

THE INTERRELATIONSHIP OF *Hyperia galba* (CRUSTACEA, AMPHIPODA) AND *Desmonema gaudichaudi* (SCYPHOMEDUSAE, SEMAEOSTOMAE) FROM THE ANTARCTIC

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ABSTRACT. This paper records the first observation of the parasitic association between the cosmopolitan amphipod *Hyperia galba* and the Antarctic scyphomedusan *Desmonema gaudichaudi*. Specimens were collected at Signy Island, South Orkney Islands, where the host, which at times exceeds diameters of 1.2 m., was most frequently noted under pack ice in spring. Both benthic and pelagic feeding of the jellyfish were observed. Ectoparasitic adult and adolescent stages of *H. galba* were found on the subumbrella around the manubrium of the scyphomedusan and were shown to feed on the epidermal tissues. Endoparasitic newly released instars, which lack eye pigment and functional swimming appendages, and instars up to 6 mm. long, were found in the terminal ramifications of the gastro-vascular system of the host. This supports the view that hyperiids with anamorphic larval development are obligative parasites and explains the absence of free-swimming young instars from the pelagic ecosystem. Egg numbers in hyperiids are high, particularly in this Antarctic population, and this may be related to the parasitic mode of life to offset high mortalities at infection of the host and emigration to new hosts. The population structure is bimodal and some form of alternation of generations could be responsible, although more sampling is required to confirm this and the timing of the reproductive cycle.

THIS paper describes for the first time the parasitic association of *Hyperia galba* (Montagu) with the large Antarctic scyphomedusan *Desmonema gaudichaudi* Lesson, established by a series of samples taken from the sea near the British Antarctic Survey biological station at Signy Island, South Orkney Islands (lat. 60°43'S., long. 45°38'W.).

H. galba is a widely distributed pelagic amphipod recorded from the Mediterranean, North Atlantic south to lat. 17°N., South Atlantic north to lat. 26°S., Arctic, Southern and Indo-Pacific Oceans (Barnard, 1932; Hurley, 1969), and the Baltic and Gulf of Finland (Haahtela and Lassig, 1967). It has been collected free swimming (Montagu, 1815; Stebbing, 1888; Walker, 1907; Brusca, 1967a, b; Haahtela and Lassig, 1967) but, as in other Hyperiidae, is commonly found in some form of symbiotic association (in the sense of Dogiel (1964)) with large planktonic invertebrates, particularly the Scyphomedusae (Bate and Westwood, 1868; Sars, 1895; Tattersall, 1907; Chilton, 1912; Stephensen, 1923; Barnard, 1932; Poulsen, 1950; Buchholz, 1953; Hardy, 1956; Nagabhushanam, 1959), where it has been observed most frequently in the sub-genital pouches (Thompson, 1847; Gosse, 1853; Hollowday, 1948; Agrawal, 1963; Laval, 1965; Metz, 1967), or less often under the bell (Dahl, 1959). However, Bowman and others (1963) suggested that *H. galba* clung to the exumbrella surface and only moved to the under surface when the medusa became moribund. Thus, if previous observations were of net-caught or stranded specimens, the amphipods would be expected on the subumbrella surface and so would be consistent with Dahl's observations. Metz (1967), using the results from 4 consecutive years of collections of *Aurelia aurita* (Linnaeus) from Isefjord in Denmark, recorded that the older stages were found among, and feeding on, the gonads whilst the younger stages were in the mesogloea. Romanes (1877) observed *H. galba* feeding on the tissues of *Aurelia* and Lambert (1936) recorded this amphipod feeding in the gastric pouches of *Aurelia*.

The association has been variously described as commensal (Hollowday, 1948), parasitic (Edwards, 1868; Sars, 1895; Agrawal, 1963, 1967; Metz, 1967), semi-parasitic (Stephensen, 1923; Poulsen, 1950), a food parasite (Orton, 1922; Hardy, 1956) and an ectoparasite (Chilton, 1912; Dahl, 1959). The latter conclusion was derived from the identification of nematocysts from the host in the stomach of *H. galba* (Dahl, 1959). Bowman and others (1963) considered that more evidence was required since the specimens that they observed adopted an inverted position (Fig. 1) on the bell which would make feeding on the tissues of the medusa difficult.

Laval (1965) described the larval development of *Vibelia armata*, *V. propinqua* and *Hyperia schizogeneios*, and indicated that, whereas epimorphic development is normal to the

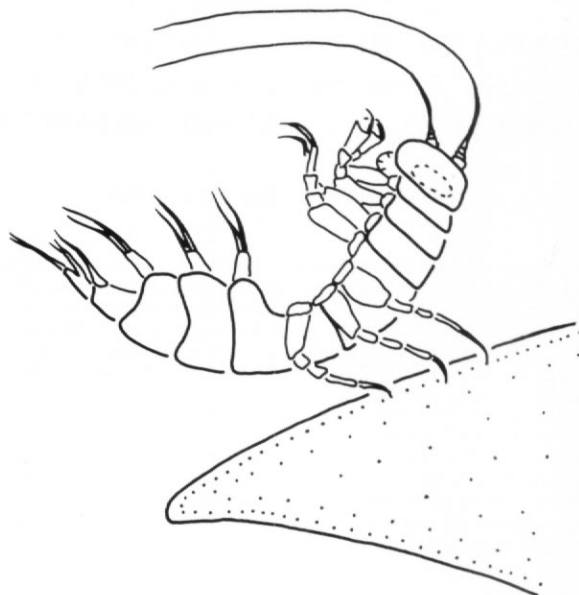


Fig. 1. Typical posture of *Hyperia galba* on Scyphomedusae (re-drawn after Bowman and others, 1963).

Amphipoda, parasitic hyperiid development is often anamorphic. The poorly differentiated larvae are released from the marsupium of the female and may undergo as many as four moults and two distinct metamorphoses before attaining the morphology characteristic of the species. These early larvae are incapable of an independent existence, being without pigmented eyes and swimming appendages, and so Laval concluded that hyperiids with anamorphic development are obligative parasites at least during the early instars.

Brusca (1967a, b), using an Isaacs-Kidd mid-water trawl as a means of collecting samples for his investigation of the ecology of pelagic amphipods off southern California, recorded that free-swimming *H. galba* were taken in 31 samples in depths of 85–1,100 m. and that there appeared to be an obvious diurnal vertical migration with concentration above the 500 m. level at night. Of 178 specimens, he found that egg production was greatest during the summer with the maximum incidence of young in the marsupia in spring. Young were released by the summer but did not enter the catchable population until autumn, and he admitted that he was unaware of where the young were during this approximate 3 month period.

METHODS

Observations of the behaviour of the jellyfish, *D. gaudichaudi*, were made whilst diving. Whenever possible, specimens were collected in a large container with as little disturbance or damage as possible and brought back to the laboratory for examination for infestation by *H. galba*.

Amphipods from individual jellyfish were preserved separately in neutralized formol saline and subsequently sexed and measured to the nearest millimetre from rostrum to telson by straightening them over a scale. The intestinal contents of adult specimens taken from the exterior, and the young instars from the interior, of *D. gaudichaudi* were examined for recognizable food organisms.

Samples of the superficial tissues of *D. gaudichaudi* were examined to determine the types and distribution of the nematocysts characteristic of the species. Parts of the lappets of the jellyfish were preserved for detailed examination to determine whether the young instars were in the gastrovascular system of the scyphomedusan or embedded in the mesogloea.

RESULTS

Occurrence

D. gaudichaudi probably occurs as a component of the macroplankton at the South Orkney Islands throughout the year but they were most frequently observed in the surface waters during the early spring, under the fast ice, or in association with drifting pack ice (Table I). This observation may be biased by the increased clarity of the water during this period (Everson and White, 1969) which would tend to increase the frequency of sightings.

TABLE I. *Hyperia galba* COLLECTIONS MADE FROM *Desmonema gaudichaudi* IN BORGE BAY, SIGNY ISLAND

Number	Date	<i>D. gaudichaudi</i>	Depth	<i>H. galba</i>	Juvenile	♀	♂
Tickell 1051	3 Jul. 1955	*?	?	+	○	○	1 14 mm.
Stammers 1268	3 Oct. 1958	†?	?	+?	?	?	?
Redfearn 82	18 Mar. 1963 15 Sep. 1966	* †	? Mid-water	○ —	○ —	○ —	○ —
White 1367	9 Nov. 1966 18 Apr. 1967 30 Jul. 1967 24 Sep. 1967 4 Oct. 1967 5 Oct. 1967	* † † † † *	Surface Shore Surface Bottom Bottom Mid-water	++ + — — — —	13 4-10 mm. ? — — —	10 11-20 mm. ? — — —	12 10-24 mm. ? — — —
White 1368	23 Oct. 1967	†	Shore	+	○	2 19 and 24 mm.	1 18 mm.
White 1369	24 Oct. 1967 25 Oct. 1967	† *	Bottom Mid-water	++ —	54 1.9-12 mm. —	50 12-24 mm. —	30 12-22 mm. —
White 1370	4 Nov. 1967 21 Nov. 1967 29 Nov. 1967	† † †	Surface Bottom Mid-water	++ — —	54 3-10 mm. —	32 11-24 mm. —	23 11-22 mm. —
White 1371	26 Sep. 1968	*	Surface	+	1 10 mm.	○	○
White 1372	27 Sep. 1968	*	Surface	+	47 2.6-9 mm.	2 22 and 23 mm.	4 14-21 mm.

* Single specimen of *D. gaudichaudi*.† Several specimens of *D. gaudichaudi*.

— Infestation not determined.

○ Not infested.

+ Infested.

Association

Examination of a large stranded specimen in Factory Cove (lat. 60°43'S., long. 45°37'W.), 9 November 1966, showed that *H. galba* was associated with *D. gaudichaudi*. A more detailed examination in the laboratory indicated that the larger specimens of the amphipod were attached to the outside of the jellyfish, whereas the young developing instars were embedded internally. Subsequently, whenever the opportunity arose, collections of *D. gaudichaudi* were made to obtain further information on the nature of this interrelationship.

The association of hyperiids with large Scyphomedusae is well known and *H. galba* has been recorded from a number of different species but not previously from *D. gaudichaudi*. Two possible earlier records were found in the Falkland Islands Dependencies Survey unpublished

reports of Tickell (1956) and Stammers (1959). Both observers recorded Amphipoda from the underside of Scyphomedusae at Signy Island. A preserved specimen collected by Tickell confirms that *H. galba* was one of the partners in the association but there is no means of confirming the host species.

Observations of the distribution of *H. galba* on *D. gaudichaudi*, in greater detail, showed that those specimens which were attached externally adopted the posture figured by Dahl (1959) but were located around the base of the manubrium rather than the exumbrella surface (Bowman and others, 1963) or the sub-genital pits as suggested by most previous authors. The juvenile instars up to 6 mm. in length were found in the terminal parts of the gastrovascular system of the jellyfish lappets (Fig. 2).

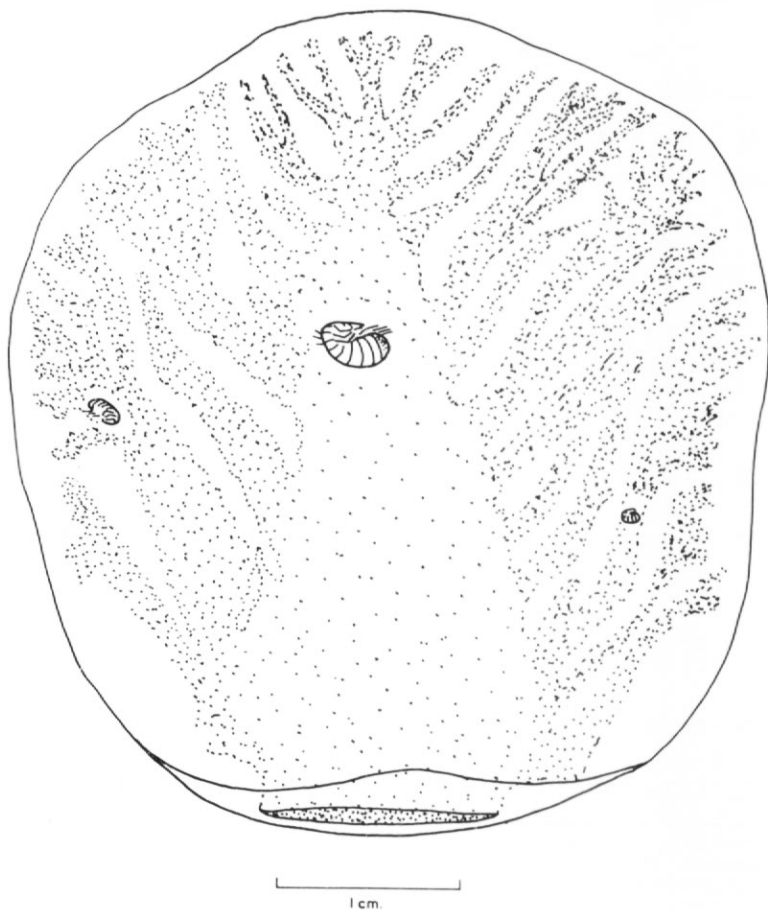


Fig. 2. Endoparasitic instars of *Hyperia galba* within the terminal ramifications of the gastrovascular system of *Desmonema gaudichaudi*.

Population dynamics

The sample size is small but in view of the circumstances and the general inaccessibility of the material it is worth examining the data available.

The size-frequency relationships for the samples from individual jellyfish are summarized as histograms (Fig. 3). The juvenile frequency distributions show a distinct bimodality which is supported by probability analysis. The break appears to correlate with the size groups found in the gastrovascular system and those to be found externally, but a continuous series of size

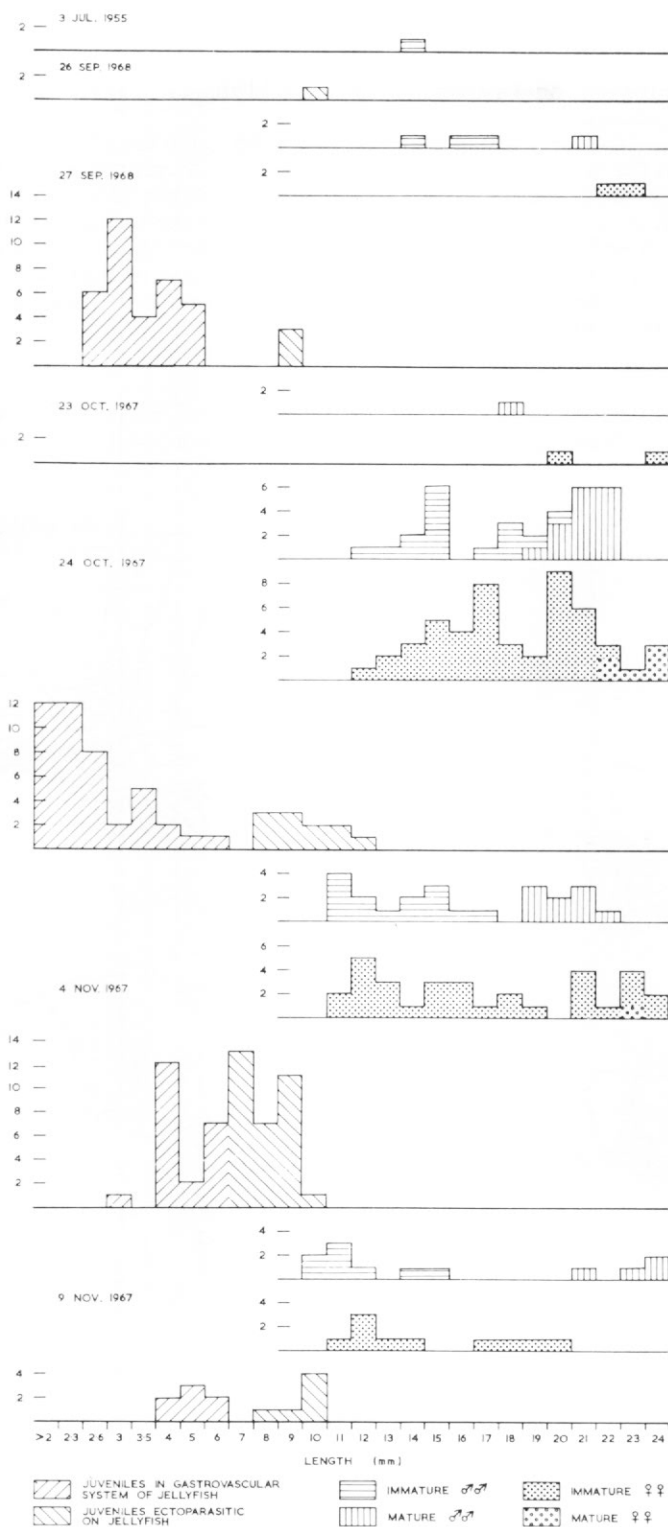


Fig. 3. Length-frequency distribution of *Hyperia galba* samples from *Desmonema gaudichaudi*.

groups through this point on 4 November 1967 would suggest that this was not necessarily a function of immigration.

The bimodal size-frequency distribution was also reflected in the adolescent and adult stages.

Development in the brood pouch is synchronous. Eight ovigerous and paedigerous females were represented in the collection. Seven were from 24 October 1967 and the other one from 4 November 1967. Again a bimodality was indicated as in the former samples the marsupial development was either early or late, i.e. five females show stages of development from the first division to gastrulation and, of the other two females, one had released its brood and the other had pre-release embryos in the brood pouch. In the female collected on 4 November 1967 development had proceeded to the blastula stage.

Development

Fig. 4 illustrates what are thought to be a natural series of instars which were taken from a single sample. These drawings show that in *H. galba* there is a progressive development and no

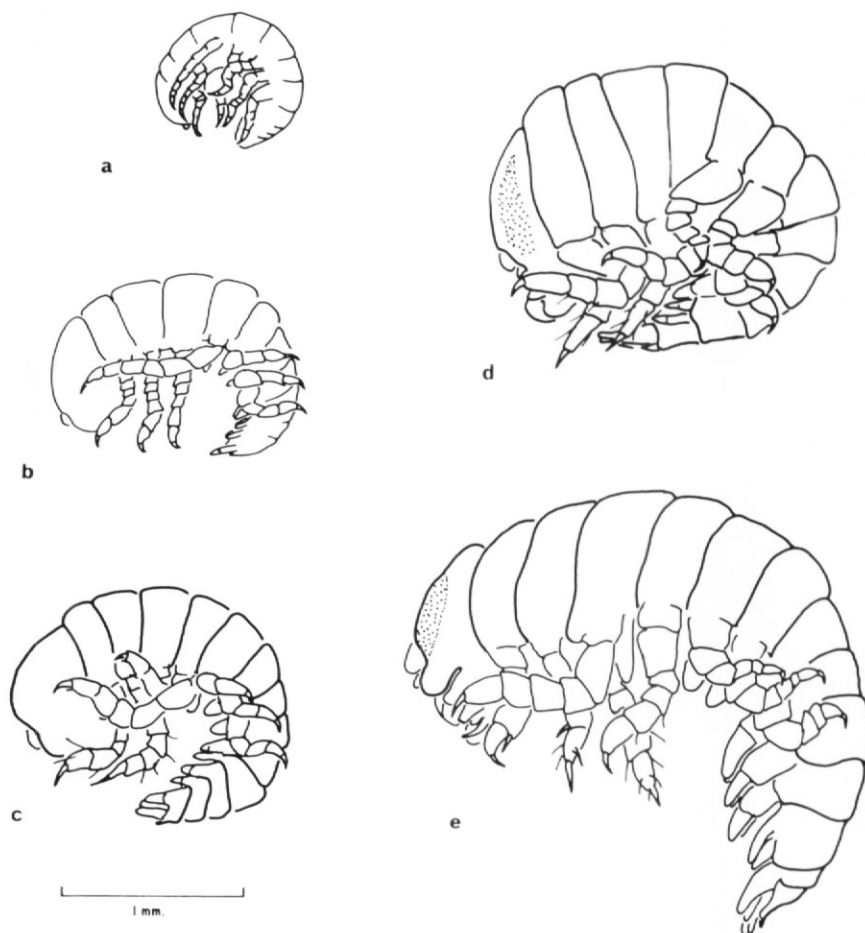


Fig. 4. *Hyperia galba*. Series of instars to show the incomplete development on release from the paedigerous female.

a, pre-release marsupial instar; b-e, instars from the gastrovascular system of *Desmonema gaudichaudi* (White 1369).

distinct metamorphosis as in *Vibelia* (Laval, 1965), but the stage at which the young *H. galba* is released from the brood pouch possesses no functional uropods, pleopods or eyes. This corresponds to the "protopleon" phase described by Laval for *H. schizogeneious*. Eye pigment develops at the third instar after release but the natatory pleopods do not develop until the juveniles are about 6 mm. long which is probably the fifth or sixth instar.

As the collection was limited to a short period of the year, it is not possible to establish the reproductive cycle of this southern population of hyperiids.

Fecundity

It was not possible to determine the brood size from examination of the contents of the marsupium, because the ovigerous females had not been preserved separately and so many of the eggs and developing instars were lost. Often the only evidence that the females were ovigerous was the large size of the oostegites and a few remaining young in the brood pouch. Examination of the ovaries of pre-ovigerous females showed that development within individuals was synchronous and so total ovum numbers were counted to give an estimate of this parameter. This was found to be 600.9 ± 137.4 ($n = 15$) and is rather higher than Metz's (1967) figure of 225 (239.5 ± 61.7 in 1960). Jensen (1958) demonstrated that for Malacostraca the total egg number is dependent on female size and Bone (1972) confirmed this principle for a benthic Antarctic amphipod *Bovallia gigantea* Pfeffer. Thus the difference in brood size is readily accounted for by the larger individual size of the ovigerous females of the Antarctic population when compared with the Danish population. J. Kane* (personal communication) recalled that egg number was very high in *Parathemisto gaudichaudi* (Guérin), especially in some of the large specimens caught south of the Antarctic Convergence.

Egg size

Thorson (1936) and others observed that marine polar invertebrates often have large yolky eggs, but hyperiids have a relatively large number of eggs and therefore would be expected to be rather smaller when compared with other amphipods (Metz, 1967).

The eggs of this southern population of *H. galba* when first deposited into the marsupium were approximately spherical, $584 \pm 37.9 \mu\text{m}$. in diameter with a mean volume of $1.042_8 \mu\text{m}^3$. This is approximately one-tenth of the egg size ($1.068_9 \mu\text{m}^3$) of the benthic Antarctic amphipod, *Bovallia gigantea*, from the same locality (Thurston, 1968, 1970).

Feeding

H. galba as live juvenile stages were removed from the terminal ramifications of the gastro-vascular system of *D. gaudichaudi* and the gut was examined. They contained no recognizable food organisms but were filled with cell debris similar to that found in the digestive system of the host; it was not possible to determine whether the amphipods were feeding on this or the host's tissues or indeed, both.

Metz (1967) considered that the ectoparasitic stages were dependent for food on the host's gonads, whereas other authors have suggested that *H. galba* is less specific and feeds on the epithelia (Dahl, 1959; Agrawal, 1967) or perhaps intercepts the host's food (Orton, 1922). Bowman and others (1963) pointed out that feeding on the external tissues would be difficult considering the posture normally adopted but Agrawal (1964, 1967), on evidence of the mouth parts, suggested that this species is well adapted to cutting off pieces of epidermal tissue.

Ten gut-content samples were taken from the ectoparasitic instars and these all contained large quantities of cell debris, but in addition variable numbers of holotrichous and atrichous haploneme nematocysts (classification after Russell (1953)). The atrichous haplonemes predominated. Capsule lengths were measured and are summarized in Tables II and III.

D. gaudichaudi was found to have a variable armament of nematocysts composed of desmonemes and haplonemes. The haplonemes were both atrichous and holotrichous. The holotrichous haplonemes predominated on the tentacles of the atrichous haplonemes at the three other sites examined (Table III).

* Jasmine Kane now Madame Georges Antonini.

TABLE II. COMPARISON OF MEAN NEMATOCYST CAPSULE LENGTH IN *H. galba* GUT CONTENTS AND FOUR SITES ON *D. gaudichaudi* BY *t* TEST

Sample* ($n = 30 : 30$)	Means	$t, p = 0.05$	t
Gut/tentacles	10.9/17.03	2.042	6.2049
Gut/subgenital pit	10.9/15.4	2.042	4.2993
Gut/bell epithelium	10.9/6.3	2.042	13.0205
Gut/manubrium	10.9/11.03	2.042	0.2503

* Differs from Table III.

TABLE III. NEMATOCYST SAMPLES FROM *D. gaudichaudi* AND *H. galba* SHOWING TYPE, LENGTH AND HOMOGENEITY

Sample site	Bell	Tentacle	Manubrium	Subgenital pit	<i>H. galba</i>
Atriches	++	+	++	++	++
Holotriches	—	++	—	+	+
Mean length* ($n = 80$)	6.39	18.39	11.13	15.45	10.78
σ	1.22	1.82	1.44	4.51	1.27
Sample	7 × 10	10 × 10	10 × 10	8 × 10	10 × 10
F	1.54	0.612	0.633	0.407	0.468
$F p = 0.05$	2.17	1.96	1.96	2.09	1.96

++ Most frequent.

+ Less frequent.

— Not observed.

* Sample size different from Table II.

D. gaudichaudi was often observed in mid-water at Signy Island and at times it was also noted at the surface when its presence was usually indicated by aggregations of birds feeding. This has also been observed at New Island, Falkland Islands (lat. 51°43'S., long. 61°17'W.), where flocks of silver grey petrels, *Fulmarus glacialis* (Smith), were seen feeding around large Scyphomedusae (personal communication from I. Everson). *D. gaudichaudi* possesses prehensile adhesive tentacles, upon which *Euphausia furcilia* were found trapped on several free-swimming specimens. However, on a number of occasions (24 September, 4 and 24 October 1967), these jellyfish were observed on the bottom substrates and a closer examination showed that they were actively engulfing members of the benthic fauna. The echinoderm, *Odontaster validus* Koehler, demersal fish, *Harpagifer bispinis* (Schneider), and nemertean, *Lineus corrugatus* McIntosh were immediately identifiable. The nototheniid fish *Trematomus newnesi* Boulenger, which was commonly found in small shoals associated with the epibenthic algal beds at Signy Island, was also found on one occasion among the folds of the manubrium of a specimen taken on 27 September 1968, and Euphausiacea were found in this position on another (Tickell, 1956). *D. gaudichaudi* seems to be both a pelagic and benthic predator, and that it frequents the benthos is supported by a photograph by G. A. Robilliard at Cape Armitage (lat. 77°50'S., long. 166°40'E.), where this species (our identification) was being held by the predatory actinarian *Urticinopsis antarctica* (Verrill) (Anonymous, 1968).

DISCUSSION

A Southern Ocean population of *Hyperia galba* has been recognized for several decades despite Ekman's (1953) contention that the species was confined to the Northern Hemisphere. However, this is the first record of its symbiosis with Antarctic Scyphomedusae, probably

because large, whole jellyfish specimens are rarely collected and *Desmonema gaudichaudi* at times exceeds 120 cm. in diameter.

It is generally accepted that this amphipod is parasitic but the degree of parasitism is conjectural and it may well be that it differs between populations. It is also probable that the nature of the interrelationship varies between different host species as implied by Buchholz (1953). Bowman and others (1963) have warned that it should not be assumed that the relationship is one of parasitism, although they concluded that *H. galba* was feeding on the tentacles or oral arms rather than on the bell of *Cyanea capillata* (Linnaeus). Hollowday (1948) considered that the relationship was synoecious, whereas Orton (1922) suggested that hyperiids on *Aurelia aurita* (Linnaeus) are opportunist, i.e. facultative, food parasites. However, Laval (1965) demonstrated that the young instars of parasitic hyperiids that he examined, on release from the brood pouch are incapable of an independent existence, and Dahl (1959) noted that nematocysts from the presumed host could be found in the gut of the instars collected externally, implying a higher grade of dependence.

Organisms that are found in the gastrovascular system of a predatory scyphomedusan would naturally be regarded as food, but the instars of *H. galba* found in this situation in *D. gaudichaudi* were not moribund and the consistency with which they occurred there indicates that this is the normal habitat during early development after release from the marsupium. Since the instars are without sight and incapable of swimming, it is probable that the ovigerous females deposit their brood in the manubrium from where they are conveyed to the extremes of the gastrovascular system by the normal ingestive mechanisms of the jellyfish, or by actively crawling. Brusca (1967b) noted that in *H. galba* the instars, between being released by ovigerous females at the 6 mm. stage, cannot be caught free-swimming and are absent from the pelagic ecosystem for a period equivalent to 3 months of the life cycle. This size is coincident with the upper size limit found for the South Orkney Islands population within *D. gaudichaudi* and so Brusca's failure to catch the young instars could be because they were endoparasitic in Scyphomedusae native to the Californian coast. This also supports the idea that dispersal to new hosts does not take place until the ectoparasitic adolescent and adult stages are reached.

Metz (1967) considered that the ectoparasitic stages of *H. galba* were dependent on the gonads for food, whereas other authors have suggested that it is less specific and feeds on the epithelia (Dahl, 1959; Bowman and others, 1963; Agrawal, 1967), or intercepts the host's food (Orton, 1922). Bowman and others (1963) pointed out that feeding on the bell itself would be difficult because of the posture adopted.

In this collection from the Antarctic, each of the intestinal tracts examined contained nematocysts typical of *D. gaudichaudi* but, because of the mean sizes of nematocyst types on the jellyfish and in the crustacean (Tables II and III), it is suggested that *H. galba* had been feeding at least in part on the manubrium. This correlates with the sites at which the specimens were most frequently observed on *D. gaudichaudi*. However, there were also considerable amounts of indeterminate cell debris in the gut samples examined and so feeding on the gonads cannot be excluded. Our conclusion is that *H. galba* is an obligative parasite on *D. gaudichaudi* which alternates between an endoparasitic juvenile stage and an ectoparasitic reproductive and dispersive phase at different stages of its life cycle. The infective stage is the newly released, poorly differentiated instar, but the precise mechanism of infection remains unknown.

There are insufficient records of the Southern Hemisphere populations to show whether *H. galba* also parasitizes other Antarctic scyphomedusans. Host specificity in the Northern Hemisphere is low since it has been collected from a variety of jellyfish and there is insufficient evidence to determine the relative dependence on each species. It is likely that the degree of parasitism may vary from host to host and it is possible that some of the associations are synoecious and occur when *H. galba* cannot find a suitable host, as suggested by Buchholz (1953).

Young endoparasitic instars are only recorded in the Northern Hemisphere from *A. aurita* (Metz, 1967). Metz concluded that the occurrence of the Danish populations of *H. galba* is completely dependent on the occurrence of the host species and suggests that those caught independently are actively seeking a new host. His hypothesis is that the ectoparasitic stages are dependent on the gonads for food and once having sterilized one host they move to another, the large eyes, particularly of the female, helping the search. Both this migration and the

probable ingestion by the host are hazards for the species and have been the major factors in selection for high egg number in this group.

Egg number in Amphipoda is usually directly proportional to female size (Jensen, 1958). The ovigerous females of the South Orkney Islands population are very much larger than their counterparts from temperate and subtropical seas, and this is reflected by an increased brood size, i.e. 225 for the Danish population (ovigerous female length, 9–13 mm.) and 600 for the Antarctic population (ovigerous female length, 22–24 mm.).

The southern Californian population (Brusca, 1967*b*) appears to have an annual breeding cycle but the marsupial period is not known. The bimodality displayed by our samples may be real or caused by small sample size. Dehnel (1955) and many other authors have recorded that polar invertebrates often have prolonged maturation and breeding cycles and may also attain a large size. Dunbar (1957) demonstrated a special case, where bimodality displayed by marine Amphipoda is an expression of two separate populations of the same species breeding out of phase with one another, as a form of alternation of generations. This may lead to the isolation of these populations and subsequent speciation. It may well be the case for *H. galba* from the Antarctic but confirmation will require more detailed year-round samples.

ACKNOWLEDGEMENTS

Our thanks are due to Sir Fredrick S. Russell who confirmed the identification of the scyphomedusan, M. H. Thurston who confirmed the amphipod species, Madame Georges Antonini, Professor M. J. Dunbar, Dr. I. Everson and Dr. G. A. Robilliard for their helpful comments, and Professor H. P. Moon and Dr. R. M. Laws for scrutinizing early drafts.

MS. received 17 May 1971

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