars this "point-of-reserve-saturation" (PRS) is identical to the end of Stage C. Zoeae fed continuously have almost doubled their biomass at this stage (Anger & Dawirs, 1982). In the megalopa, the transition between intermoult and early premoult coincided with a maximum in biomass (Anger & Dawirs, 1982; Anger et al., 1983).

Summarizing, postmoult and intermoult may be considered combined as the period of cuticle formation, of reserve accumulation, and of rapid tissue growth.

The beginning of premoult is initiated by apolysis, the characteristic event of Stage D_0. With the exception of Dexter (1981; see above), this definition has been used consistently throughout the literature.

The following phase, D_1, is generally considered the period of setogenesis (e.g. Stephenson et al., 1968; Herp & Bellon-Humbert, 1978; Buchholz, 1982). There are probably two types of setogenesis: (1) epidermal invagination, and (2) stepwise formation of a doublewalled tubule in the interior of the epidermal tissue (Dexter, 1981). D_1 may be subdivided into two or more stages, the subdivisions being based on the increasing depth of invagination. Maximum depth is generally considered the sign for the end of D_1 (Stephenson et al., 1968; McNamara et al., 1980). Buchholz (1982) defined this time (D_1''') by the occurrence of secondary bristles. In *H. araneus* zoeae, however, secondary spinules were found already at the end of Stage D_0.

The two types of setogenesis were described by Drach (1944) and by Stephenson et al. (1968), respectively. Invagination appears to be the normal case in spines and short setae. The tubule type was observed in the natatory setae of the zoeal maxillipeds and in developing megalopal antennae of *H. araneus.* Although Dexter (1981) proposed a generalized scheme of setogenesis, many details of larval morphogenesis still remain unclear. The connections between the moult cycle and morphogenesis also require further analysis, since they appear to be partly independent processes (McConaugha, 1982).

Late premoult (D_{2-4}) is characterized by the formation of new cuticle. Partial degeneration of the old cuticle in Stage D_3 as known from adult crustaceans (e.g. Drach & Tchernigovtzeff, 1967) was not clearly observed microscopically in larval *H. araneus,* but it was suggested by mechanical probing of the carapace with forceps. Freeman & Costlow (1980) reported degeneration "in some regions" of the exoskeleton of *R. harrisii* larvae, however, without describing their observation in more detail. It must remain doubtful as to what extent this phenomenon plays a role in larval crustaceans.

Herp & Bellon-Humbert (1978) found setal extrusions during late premoult. They may have been caused by mechanical damage, when appendages were dissected. They have never been observed before ecdysis in *H. araneus* larvae. Dexter (1981) observed setal eversion only during ecdysis or shortly after it. Presumably, it is a typical event of Stage A.

The time schedule for moult cycle events given in Figure 23 can be compared with only very few literature data: the figures estimated for the zoea I instar are similar to those found by McNamara et al. (1980) in Stage I *Macrobrachium olfersii*. The time spans observed in the zoea II and megalopa can be compared to the last zoeal instar (IV) and megalopa in *R. harrisii* (Freeman & Costlow, 1980). From these data similar tendencies may be derived, i.e. relative prolongation of postmoult and intermoult with contemporaneously decreasing premoult durations from instar to instar. It is too early, however, to make generalizations or draw conclusions. Further studies including more species are necessary to estimate whether the present findings are specific for *H. araneus* or in any way typical for other decapod larvae. The megalopa instar will be the subject of closer examination, including histological techniques, as the present observations supply only preliminary information on its development. Additionally, the accelerating or retarding effects of external factors such as nutrition or temperature on the stages of the moult cycle will be investigated to gain better understanding of larval response patterns to those factors.

Acknowledgements. I am grateful to Mr. G. Sahling and Ms. B. Lämmel for processing the photographic material, and to Mr. M. Janke and Dr. E. Wahl for providing *Artemia* nauplii. My sincere thanks are also due to Dr. M. Rieper for correcting the manuscript.

LITERATURE CITED

Anger, K. & Dawirs, R. R., 1981. Influence of starvation on the larval development of *Hyas araneus* (Decapoda, Majidae). – Helgoländer Meeresunters. *34,* 287–311.

Anger, K., Dawirs, R. R., Anger, V. & Costlow, J. D., 1981. Effects of early starvation periods on zoeal development of brachyuran crabs. – Biol. Bull. mar. biol. Lab., Woods Hole *161,* 199–212.

Anger, K. & Dawirs, R. R., 1982. Elemental composition (C, N, H) and energy in growing and starving larvae of *Hyas araneus* (Decapoda, Majidae). – Fish. Bull. U. S. *80,* 419–433.

Anger, K., Laasch, N., Püschel, C. & Schorn, F., 1983. Changes in biomass and chemical composition of spider crab *(Hyas araneus)* larvae reared in the laboratory. – Mar. Ecol. Prog. Ser. *12,* 91–101.

Broad, A. C. & Hubschman, J. H., 1963. The larval development of *Palaemonetes kadiakensis* M. J. Rathbun in the laboratory. – Trans. Am. microsc. Soc. *82,* 185–197.

Buchholz, F., 1982. Drach's molt staging system adapted for euphausiids. – Mar. Biol. *66,* 301–305.

Christiansen, M. E., 1973. The complete larval development of *Hyas araneus* (Linnaeus) and *Hyas coarctatus* (Decapoda, Brachyura, Majidae) reared in the laboratory. – Norw. J. Zool. *21,* 63–89.

Dawirs, R. R., 1983. Respiration, energy balance and development during growth and starvation of *Carcinus maenas* L. larvae (Decapoda: Portunidae). – J. exp. mar. Biol. Ecol. *69* 105–128.

Dexter, B. L., 1981. Setogenesis and molting in planktonic crustaceans. – J. Plankt. Res. *3,* 1–13.

Drach, P., 1939. Mue et cycle d'intermue chez les Crustacés Décapodes. – Annls Inst. océanogr., Monaco *19,* 103–391.

Drach, P., 1944. Etude préliminaire sur le cycle d'intermue et son conditionnement hormonal chez *Leander serratus* (Pennant). – Bull. biol. Fr. Belg. *78,* 40–62.

Drach, P. & Tchernigovtzeff, C., 1967. Sur la méthode de la détermination des stades d'intermue et son application générale aux Crustacés. – Vie Milieu (A) *18,* 595–610.

Freeman, J. A. & Costlow, J. D., 1979. Hormonal control of apolysis in barnacle mantle tissue epidermis, in vitro. – J. exp. Zool. *210,* 333–345.

Freeman, J. A. & Costlow, J. D., 1980. The molt cycle and its hormonal control in *Rhithropanopeus harrisii* larvae. – Devl. Biol. *74,* 479–485.

Herp, F. van & Bellon-Humbert, C., 1978. Setal development and molt prediction in the larvae and adults of the crayfish, *Astacus leptodactylus* (Nordmann, 1842). – Aquaculture *14,* 289–301.

Huner, J. V. & Colvin, L. B., 1979. Observations on the molt cycle of two species of juvenile shrimp,

Penaeus californiensis and *Penaeus stylirostris* (Decapoda: Crustacea). – Proc. natn Shellfish. Ass. *69,* 77–84.

McConaugha, J. R. & Costlow, J. D., 1981. Ecdysone regulation of larval crustacean molting. – Comp. Biochem. Physiol. *68A,* 91–93.

McConaugha, J. R., 1982. Regulation of Crustacean morphogenesis in larvae of the mud crab, *Rhithropanopeus harrisii.* – J. exp. Zool. *223,* 155–163.

McNamara, J. C., Moreira, G. S. & Moreira, P. S., 1980. Respiratory metabolism of *Macrobrachium olfersii* (Wiegmann) zoeae during the moulting cycle from eclosion to first ecdysis. – Biol. Bull. mar. biol. Lab., Woods Hole *159,* 692–699.

Rao, K. R., Fingerman, S. W. & Fingerman, M., 1973. Effects of exogenous ecdysones on the molt cycles of fourth and fifth stage American lobsters, *Homarus americanus.* – Comp. Biochem. Physiol. *44A,* 1105–1120.

Stephenson, J. R., Guckert, R. H. & Cohen, J. D., 1968. Lack of correlation of some proecdysial growth and developmental processes in the crayfish. – Biol. Bull. mar. biol. Lab., Woods Hole *134,* 160–175.

Tchernigovtzeff, C., 1965. Multiplication cellulaire et régénération au cours du cycle d'intermue des crustacés décapodes. – Archs Zool. exp. gén. *106,* 377–497.

Uhlig, G. & Heimberg, S. H. H., 1981. A new versatile compression chamber for examination of living microorganisms. – Helgoländer Meeresunters. *34,* 251–256.