Postembryonic development of the parasitic amphipod *Hyperia galba**

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ABSTRACT: *Hyperia galba* Montagu is associated with gelatinous zooplankton as are many species of the Hyperiidea. The hosts preferred in the European seas are the large scyphomedusae *Aurelia aurita, Chrysaora hysoscella, Rhizostoma pulmo, Cyanea capillata* and *Cyanea lamarckii*, which harbour the first developmental stages. The anamorphic development produces young that are incapable of swimming at the time of hatching. They are characterized by an embryonic abdomen without extremities and external segmentation; the eyes are not completely developed and the mouth is primitive lacking bristles, molar and incisor. The postembryonic development, described in detail, is subdivided into two phases: the pantochelis phase and the protopleon phase; the former comprises only one stage; the latter can be subdivided into four stages. In the course of postnatal development the larval organs are reduced and characters typical of the adult are gradually differentiated. *H. galba* plays an important role as obligatory endoparasite of scyphomedusae at least during the first stages of development; without a host this amphipod cannot survive, neither benthically nor in the plankton. The transition from life in the female's marsupium to endoparasitism in the jellyfish generally occurs during stage of the postembryonic development which is the first stage of the protopleon phase. The specific adaptations of its reproductive biology to a parasitic mode of life such as moult inhibition under starvation, development of larval organs and the behavioural patterns of the females as well as the young are described. Further, the influence of external factors such as temperature and food supply on the course of development is examined.

INTRODUCTION

The representatives of the suborder Hyperiidea differ from other amphipod suborders not only in their mode of life but also in the course of their postembryonic development. After epimorphic embryonic development the freshly hatched gammarids resemble the adults to a large extent attaining their final shape by length increment and increasing segmentation of the antennae and the pleopods. Unlike the gammarids, the hyperiids exhibiting an anamorphic development hardly resemble the adults in their morphology at the time of hatching. The only exceptions known until now are *Hyperoche medusarum* (von Westernhagen, 1976) and *Parathemisto gaudichaudi* (Kane, 1963; Sheader, 1977). Extensive descriptions of the postembryonic development of hyperiid amphipods have been published for only a few species (Kane, 1963; Laval, 1963, 1965, 1968, 1980; Harbison, 1976).

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* Dedicated to Prof. Dr. H. Mergner on the occasion of his 70th birthday.

Protopleon stages of hyperiids have been roughly sketched in the literature, but a detailed description of the stages as well as of the complete larval development is so far lacking.

Early postembryonic stages of *Hyperia* have been referred to by Gosse (1853; Pl. XXII, Fig. 15): "... the larvae ... are not larger than a grain of sand, shaped somewhat like a toad, with the abdomen distinctly separated, narrow, and bent abruptly under, in the manner of the Brachyura." His illustration shows a young at the protopleon stage. Bate & Westwood (1868) gave only a general description of the young hyperiids: "The head of the young animal is small and the eyes, consequently, are not much developed. The body is very large, while the tail is narrow and straight and lies compressed beneath the body." Bovallius (1889) described a late protopleon stage of *Hyperia medusarum* as "the young just hatched".

Hollowday (1947) depicted as an "advanced embryo" with a body diameter of 590 μm a young of *Hyperia galba* apparently in stage II and the first protopleon stage, respectively. White & Bone (1972) reported on the larvae of the same species and gave sketches of them. The "pre-release marsupial instar" described by White & Bone represents a pantochelis stage while those found within the gastrovascular system correspond to protopleon stages. The description of the development given by White & Bone appears doubtful; the authors describe pleopods able to function for individuals at a minimum body length of 6 mm and assign them to the fifth or sixth instar. Goormaghtigh & Parmentier (1973) characterized the young of *Hyperia galba* as follows: "A l'éclosion, le jeune est presque entièrement formé. Au course de son développement ultérieur, il subit une mue par an." It is doubtful whether or not the organism dealt with is actually *H. galba*, as cited by the authors.

Hyperia lives parasitically on scyphozoans (Romanes, 1877; Pirlot, 1932; Alvarado, 1955; Dahl, 1959a, b; Metz, 1967; White & Bone, 1972; Rasmussen, 1973; Sheader, 1973; Thiel, 1976; Möller, 1978/79). The hosts preferred are – at least in the European seas – the comparatively large medusae of the species *Aurelia aurita, Chrysaora hysoscella, Rhizostoma pulmo, Cyanea lamarckii* and *Cyanea capillata*. Although Sokolowsky (1900) mentioned that in the waters around Helgoland, *H. galba* is not rarely seen, this species as well as other hyperiids has been disregarded in studies of pelagic organisms carried out in the German Bight. Since Hollowday's (1947) conclusion that little is known concerning the life history and reproductive periods of *H. galba* the situation has not changed very much.

The present publication is concerned with the reproductive biology of this parasitic amphipod. Investigations of its life cycle (Dittrich, 1986) have been carried out to explore to what extent *H. galba* ist adaptated to the parasitic way of life.

MATERIAL AND METHODS

The animals investigated were caught in the waters of the German Bight around Helgoland. During the months August to October ovigerous females were isolated from scyphomedusae. The eggs were rinsed out of the marsupium by means of a pipette and kept in shallow glass dishes at constant temperature.

The newly hatched hyperiids were kept individually in small glass vessels with a volume of about 50 ml filtered seawater. Rearing young *Hyperia* turned out at first to be

difficult because generally they lie on the bottom of the culture vessel and move – if at all – rather clumsily; food particles such as *Artemia* nauplii and tissue of medusae can be taken up only when in available reach of the young. Therefore, food organisms such as *Artemia*, being too agile alive, were fed after being frozen.

In the course of daily inspections, the exuviae cast off were collected and investi-. gated microscopically. It was possible to observe in detail the complete development of individuals. Some of the young hyperiids were fixed in 4 % glutaraldehyde after having reached a certain stage of development. For the electron microscopic investigation the samples were dehydrated in an alcohol series and dried using the "critical point"-method. A 5-minute gold sputtering, necessary for scanning electron microscopic obser-vations, followed.

RESULTS

Stages in the postembryonic development

The anamorphic development of *Hyperia galba* can be subdivided into two phases. According to the definition of Laval (1965, 1980), they can be defined as follows: (1) The pantochelis phase. Metasoma and urosoma are embryonic. The only extremities developed are the peraeopods. (2) The protopleon phase. The metasoma is segmented and bears incomplete pleopods. The urosoma is still undifferentiated.

The pantochelis phase

S t a g e I : The first postembryonic stage is characterized by a more or less spherical body showing no trace of pigmentation. The diameter of the body is approximately 0.5 mm (Fig. 2). This stage is found exclusively within the marsupium of the females. The eyes are not yet fully developed. The only extremities developed are the peraeopods represented in complete number. The embryonic abdomen bears no extremities and shows no external segmentation. The mouth parts are scarcely differentiated structures lacking bristles as well as the molar and the incisor (Fig. 1a). Apparently, solid food is not consumed at this stage; obviously, the supply is effected by the yolk store available in large amounts in the gut.

The protopleon phase

S t a g e II : Immediately after the first moult the young individuals stay in the marsupium; during the course of this stage they are released and deposited near the gonads and the canals of the gastrovascular system of the host. When passing over to stage II, the length increment is comparatively small; therefore, apparently, no young are evacuated from the marsupium because of lack of space therein.

As in stage I, the first and second gnathopods bear two spines at the ventro-distal margin of the propodus (Fig. 3d). There are two possible explanations of the function of these accessory prehensile organs: on the one hand they play an important part as an auxiliary organ when hatching; in gammarids the egg membrane is ruptured at the point of hatching by means of the hatching spines of the urosoma (Sheader, 1977); in young *Hyperia galba* this part of the body is of little importance because of its embryonic development. On the other hand, these grasping organs may secure the young in the marsupium which among hyperiids is formed by oostegites lacking any bristles. This assumption is supported by the fact that species inhabiting exposed areas show similar
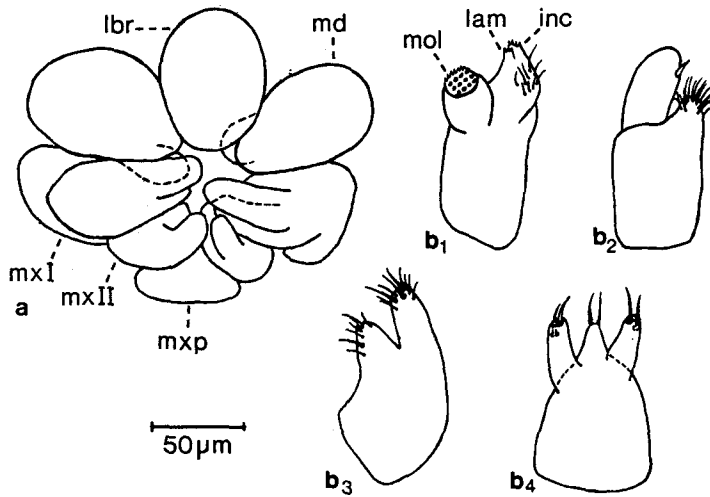
Fig. 1. Mouth parts of *Hyperia* larvae. a: Stage I; general view; b: Stage II; b_1: mandible; b_2: first maxilla; b_3: second maxilla; b_4: maxilliped. Abbreviations: inc = incisor, lam = lacinia mobilis, lbr = labrum, md = mandible, mol = molar, mxI = first maxilla, mxII = second maxilla, mxp = maxilliped

adaptations; the algae-inhabiting gammaridean species such as *Hyale pontica, Micro-deutopus chelifer* and *Pereionotus testudo* show — even in the adult stage — similar structures on the gnathopods to those of *H. galba* (Dittrich, 1983). From stage III on, these structures are no longer present in *Hyperia* individuals.

The mouth parts develop first bristles, and the mandibles bear a minute molar and a small incisor (Fig. 1b, 3b). The pleon is segmented, the urosoma not yet. The uropods and pleopods are recognizable as singly-lobed structures (Fig. 3c).

S t a g e   I I I : The third developmental stage as well as the following stages do not take place within the marsupium but on the scyphomedusae. The body is now slightly extended and attains a length of about 0.9 mm. The two thornlike protrusions on the first and second gnathopods have not developed any further. The pleopods are bilobate (Fig. 4) and, like the uropods, display a positive allometric growth during the next stages. Unlike the pleopods which are of equal length, the uropods already differ in size thus corresponding to their structure at the adult stage.

S t a g e   I V : With the third postembryonic moult, morphological changes take place mainly in the abdominal region (Fig. 5). The pleopods and uropods undergo further differentiations; nevertheless, the rami are not yet separated from the pedunculus. The urosoma is — at least externally — still unsegmented.

S t a g e   V : Having reached a total body length of about 1.7 to 1.9 mm (Fig. 6a), most of the individuals form the first pigment, namely the red component, within the chromatophores. In the eyes, the pigments are deposited in a small kidney-shaped, light red structure. The urosoma is segmented and bears uropods, of which the rami and the pedunculus are developed completely; generally they are separated from each other only in the third pair of uropods (Fig. 6b). In most of the pleopods, the rami are separated from the pedunculus; frequently, the pleopods show first plumose bristles at the tip of the rami which are not yet further segmented. Occasionally, the insides of the pleopod pedunculi
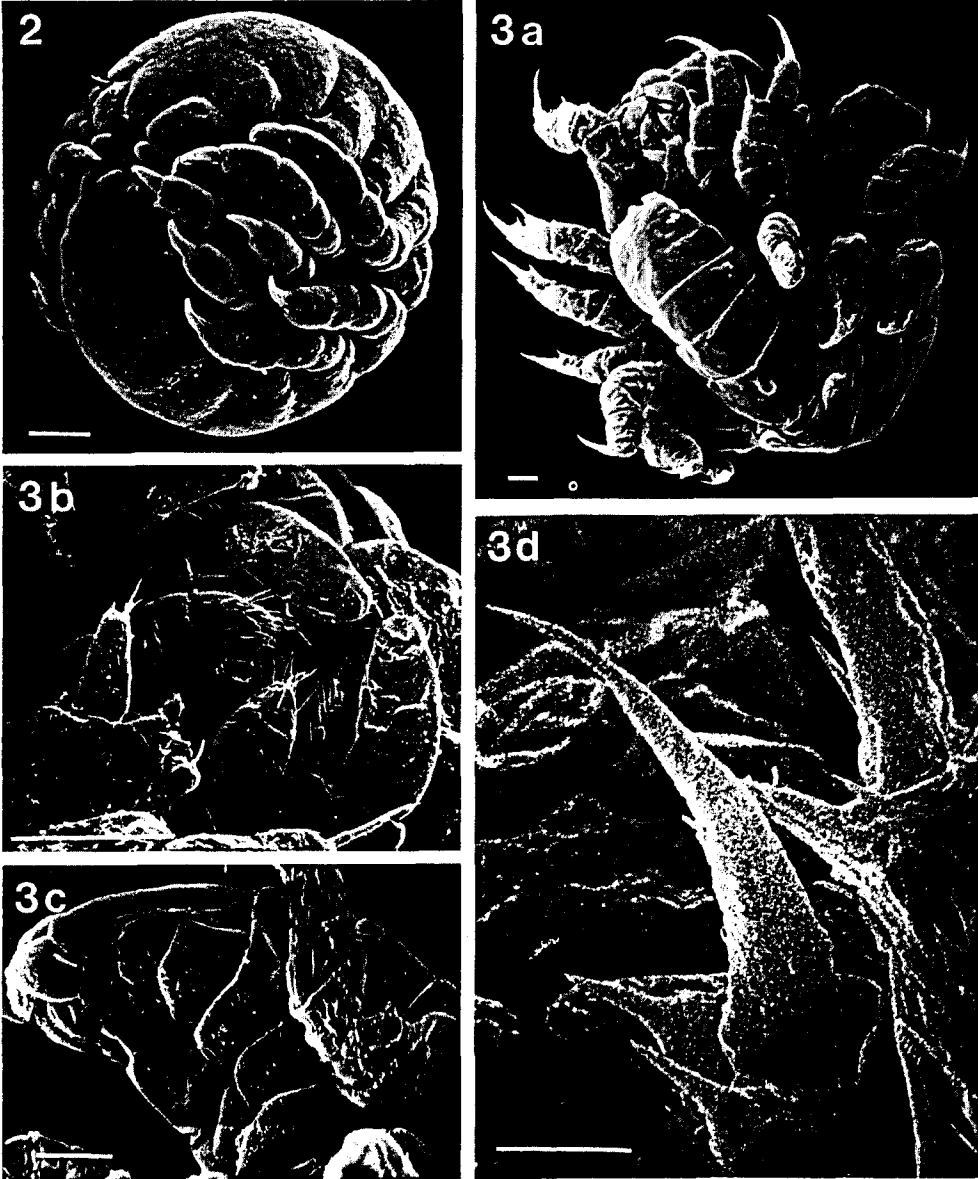
Fig. 2. Stage I (newly hatched *Hyperia* larva)

Fig. 3. Stage II; a: habit; b: mouth parts; c: abdomen; d: prehensile structures on the propodus of the 1st and 2nd gnathopods.
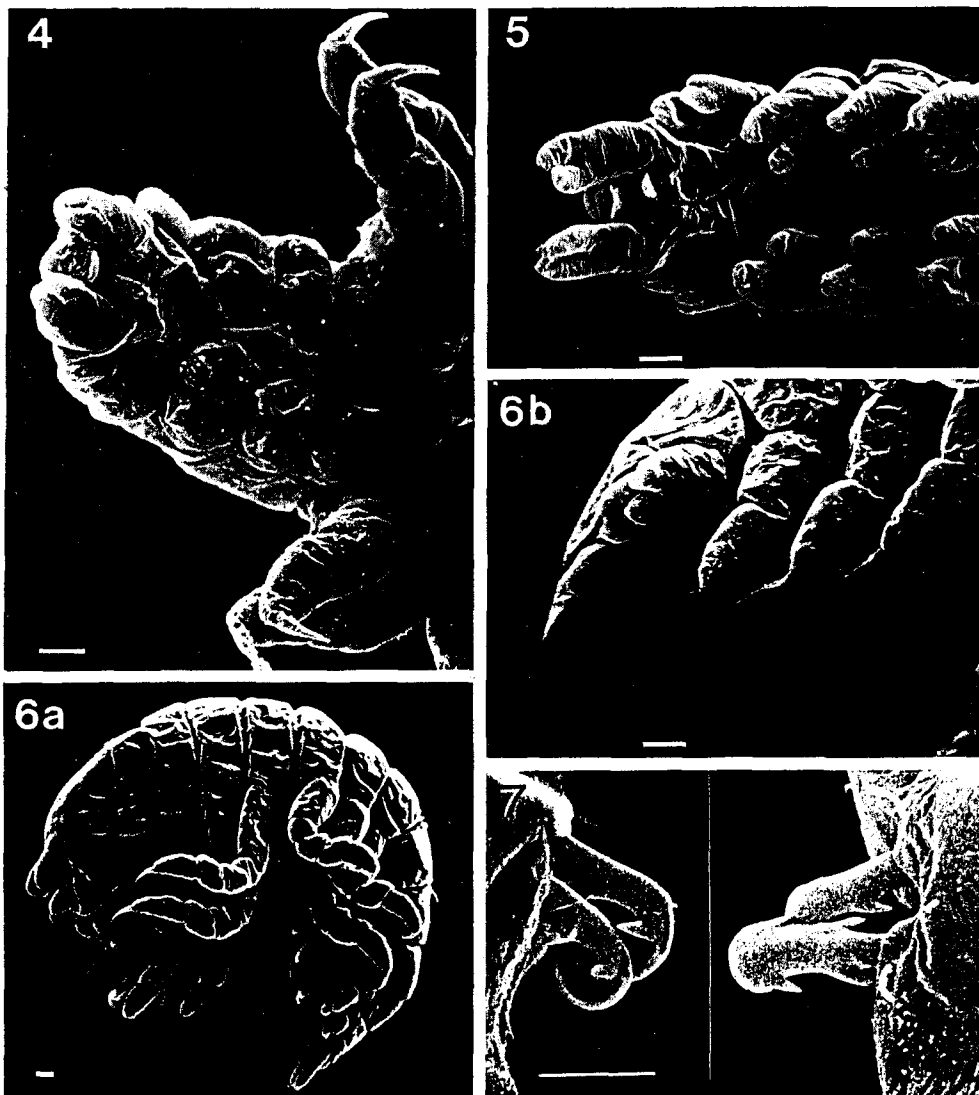Bars indicate 0.1 mm

Fig. 4. Stage III; abdomen (ventral view)

Fig. 5. Stage IV; abdomen (ventral view)

Fig. 6. Stage V; a: habit; b: abdomen (lateral view)

Fig. 7. A pair of coupling spines on the pleopods.
Bars indicate 0.1 mm except in Figure 7 where it is 0.01 mm

Table 1. Survey of the formation and differentiation of morphological characters in the course of the postembryonic development. +: character developed; −: character not developed; (+): character developed sometimes

Phase	Pantochelis		Protopleon			Juvenile
Stage	I	II	III	IV	V	⟶
Total body length [mm]	0.5	0.7	0.9	1.4	1.7	2.0
Occurrence in the marsupium	+	+/−	−	−	−	−
Yolk in the gut	+	+	−	−	−	−
Additional prehensile structures on the gnathopods	+	+	−	−	−	−
Mouth parts equipped with bristles	−	+	+	+	+	+
Pleon segmented	−	+	+	+	+	+
Pigments in chromatophores and eyes	−	−	−	(+)	+	+
Pleopods differentiated	−	−	−	−	(+)	+
Pleopod rami segmented	−	−	−	−	(+)	+
Pleopods with plumose bristles	−	−	−	−	+	+
Uropods differentiated	−	−	−	−	(+)	+
Coupling spines ("retinaculae")	−	−	−	−	(+)	+
Capability of swimming	−	−	−	−	−	+
Mandibular palp	−	−	−	−	−	(+)

show retinaculae ("coupling spines") (Fig. 7) which, because of their small number, do not allow coordinated beating of the pleopods and therefore do not permit swimming.

After the fifth postembryonic moult, all species-specific characters are developed with the exception of the mandibular palp (Table 1). The pleopods are always separated into the pedunculus and the rami equipped with plumose bristles; further development of coupling spines enables the pleopods to coordinate beating. The urosoma is segmented and bears differentiated uropods. According to the above given definition of the pantochelis and protopleon phase, the latter is completed with the fifth postembryonic moult. The first juvenile stage is characterized by the complete segmentation of the abdomen and the presence of differentiated pleopods and uropods.

Temperature dependence of the postembryonic development

The postembryonic development shows a distinct temperature dependence. Figure 8 depicts the mortality rate at the end of postembryonic development; that is, the percentage of young that have not survived this period of development at different temperatures. The chance of survival is greatest at 5 °C. Temperature increase up to 20 °C is accompanied by a slow rise of the mortality rate up to 64 %; a temperature decrease only slightly beneath 5 °C results in a rapid rise of mortality which at 0 °C amounts to 100 %. When kept at 0 °C, the newly hatched young survive up to 108 days but do not undergo a moult and die during the first postembryonic stage.

The temperature of about 20 °C is extremely unfavourable for this arctic-boreal species and results in an increase of the intermoult phase from stage III compared with the corresponding intervals at lower temperatures (Table 2, Fig. 9). All young kept at this high temperature die during the juvenile phase at the latest and never attain the adult
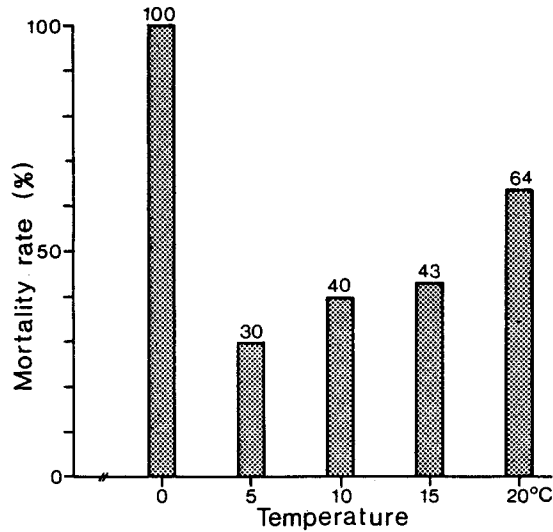
Fig. 8. Temperature dependence of mortality rate of young *Hyperia galba* at the end of postembry-
onic development

stage. The first moult which terminates the pantochelis stage is generally accomplished
one day after hatching at a temperature of 20 °C; when the animals are kept at 5 °C,
moulting occurs on an average after 2.3 days (Table 2). While the postembryonic
development of the young hyperiids takes on an average 48 days at a temperature of 5 °C,
this process requires only 30 days at 10 °C and just 23 days at 15 °C. Animals kept at 20 °C

Table 2. Temperature dependence of duration of developmental stages. i: intermoult period (days),
mean ± standard deviation; a: medium age (days) at the end of the stage concerned; n: number of
individuals investigated

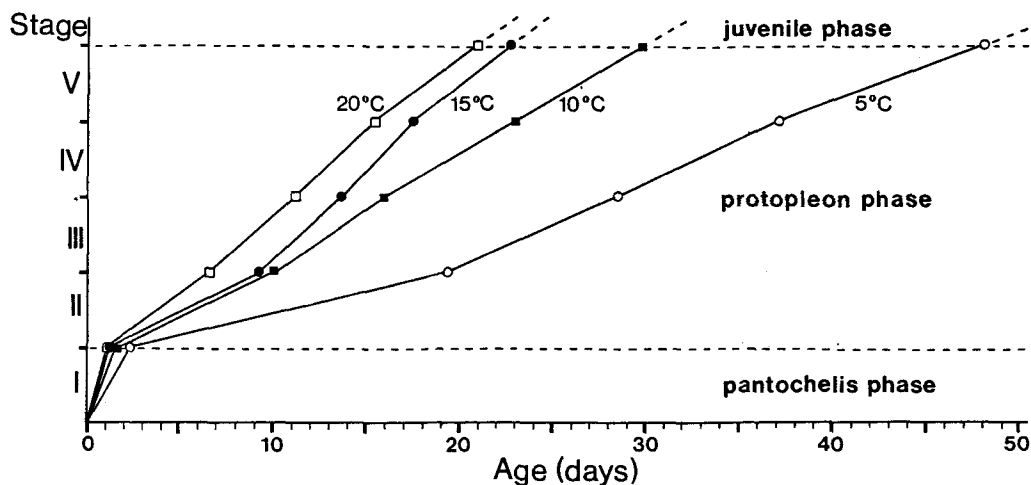| t (°C) Stage		I	II	III	IV	V
0		∞	–	–	–	–
5	i	2.3 ± 0.5	17.0 ± 2.2	9.1 ± 0.9	8.7 ± 0.5	11.0 ± 1.2
	a	2.3	19.3	28.4	37.1	48.1
	n	7	7	7	7	7
10	i	1.4 ± 0.5	8.5 ± 0.9	6.0 ± 1.6	7.0 ± 1.3	7.1 ± 1.3
	a	1.4	9.9	15.9	22.9	30.0
	n	18	17	16	14	13
15	i	1.1 ± 0.4	8.1 ± 0.9	4.4 ± 0.9	3.9 ± 0.9	5.2 ± 0.7
	a	1.1	9.2	13.6	17.5	22.7
	n	21	20	18	18	18
20	i	1.0 ± 0	5.5 ± 0.9	4.6 ± 1.1	4.3 ± 0.8	5.5 ± 0.8
	a	1.0	6.5	11.1	15.4	20.9
	n	8	8	8	8	7

Fig. 9. Temperature dependence of course of postembryonic development of *Hyperia galba*. Each point marks a moult (medium value; for number of animals investigated see Table 2)

complete this development within approximately 21 days. Development times at 15° and 20 °C do not differ statistically; therefore, the velocity of development does not follow the Q_{10}-rule. Obviously, the development of this arctic-boreal species is hampered by higher temperatures.

Reproductive adaptations to parasitism

The transition from life in the female's marsupium to endoparasitism in the medusae occurs in stage II and influences the morphological development considerably. This stage always lasts much longer than all other stages, no matter whether the young are fed well or badly (Table 2). Individuals kept under starvation after hatching undergo the moult which brings them to stage II; further development stagnates until death occurs. This period of time is temperature-dependent and lasts under laboratory conditions at 5 °C maximally 58 days (Fig. 10). The LT_{50}-value, representing the time elapsed until 50 % of the test animals have died, reaches its maximum with 48 days at this temperature level (Fig. 11). Young in stage II do not moult when starved and therefore do not grow. Kept under normal feeding conditions, the young show a relatively high increase in body length when passing over to stage III. Observations of ovigerous females revealed that the offspring is always released after the first moult, that is to say, during the first protopleon stage. When offered unsuitable substrates such as actinians, sponges, ascidians or scyphopolyps, the females cling to the substrate while showing the typical brightening of body colour but they suppress the release of young out of the marsupium. When the same females have living or dead medusae or even pieces of them at their disposal, they release the progeny mostly a short time after coming in contact with the substrate. Contrary to many gammarids and some hyperiid species such as *Vibilia armata* and *Lestrigonus schizogeneios* (Laval, 1980), the young *Hyperia galba* do not leave the marsupium actively but are placed on the host with the active support of the female. In many cases, the females bite small holes into the host tissue in which the young are
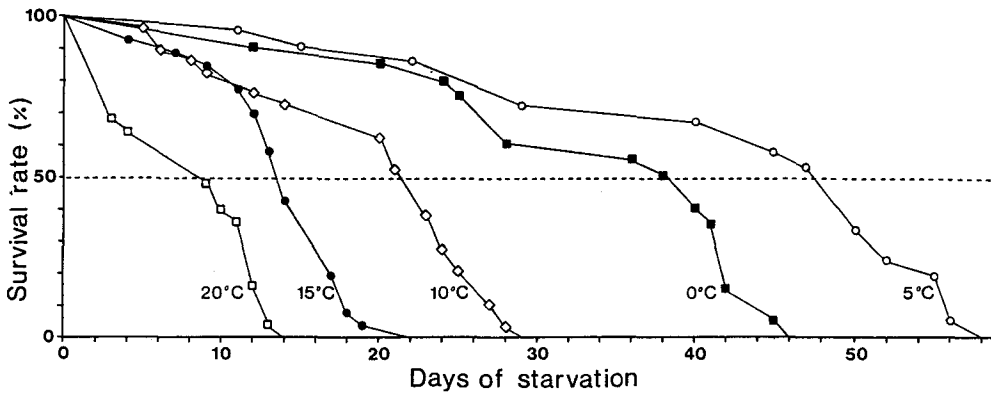
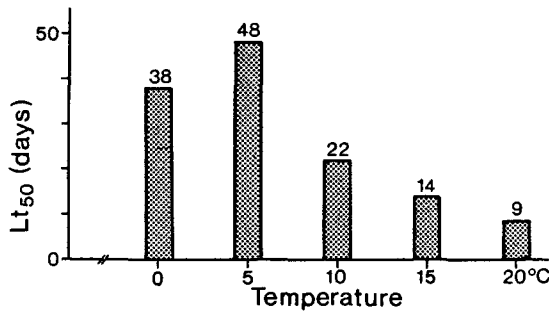Fig. 10. Temperature dependence of survival period of starved *Hyperia galba*

Fig. 11. LT$_{50}$ of *Hyperia galba* following hatching and under starvation at different temperatures

placed singly; sometimes the females seem to press the young into these holes until they themselves have found a hold on the host. Unlike some gammarid species such as *Marinogammarus obtusatus* and *M. finmarchicus* (Sheader & Chia, 1970) young *H. galba* never try to reenter the marsupium once they have left it. Generally the young start with the uptake of food immediately after being released on the host and undergo the moult leading to stage III. For this development, the uptake of nutritious food such as the gonads or the predigested content of the gastrovascular system of the medusae is necessary; feeding on only mesogloea does not suffice.

It is striking that medusae heavily infested with young *Hyperia* in the gastrovascular system rarely show damage of the wall tissue. Probably, the damage to tissue is only low and can be repaired because of the coelenterates' great ability to regenerate; possibly the young feed primarily on the content of the canals of the gastrovascular system. Although they live and feed in the gastrovascular system, the young leave the canals prior to moulting; the exuviae of larvae reared on hydromedusae or small scyphomedusae were always found within the mesogloea or on the surface of the umbrella.

Apparently, the females do not release the young from the marsupium all at once. Under laboratory conditions, they release just 5–10 young within 3–5 minutes and then swim around several minutes before they continue to release the progeny. From this

observation, it can be deduced that under natural conditions the female moves around – at least on the same medusa – and therefore prevents too dense crowding of young. Possibly the female moves to another host and·so avoids severe competition for food among the progeny. Of course, the distribution of the young on several hosts has the advantage of a greater survival chance at least for a part of the brood; nevertheless, it is rather risky because of the sometimes very small abundance of the host animals.

Choice of hosts

Adult *Hyperia galba* cling not only to coelenterates but also – even though for only a short time – to a variety of animals such as sponges, asteroids, nudibranchs and ascidians. The fact that scyphomedusae as well as scyphopolyps are accepted as substrate gives rise to the question of whether the latter also can serve as host for the uptake of young *H. galba*. Laboratory observations revealed that the young in stage I or II do not survive on scyphopolyps; generally, they die within few hours or are soon gorged by the polpyps.

When freshly hatched *H. galba* individuals are deposited on a hydromedusa such as *Phialidium* or another species (with a diameter of about 1.5 cm), a single young amphipod eats up its host within 2–3 weeks (at 10 °C). Obviously, the regeneration ability of the small hydromedusae does not suffice to replace the loss in substance due to the heavy infestation with *Hyperia*. The young are then in a developmental stage – generally stage III – that does not enable them to actively seek a new host. Therefore, apparently a minimum size of the host animal is necessary to ensure the development of the young, at least to a stage capable of swimming. To a large degree, this is guaranteed by the choice of scyphomedusae as hosts.

DISCUSSION

The association of *Hyperia galba* with the large scyphomedusae permits the former an anamorphic development that results in young incapable of swimming at the time of hatching. These young differ considerably from the newly hatched young of the hyperiid species *Hyperoche medusarum* which are more highly developed, attacking herring larvae soon after being released from the marsupium (von Westernhagen, 1976); in contrast, the young of *Hyperia galba* are not able to search actively for food. The close relationship between host and parasite becomes obvious especially in reproduction, since the females deposit their offspring only on scyphomedusae. This is paralleled by the development of *Hyperoche medusarum*, the first brood of which is released at a time when herring larvae hatch, the latter then serving as food organisms (von Westernhagen, 1976). Within the annual cycle the first larvae of *Hyperia* can be found when medusae with mature gonads appear; in the German Bight these are first the medusae of *Aurelia aurita*, later followed by *Chrysaora hysoscella*, *Cyanea capillata*, *Cyanea lamarckii* and *Rhizostoma pulmo*. For the young hyperiids, a medusa represents "...une cavité incubatrice secondaire..." (Laval, 1968) and protects them from sinking and from predators.

Freshly hatched *Hyperia galba* hardly show any similarity to the adults. Their completely different habit with budlike structures of the extremities as well as the temporary formation of additional prehensile organs characterizes the first stages of the postembryonic development. On the basis of their morphology, the first postnatal stages of gammarids are described as juveniles; this of course gives rise to the question whether

it is justified to describe the corresponding stages of *Hyperia galba* as larvae. Per definitionem a larva is a developmental stage (1) that lacks certain organs typical of the adults; (2) that has organs structured morphologically in another way than the adult's organs; (3) that develops certain organs only within this phase of development. Larvae often live in another habitat than the adults. *Hyperia galba* fulfills every one of these criteria. At the time of hatching, the young lack completely developed visual organs and abdominal extremities as well as the segmentation of the abdomen and – at least in stage I – the structuring of the mouth parts; on the gnathopods, larval grasping organs are developed which are no longer present after the second moult. While the adults show a certain degree of flexibility in choosing their hosts, the larvae are – especially because of their inability to swim – obligatory endoparasites; in the absence of hosts they cannot survive.

When larvae occur, the indirect development leads through a metamorphosis to the adult. This can be a sudden change which is typical of holometabolic insects; however, more common is the gradual change, which is characterized by a gradual growth of adult organs and the breakdown of typical larval organs (Schwartz, 1973). In the course of their larval development, young *Hyperia galba* show a gradual metamorphosis which leads them through several juvenile stages to the adult phase. According to Laval (1980), the young of those hyperiids that develop a pantochelis and a protopleon phase have performed two metamorphoses during transition to the juvenile phase: "When a pantochelis stage is present, it is followed through a metamorphosis (a major, non-gradual change in shape) by a protopleon stage. The protopleon phase ... itself ends with a metamorphosis. This metamorphosis gives rise to the juvenile phase, where the young ... corresponds to the hatching stage of gammarids."

The females' care of the young plays an important role in the distribution of *H. galba* and its settlement on new host medusae. White & Bone (1972) realized in fact that "the infective stage is the newly released, poorly differentiated instar ..."; however, they noted that "... the precise mechanism of infection remains unknown". Many crustaceans produce planktonic larvae – e.g. the nauplii of the cirripedes and the zoëae of the decapods –, which may be drifted away by currents. When they are capable of active swimming they are – often only to a restricted extent – also able to choose the substrate as well as the place for settling. Like the larvae of most of the hyperiid species the larvae of *Hyperia galba* are also incapable of doing this. They are deposited by the female on a suitable substrate. The possible delay in release of young out of the marsupium – this depends on the female – and the stagnation in their development when starved can be regarded as an adaptation to parasitism. This enables the females to search for a suitable host for their progeny. When there is no adequate food at the disposal of the larvae, such as they generally find on medusae or – in laboratory culture – in *Artemia* nauplii, they do not moult although they survive for quite a long time. This would be important if ovigerous females did not find a suitable host within a short time. If a further moult took place, the considerable length increment after shedding of the exuviae would result in an inevitable loss of progeny because of lack of space in the marsupium and mutual displacing of the larvae.

Compared with the Gammaridea, the initial phase of development in the marsupium of the Hyperiidea differs considerably within the species. Comparative morphological investigations of these two amphipod suborders allowed Pirlot (1932) to become con-

vinced that the suborder Hyperiidea does not represent a natural systematic whole but unites the descendants of several evolutionary lines: "... les Hypérides représentent un group non naturel, dans laquel sont réunis les descendants de différent souches d'Amphipodes, qui ont conquis les espaces pélagiques en s'attachant comme inquilins ou parasites à des formes du macroplankton." Detailed studies convinced Laval (1965, 1980) of this hypothesis too. His statement that "... Hypérides à développement anamorphe sont obligatoirement parasites, au moins dans les premiers stades..." (Laval, 1965) concerns almost all hyperiid species described until now; the only exceptions known are the hyperiid species with epimorphic development: *Parathemisto gaudichaudi* (Kane, 1963; Sheader, 1977) and *Hyperoche medusarum* (von Westernhagen, 1976). The morphological and ecophysiological similarities within this suborder can be accounted for with the polyphyletic evolution of this group. Except for *Hyperia galba*, a pantochelis stage at the beginning of the postembryonic development is known only within the hyperiid species *Vibilia armata, Bougisia ornata, Hyperoche mediterranea* and *Dairella latissima (= D. bovallia)* (Laval, 1980). The young of several species such as *Lestrigonus schizogeneios* and *Phronima sedentaria* hatch as protopleon stages (Laval, 1980). As different as the developmental stage of the freshly hatched hyperiids is the further course of development and the species-specific number of protopleon stages. Thus *Vibilia armata* and *V. propinqua* develop three protopleon stages; *Bougisia ornata* and *Lycaeopsis themistoides* only two, however; in the development of *Hyperia schizogeneios* there occurs just one protopleon stage (Laval, 1965, 1968). While the larvae of *Lestrigonus schizogeneios* and the genus *Vibilia* do not moult in the marsupium, the larvae of *Phronima sedentaria* (Laval, 1968, 1980) as well as those of *Hyperia galba* moult once. The larvae of *Parathemisto gaudichaudi* even moult twice before leaving the female's marsupium (Sheader, 1977); the release of the progeny is supported by the length increment from 0.35 mm (embryo) to 2.8 mm (stretched young) (Kane, 1963) which runs parallel with an increase of brood volume and an increasing activity of the young.

At the time of reproduction of *H. galba*, the gonads of the host medusae – the organs by far the most rich in energy – are crowded densely with young still incapable of swimming. The maximum number of larvae per medusa never reaches the number of eggs and young, respectively, found within the marsupium of a single female (Dittrich, 1986). The following conclusions can be drawn:

(1) The loss of larvae is significant. The question as to the reasons can be answered only speculatively. The possibility considered by Metz (1967) that "... a certain number of young leave the host medusa immediately after hatching", can – with knowledge of the larval development – be discarded: the larvae cannot leave their host before having finished the larval development and must be reduced in number while still within the medusa; cannibalism of the larvae or digestion on the part of the host may account for this.

(2) The females do not deposit all larvae on one medusa but distribute them on several hosts. This assumption is supported by the observation that females kept in the laboratory release only a small number of larvae before they swim around a short time and go on releasing the progeny. "Not putting all her eggs into one basket..." (Laval, 1980) reduces the probability that the young of a single brood are lost all at once. Generally, the larvae isolated from a medusa develop equally or can be subdivided into few, differently developing groups. This supports the hypothesis that several females

release the larvae on one medusa and do not necessarily search for a medusa not occupied by *Hyperia* larvae.

The size of the scyphomedusae used as hosts guarantees the nourishment of many *Hyperia* larvae until they have reached the juvenile phase. When the hosts are very small – e.g. the leptomedusae infested with *Lestrigonus schizogeneios* – the females release only few larvae per host to ensure their food supply until the larval development is completed. The females of *Vibilia* even deposit just a single larva on a salp of *Salpa fusiformis* and *Thalia democratica* (Laval, 1963, 1980).

Freshly hatched gammarids resemble the adults in their habit to a large degree; this developmental stage is comparable with the first juvenile stage of *Hyperia galba*. Only then are the young hyperians able to move around by actively swimming and to search for a new host if necessary. This can also be concluded from the size distribution of *Hyperia* found independently on medusae in plankton samples around Helgoland: the smallest of these individuals had a total body length of 2.6 mm (Dittrich, 1986).

Obviously because of their very thin cuticle, freshly hatched *Hyperia* larvae are very sensitive to the contents of the nematocysts. When larvae of stage II are deposited on scyphopolyps of *Aurelia aurita* they become paralyzed shortly after coming into contact with the tentacles or are directly gorged by the polyps. This may account for the observation that females deposit the larvae particularly within the gonads or subgenital pouches and on the mesogloea, thus on those parts of the body that are not equipped with nematocysts. The behaviour of the larvae, that is to say their immediate burrowing into the host's tissue, brings them out of range of the nematocysts. According to Laval (1980), the immunity probably is due to a property of the cuticle: "The waxes responsible for the hydrophobous character of the cuticle (a character present in all hyperiids) are perhaps related to this inhibition." Mauchline & Ballantyne (1975) described pore-like structures on the surface of adult *Hyperia galba* and interpreted them as glandular openings; probably they correspond to those of the subcutaneous glands found by Briggs (1977) on the copepod *Paranthessius anemoniae*. Briggs supposes that these glands secrete a substance which is responsible for the immunity of the copepods towards the nematocysts of the sea anemone *Anemonia sulcata* inhabited by them. Whether freshly hatched *Hyperia galba* have such glands and to what extent they are able to aquire immunity towards nematocysts should be the subject of further investigations. Though different studies have been carried out, the character of the larvae that leads to immunity towards the content of the gastrovascular system of the medusae is still unknown (Vader, 1983).

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