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Aspects of the Life-Cycle of the Antarctic Fish Parasite *Gnathia calva* Vanhöffen (Crustacea: Isopoda)

J.-W. Wägele

Arbeitsgruppe Zoomorphologie, Fachbereich 7, Universität Oldenburg, Postfach 2503, D-2900 Oldenburg, Federal Republic of Germany

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Summary. The life-cycle of the Antarctic fish parasite *Gnathia calva* Vanhöffen, 1914 (Crustacea, Isopoda) is described. Three larval instars (pranizae) were discerned. Each instar sucks blood from benthic fishes once and then rests hidden for a period of up to 2 years. Pranizae, that have fed, have swollen pereonites, they bear symbiotic bacteria in a rectal vesicle. The third instar is frequently found within small hexactinellid sponges, where they moult and metamorphose into mature specimens. Within the sponges usually a single male is found together with several females and immature adults. On occasions, a premale moults into a second male and an intraspecific fight eliminates one of the males. Adult stages do not feed.

Introduction

Gnathia calva Vanhöffen, 1914 is a common Antarctic gnathiid species, that has been discovered practically everywhere where samples were taken from the littoral of the Weddell Sea and the Antarctic Peninsula (depth range: 124 to 661 m; Wägele 1987a). Most of the specimens were found in small hexactinellid sponges, some also occurred in sediment samples. *Gnathia calva* is a fish parasite, whose larval stages, the pranizae, use specialized mouthparts to suck blood from their host. The digestive tract is adapted to this mode of living, the anterior hindgut being a highly dilatable reservoir; in the posterior hindgut a "rectal vesicle" filled with symbiotic bacteria is present (Juilfs and Wägele 1987).

New data obtained from samples of Antarctic benthos and during two years of observation of living animals complete our knowledge of the life history of this species.

Materials and Methods

The material was collected by means of an Agassiz trawl during the cruises of *RV Polarstern* in the seasons 1982/83, 1983/84 and 1984/85. Specimens from the season 1984/85 were kept alive. A redescription of *G. calva* together with the localities was published elsewhere (Wägele 1987a).

The animals were immediately sorted on deck. All small hexactinellid sponges (height 2–3 cm), which were found to often contain *G. calva*, were opened and the contents kept in separate glass containers. Subsamples of sediment from the same localities were fixed with formaline and sorted later, some living specimens were sacrificed for electron microscopy. All living animals were counted immediately and their sex was determined; these specimens were not used for the analysis of length frequencies. The total length was measured from the tip of the frontally projecting mouthparts to the telsonic apex.

Living animals were kept in a temperature-controlled container at 0 to −1 °C on board of *RV Polarstern* and later transported within the container to Oldenburg University. Fish from the Weddell Sea were also kept in the same container; they were used to feed the praniza stages. To avoid the need to maintain a culture of natural sponges, which is extremely difficult, artificial "sponges" were used to provide a suitable habitat for *G. calva* (Fig. 1). These consist of the upper half of test tubes with a screw plug, which hung in a box of black plastic. The inside of the tubes and the lower opening are covered with gauze, onto which the animals can cling. The plug has a small opening, the artificial "osculum". The "osculum" was always closed by a piece of industrial sponge. Filtered water passes through the lower opening of the tubes and leaves the artificial "sponge" through the "osculum". This arrange-

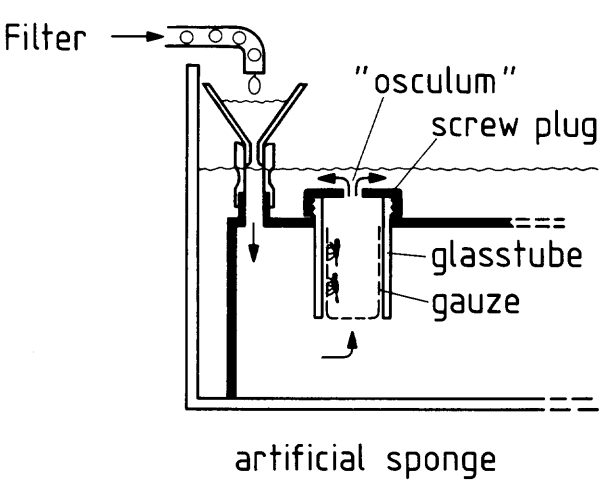

Fig. 1. Apparatus used to keep *G. calva* alive. The glass tubes with *G. calva* were kept in the dark in filtered artificial seawater at −1 °C

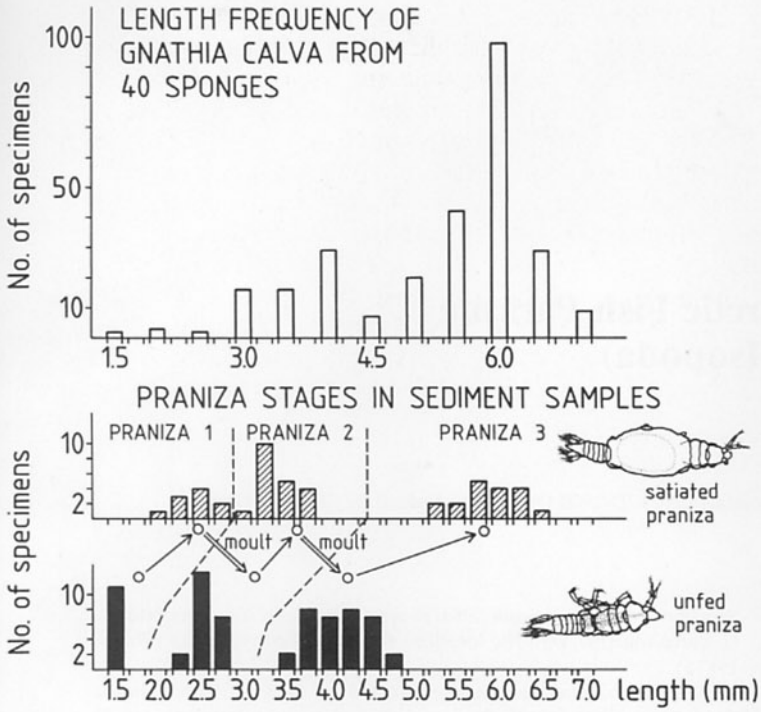

Fig. 2. Length frequencies of *G. calva* found in sponges (*above*) and in sediment samples (*below*). Sponges contain for the most part preadult and adult specimens, sediment samples the larval stages (pranizae), of which three instars could be discerned

ment allows the animals to move in a habitat very similar to that in which they were discovered.

No special care was taken to keep the water sterile, but to avoid frequent manipulations, the controls, for which the animals were extracted from their tubes, were carried out at intervals of 5 to 6 weeks.

Results

Most of the *G. calva* extracted from hexactinellid sponges were transferred to aquaria, but some were fixed in formaline for further analysis. These sponges have an average height of 2.35 ± 0.9 cm (maximum: 7 cm) and a greatest diameter of 1.48 ± 0.5 cm ($n = 30$). If gnathiids are present, typically a single male of *G. calva* is found close to the osculum, the head directed towards the opening of the sponge, in company of several breeding females and immature specimens, i.e. the sponges contain a "harem" with its male. In a subsample containing 41 small sponges, 29 were inhabited by *G. calva*, i.e. 70.7%. No correlation between the size of the sponges and the number of gnathiids was found. The following numbers are the result of the study of 95 inhabited sponges.

Figure 2 presents the length frequencies of the specimens found in 40 sponges. Most animals are adult males, females or large pranizae of about 6 mm length. Smaller stages are less frequent, the small first praniza stage is only rarely found. Most of the smaller pranizae were obtained from sediment samples. Figure 2 shows the length frequency of young *G. calva* found in our samples from the

Table 1. Composition of "harems"

No. of males in single sponges	
Sponges studied	95
Only 1 male present	66.3%
2 adult males present	3.1%
1 or 2 immature males present	11.6%
No males present	28.4%
Solitary males without company	6.3%
No. of immature specimens and of females	
Average no.	8.07
Maximum	43

Weddell-Sea. When satiated stages with dilated pereonites 4 to 6 are differentiated from unfed stages, which have a slender body and shorter pereonites 4 to 6, three praniza-stages can be distinguished. The satiated stages are always longer than the unfed specimens, often nearly as long as the specimens of the next instar. The unfed stages suck blood and increase in length by the extension of the elastic cuticle of the central pereonites, and then after a moult are transformed into the next, larger,

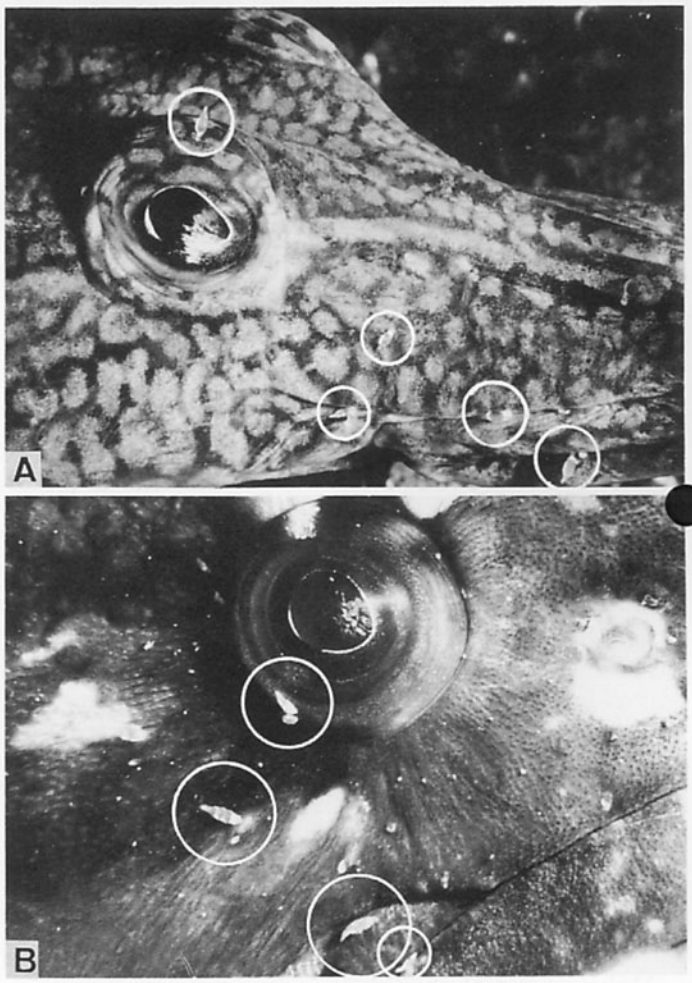

Fig. 3. Pranizae on the heads of Antarctic fish (Bathy draconidae (**A**) and a Nototheniidae (**B**) from underwater photographs from the area of South Bay, Doumer Island (courtesy of A. Larrea, Santiago de Chile)

slender (unfed) praniza. The third praniza reaches the size of the adults, most of these specimens are already found within the sponges.

Feeding experiments in larger aquaria proved that the first praniza is an active swimming stage, which rests for many hours on the ground but from time to time swims short distances. They successfully attached to a small individual of *Notothenia nudifrons* Lönnberg, 1905 and sucked blood or lymphatic, colourless fluid. *Notothenia gibberifrons* Lönnberg, 1905, *Dolloidraco longedorsalis* Roule, 1913, and several benthic species from the North Sea were not accepted in the course of the experiments. Underwater photographs obtained by Chilean divers (Fig. 3) have demonstrated that benthic fishes are the natural hosts of Antarctic gnathiids. These photographs show pranizae on a bathydraconid and on a nototheniid fish. Pranizae have also been found in the gut of a Weddell seal, together with a large number of otoliths of channichtyids and of *Trematomus* spec. supporting the association between gnathiids and Antarctic fish (data from Dr. J. Plötz, Institute of Polar Research, Bremerhaven).

Some specimens of *G. calva* were maintained for more than two years in artificial sponges. As adult males, females and satiated third pranizae do not feed, their cultivation is not difficult. The following results are based on observations of living animals. The animals moult

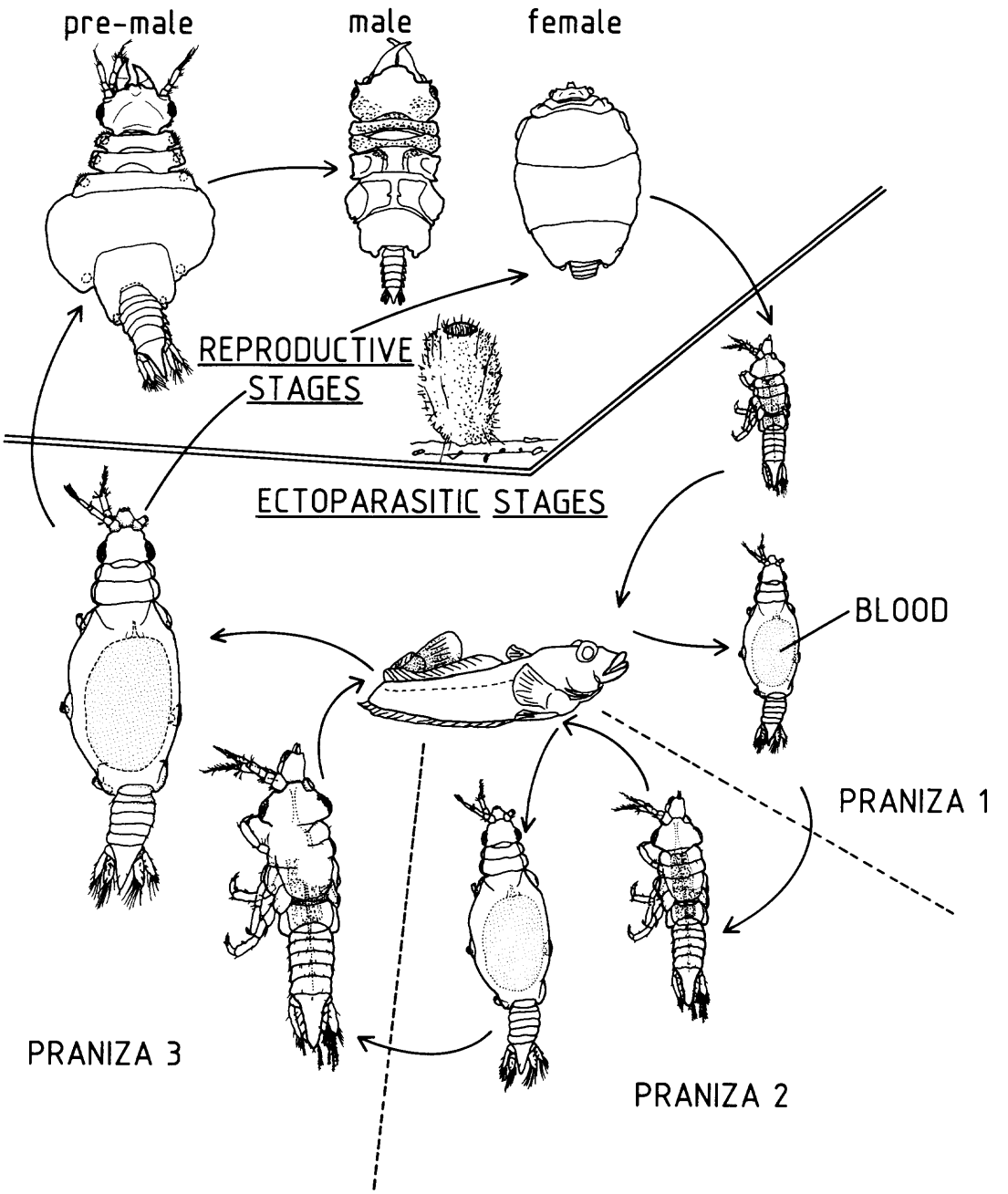

Fig. 4. Schematic representation of the life-cycle of *G. calva*

at any time of the year, but the release of young larvae from ovigerous females was observed in 22 of 25 cases between February and May, an indication of seasonal reproductive activity. The females which produce an average of 129.3 ± 28.4 ($n = 28$) eggs, diameter 0.32 ± 0.016 mm ($n = 150$). Six females laid eggs in captivity, the larvae were released after an incubation of about 12 months; animals were checked every 5 to 6 weeks, so the exact time cannot be specified. During the time between January 1985 and March 1987, several males survived without signs of starvation, ovigerous females lived until the release of their offsprings and died 2–3 months later.

A praniza of the third instar lived 2 years without moulting. It was observed, that this instar can moult into an immature male, in three cases a transformation of a third praniza into a mature male within 6 weeks took place, each time the animals lived in a tube where no mature male was present. One or two immature males were experimentally placed in a tube together with a single mature male. In one case the adult male tolerated the immature specimens during two years. But when two mature males were present (observed in 4 cases), intraspecific fights obviously lead to the death of one of the rivals. The defeated males always lost their legs, which were bitten off by the stronger animal. One tube contained two males for a period of 6 months until one was killed; the other three pairs of males coexisted for a maximum of 6 weeks.

Figure 4 is a summary of the life-cycle of *G. calva*: The pranizae live initially outside sponges, sucking blood of fishes in the initial phase of each instar and then resting in some hidden place for a time of up to two years (observed in praniza 3). The third praniza penetrates into small hexactinellid sponges, where it moults into a mature female or an immature male.

It is not known if these stages are attracted by sponges inhabited by other specimens, especially by mature males, and it is not known if the sex is already determined in the third pranizae.

Females with reduced mouthparts and a secondary marsupium (Wägele 1987a) have their ovaries filled with eggs. The time of copulation, after which eggs are transferred into the marsupium, was not observed. Ovigerous females have to live for more than one year, until the young are released from the brood pouch.

Few pranizae moult into pre-male stages, which coexist with the male adult unmolested in the harem. They may live for two years before they moult into a mature male. In this case an intraspecific fight leads to the elimination of one of the two males. A single male can be the guard of up to 43 female or immature specimens. A mature male can live for more than two years.

All these preadult and adult stages exist on the basis of the blood they ingested during the last praniza stage. Symbiotic bacteria (Juilfs and Wägele 1987) may provide *G. calva* with essential substances (vitamins, amino acids?).

Released young have to leave the sponges and search for a host. It is not known if they already bear symbiotic bacteria in the rectum.

Discussion

The biology of gnathiids still is not fully understood. Hesse (1864) observed the transformation of pranizastages into males (ancées mâles) and described essential aspects of the life cycle, such as the swimming and feeding activities of the larvae. Wagner (1866) concentrated on the description of morphological characteristics, Dohrn (1870) found males and females of *"Anceus maxillaris"* together in crevices and described aspects of their general anatomy. He postulated that the plate-like pylopods of the males could possibly play a role in feeding, a mere speculation, while he observed that the mandibles were used only for defense. Smith (1904) described for *Gnathia maxillaris* (Montagu, 1804) the transformation of pranizae into adults. In *G. maxillaris* also adult specimens vary in size and it seems that the size of the adult "is dependent on the size of the praniza that undergoes metamorphosis" (Smith 1904, 473). Monod's important monograph on the Gnathiidea (Monod 1926) clarifies several taxonomic problems, the homology of mouthparts and somites, aspects of the ontogeny and the anatomy, including a short description of the mysterious "rectal vesicle". It was known that the first stages ingest blood and "grow" by a stretching of the integument of the pereonites 3 to 5 when the anterior hindgut is filled. Besides these first pranizae, some "giant segmented larva" (Smith 1904), also known as genus "*Zuphea* Risso, 1826", had been described. These stages also suck blood, but Monod (1926) was uncertain of their origin. Mouchet (1928) discovered the three larval instars of *Paragnathia formica* (Hesse, 1864) and the origin of the *Zuphea.*

The existence of "harems" was already known for *Paragnathia formica* (Monod 1926). Males of this species burrow in the mud of estuaries, groups of few immature specimens and females live together with one male in a small chamber. Monod supposed that female pranizae search actively for chambers occupied by a male.

Finally, Stoll (1962) completed the description of the life-cycle of *Paragnathia formica*: There are three instars of larvae, which succeed one another in the same way as in *G. calva*. During the process of digestion, at first the anterior hindgut is swollen and filled with blood, then the digestive glands increase in size while the gut shrinks. Finally, a moult transforms the formerly swollen praniza into an unfed next instar. In *P. formica*, digestion by the first two instars takes up to 6 to 7 weeks and the third instar may exist for 4 months; this is a much shorter period than in *G. calva,* where similar processes may take up to 2 years. Single males of *P. formica* often live for 12 months and rarely up to 20 months (Amanieu 1963). The embryonic development of *P. formica* is completed in only 1 to 2 months and the whole cycle from egg to egg lasts

about 1 year. In *G. calva* the cycle may need 4 to 5 years to reach maturity; 1 year for the embryonic development and possibly 3 to 4 years for the larval stages. Male specimens may live for more than six years (4 to 5 years until maturation, at least two years as a guardian of a "harem").

Of course the retardation of the life cycle of *G. calva* is a product of the low temperatures, with the present data it cannot be calculated at what degree a metabolic compensation occurs in comparison with *P. formica.* In *P. formica*, digestion stops when fed pranizae are kept at 4 °C for 4 months (Stoll 1962); in *G. calva* slow digestion is possible at −1 °C.

In comparison with other Antarctic isopods (White 1970; Luxmoore 1982; Wägele 1987b), the embryonic development of *G. calva* lasts only 12 instead of 20 to 23 months (in Serolidae and *Glyptonotus*), and the eggs are much smaller (diameter 0.3 mm instead of 1.5 to 3 mm).

Eggs of comparable size (0.3 to 0.5 mm) are found in most temperate isopods, in *Limnoria lignorum* (Rathke, 1799) they develop at 6 °C in about 3 months (Sømme 1940), in *Asellus aquaticus* (Linnaeus, 1758) at 4.5 °C in more than 4.5 months (Andersson 1969); but a duration of nearly 1 year (at 11.5 °C) is only found in the stygobiont *Caecosphaeroma burgundum* Dollfus, 1898 (Daum 1954). The life-cycle of *G. calva* is probably somewhat shorter than in the large Antarctic species of *Glyptonotus* and *Serolis*, but it is prolonged in comparison with the temperate gnathiid *P. formica.*

Some interesting questions remain unanswered. 1) The percentage of males of *G. calva* in the sponges is very low (♂ : ♀ = 1 : 8), but it is not known, if the sex-ratio in the larval stages is the same. 2) During the experiments the suspicion arose that moulting of pre-males to males may be inhibited by the presence of a mature male. This needs confirmation. 3) It is not known if the pranizae are attracted by mature specimens and how a harem comes into being. In theory, physiological sex determination would be an appropriate mechanism to regulate the composition of a harem. These and further details could be investigated with faster growing gnathiids from temperate regions. For the Antarctic benthos it would be interesting to have quantitative data on abundance of the species and the rate of infestation of benthic fish. Nothing is known about the habitats and habits of the other Antarctic gnathiids, of their hosts and of interspecific interactions.

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