

## The associations of Amphipoda Hyperiidea with gelatinous zooplankton— II. Associations with Cnidaria, Ctenophora and Radiolaria\*

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**Abstract** We have collected representatives of 12 of the 22 families of Amphipoda Hyperiidea while SCUBA diving. We have found that members of five families (Paraphronimidae, Lycaeopsidae, Pronoidae, Parascelidae and Platyscelidae) are associated only with siphonophores. Species within the Hyperiidae and Brachyscelidae are associated primarily with medusae, as are some members of the Lycaeidae. Members of the Oxycephalidae are often found with ctenophores, but are frequently found free-living or with other gelatinous organisms. Members of the Phronimidae fashion their barrels from a number of different gelatinous zooplankters. We have collected members of the Phrosinidae, but not in association with gelatinous zooplankton. Taken together with members of the Vibiliidae, which have been found only on salps, the families we have collected include all of those expected to be accessible to our collecting technique. In many cases, the association between amphipod and host is highly specific. Our collections have led to the conclusion that most, if not all, hyperiid amphipods are associated with gelatinous zooplankton during some portion of their life histories. A knowledge of the nature of these interactions is essential to an understanding of the evolution of the group.

### INTRODUCTION

IN THE first paper of this series (MADIN and HARBISON, 1977) we showed that many species within two hyperiid amphipod genera (*Vibilia* and *Lycaea*) are obligate symbionts of salps. In addition, we collected members of four other genera (*Parathemisto*, *Brachyscelus*, *Oxycephalus*, and *Phronima*) with salps. However, salps are but one of the many types of gelatinous zooplankton found in the open ocean, and other organisms, such as medusae, siphonophores, colonial radiolarians, and ctenophores, also harbour hyperiid amphipods. In fact, one of the first hyperiid amphipods to be described, *Hyperia medusarum* (MÜLLER, 1776), was collected in association with a jellyfish (STRØM, 1762).

By the middle of the nineteenth century, a number of observations had been made on the nature of associations between hyperiid amphipods and gelatinous zooplankton (see Table 9). These records led MILNE-EDWARDS (1840) to suggest that hyperiid amphipods might, in general, be associated with medusae and fish. Pursuing this line of reasoning, BATE (1861) further speculated that the parasitic mode of life of hyperiid amphipods should have a considerable influence on their morphology. Much later, PIRLOT (1932) implied that the evolution of hyperiid amphipods could not be understood without a knowledge of their hosts, and of how they interact with them. In his view, many morphological similarities within the Hyperiidea are due to convergence, since the group is polyphyletic in origin. In particular, he noted that the mouth-parts of widely divergent species are much reduced, and appear to be modified for the consumption of soft-bodied organisms.

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Despite this long history of speculation concerning the mode of life of hyperiid amphipods, surprisingly little is known about their host specificities. Most researchers have been primarily interested in taxonomy rather than the life histories of these amphipods. Further, most studies have relied on nets for collecting organisms. Unfortunately, sampling with nets obscures associations. STEPHENSEN (1925) specifically stressed that the *Thor* collections, the most extensive collection of hyperiid amphipods up to that time, contributed nothing to an understanding of the relationships between hyperiid amphipods and their hosts.

Consequently, most records of associations of hyperiid amphipods with gelatinous zooplankton are limited primarily to observations made in the nineteenth century before the popularization of net-sampling (Table 9). In the course of our collections of gelatinous zooplankton using SCUBA diving, we have observed a number of associations between hyperiid amphipods and gelatinous zooplankton which hitherto have not been reported.

In this paper, we present a comprehensive over-view of the symbiotic relationships we have observed between hyperiid amphipods and gelatinous zooplankton other than salps. We also discuss the relatively limited number of occasions when we have collected hyperiid amphipods that were not associated with other zooplankton. Our collections have led to the conclusion that PIRLOT (1932) and those before him were correct in believing that all hyperiid amphipods are intimately associated with gelatinous zooplankton at some time in their lives. We therefore discuss ways in which the morphology of hyperiid amphipods could be influenced by their varied life-styles.

#### METHODS

Gelatinous zooplankton and their associated amphipods were collected with hand-held jars while SCUBA diving in the upper 30 m of oceanic waters. In several instances, the living amphipods were studied in the field, but usually their behaviour was observed on shipboard using a dissecting microscope. After initial observations, each gelatinous zooplankter was preserved with 10% sodium borate buffered Formalin in seawater and carefully examined for associated amphipods. The amphipods were measured and drawn using a Wild M-5 stereomicroscope with drawing-tube attachment.

Hyperiid amphipods are relatively easy to identify to genus, but identification to species is beset by numerous difficulties, due to the confused state of the literature. We therefore present our criteria for identification to species as we discuss each genus. Our presentation of data is organized around the hyperiid amphipods rather than around their hosts, since most associations we have observed are specific to higher taxa of host organisms. Whenever possible, we present colour notes and behavioural observations.

Siphonophores were identified to species (by DCB) using TOTTON's (1965) synopsis, in conjunction with original descriptions for some groups. For identification of species within the subfamily Sulculeolarinae, the recent review by STEPANYANTS (1973) was also employed.

#### RESULTS

A list of stations where the hyperiid amphipods discussed in this paper were collected is given in our first paper (MADIN and HARBISON, 1977), with an accompanying map. Altogether, members of twelve families have been collected while SCUBA diving. This represents over half of the presently recognized families of Hyperiidea. The associations we have observed are detailed in Tables 1 to 8.

Table 1. Associations of the family Hyperiidae with gelatinous zooplankton. Locations of stations are given in MADIN and HARBISON (1977).

Amphipod species	Host species	Number of amphipods (m) (f) (j)			Station number
<i>Hyperoche mediterranea</i>	<i>Beroë cucumis</i>	-	1	1	304
<i>Iulopsis loventi</i>	<i>Panacea conica</i>	-	1	-	374
* <i>Lestrigonus schizogeneios</i>	<i>Aequorea</i> sp.	1	-	-	277
* <i>L. schizogeneios</i>	<i>Aequorea</i> sp.	1	-	3	277
* <i>L. schizogeneios</i>	<i>Aequorea</i> sp.	-	1	-	294
<i>L. schizogeneios</i>	marine snow	1	-	-	341
<i>Lestrigonus</i> sp.	<i>Aequorea</i> sp.	-	-	3	274
* <i>Lestrigonus</i> sp.	<i>Aequorea</i> sp.	-	-	2	274
* <i>Lestrigonus</i> sp.	<i>Aequorea</i> sp.	-	-	1	276
* <i>Lestrigonus</i> sp.	<i>Aequorea</i> sp.	-	-	1	281
<i>Lestrigonus</i> sp.	<i>Aurelia</i> sp.	-	-	25	290
<i>Lestrigonus bengalensis</i>	<i>Eirene pyramidalis</i>	6	6	55	290
<i>L. bengalensis</i>	<i>Eirene pyramidalis</i>	-	2	-	290
<i>Lestrigonus crucipes</i>	<i>Pelagia noctiluca</i>	-	10	52	297
<i>L. crucipes</i>	<i>P. noctiluca</i>	4	5	35	297
<i>L. crucipes</i>	<i>P. noctiluca</i>	2	13	29	297
<i>L. crucipes</i>	<i>P. noctiluca</i>	4	4	43	297
<i>L. crucipes</i>	<i>P. noctiluca</i>	-	1	46	364
<i>L. crucipes</i>	<i>P. noctiluca</i>	-	1	-	365
<i>L. crucipes</i>	<i>P. noctiluca</i>	-	1	-	365
<i>L. crucipes</i>	<i>P. noctiluca</i>	1	-	-	365
<i>L. crucipes</i>	<i>P. noctiluca</i>	1	-	-	365
<i>L. crucipes</i>	<i>P. noctiluca</i>	1	-	-	365
<i>Lestrigonus</i> sp.	<i>P. noctiluca</i>	-	-	2	299
<i>Hyperietta stebbingi</i>	marine snow	1	-	-	370
<i>H. stebbingi</i>	marine snow	-	1	-	377
<i>H. stebbingi</i>	<i>Callisnoea</i> sp.	1	-	-	377
<i>H. stebbingi</i>	egg mass	2	-	-	377
<i>H. stebbingi</i>	<i>Callisnoea</i> sp.	1	-	-	377
<i>H. stebbingi</i>	<i>Callisnoea</i> sp.	-	3	-	380
<i>H. stebbingi</i>	<i>Callisnoea</i> sp.	-	1	-	381
<i>Hyperietta stephenseni</i>	egg string of <i>Navolina</i>	1	-	-	366
<i>H. stephenseni</i>	radiolarian colony	1	-	-	377

\*Co-occurred with *Brachyscelus rapacoides* and *Brachyscelus* sp. on the same medusa.

## Family Hyperiidae DANA, 1852 (Table 1)

Four genera have been collected by us, although only two of them (*Lestrigonus* and *Hyperietta*) were collected at more than one station.

### 1. Genus *Hyperoche* BOVALLIUS, 1887

The single specimen we collected was identified to species from STEUER's (1911) description and key. It closely resembles STEPHENSEN's (1924, p. 79) 'large specimen' of *Hyperoche mediterranea* SENNA, 1906.

*Hyperoche mediterranea*: 1 ♀, 3.7 mm. This amphipod was clinging to the outer surface of a ctenophore. We could discern no damage to the host, although both juveniles and adults have been reported to burrow into ctenophores (FLORES and BRUSCA, 1975).

### 2. Genus *Iulopsis* BOVALLIUS, 1887

Identified to species on the basis of BOVALLIUS' (1889) key and figures.

*Iulopsis loventi* BOVALLIUS, 1887: 1 ♀, 5.8 mm. This amphipod was almost as large as the medusa, and was sitting in the center of the subumbrellar surface, blocking the mouth. A few

hours after collection, the amphipod began eating parts of the medusa (the tentacles and gonads), using peraeopods 1 and 2 as shears. Peraeopods 3 and 4 were used for frequent wiping of the eyes and telson, a behaviour pattern we have observed in many other groups of hyperiids. These peraeopods, together with peraeopods 5, 6, and 7, were also used for clinging to the medusa.

### 3. Genus *Lestrigonus* MILNE-EDWARDS, 1830

Individuals were identified to species using BOWMAN's (1973) key and figures.

*Lestrigonus schizogeneios* (STEBBING, 1888): 3 ♂, 3.0, 4.2, 5.9 mm; 1 ♀, 2.2 mm; 3 juv., 1.4, 1.7, 1.7 mm. We have collected this species only with the medusa, *Aequorea* sp., and on a delicate aggregation of particulate organic matter of indeterminate origin ('marine snow').

*Lestrigonus* sp.: 32 juv., 0.7 to 2.1 mm. These juveniles were not accompanied by more mature specimens and thus could not be assigned to species. It is possible that specimens found on *Aequorea* sp. are *L. schizogeneios*. Some of these amphipods were found burrowed into the mesogloea of the host. *Lestrigonus schizogeneios* and juvenile *Lestrigonus* sp. co-occurred with *Brachyscelus rapacoides* STEPHENSEN, 1925 and *Brachyscelus* sp. at Stas. 274, 276, 277, 281 and 294 (compare Tables 1 and 3).

*Lestrigonus bengalensis* GILES, 1887: 6 ♂, 2.8 to 3.8 mm; 8 ♀, 2.2 to 3.0 mm, 55 juv., 0.7 to 2.1 mm. This species was found only at Sta. 290 on *Eirene pyramidalis* (AGASSIZ, 1862). We assume that the juveniles, which obviously belong to the genus *Lestrigonus*, are the same species as the adults.

*Lestrigonus crucipes* (BOVALLIUS, 1889): 13 ♂, 3.5 to 4.7 mm; 35 ♀, 3.7 to 4.8 mm; 205 juv., 1.3 to 3.5 mm. This species was collected at three stations, always with the scyphomedusa *Pelagia noctiluca* (FORSKÅL, 1775). Two juvenile *Lestrigonus* sp. were collected with *P. noctiluca* at another station. The parasitic behaviour of *L. crucipes* closely resembles that described by LAVAL (1968a, 1972) for *L. schizogeneios*. The living amphipods are grey, in contrast to the yellow-brown colour of *L. schizogeneios*.

### 4. Genus *Hyperietta* BOWMAN, 1973

Individuals were identified to species using BOWMAN's (1973) key and figures.

*Hyperietta stebbingi* BOWMAN, 1973: 5 ♂, 2.9 to 3.7 mm; 5 ♀, 1.8 to 2.9 mm. This species has been collected primarily on radiolarian colonies. It is possible, therefore, that the 'marine snow' on which specimens have been found twice were the remnants of radiolarian colonies.

*Hyperietta stephensi* BOWMAN, 1973: 2 ♂, 3.4, 3.4 mm.

### Family Paraphronimidae BOVALLIUS, 1887 (Table 2)

#### 5. Genus *Paraphronima* CLAUS, 1879a

Identification to species within this genus was based both on BOVALLIUS' (1889) key and the synonymy of STEPHENSEN (1924).

*Paraphronima crassipes* CLAUS, 1879b: 8 juv., 2.2 to 5.3 mm. These specimens were collected on one occasion on the siphonophore, *Rosacea cymbiformis* (CHIAJE, 1822), co-occurring on this host with *Symprone parva* CLAUS, 1879b (see Table 4). Most of the *Paraphronima* were found in the hydroecia of the bracts. These specimens were difficult to see, in contrast to the prominent *S. parva*, and were not discovered until after preservation.

Table 2. Associations of the families Paraphronimidae, Phronimidae, Phrosinidae, Lycaeopsidae, and Lycaeidae with gelatinous zooplankton other than salps

Amphipod species	Host species	Number of amphipods (m) (f) (j)			Station number
<b>Paraphronimidae</b>					
<i>*Paraphronima crassipes</i>	<i>Rosacea cymbiformis</i>	-	-	8	321
<b>Phronimidae</b>					
<i>Phronima coletti</i>	in barrel	-	1	-	280
<i>Phronima coletti</i>	in barrel	-	1	-	295
<i>Phronimella elongata</i>	no host	-	1	13	298
<i>Phronima coletti</i>	in barrel	-	1	-	299
<i>Phronima pacifica</i>	in barrel	-	1	47	321
<i>Phronima pacifica</i>	in barrel	-	1	20	321
<i>Phronima sedentaria</i>	in barrel	-	1	-	340
<i>Phronima solitaria</i>	in barrel	-	1	-	350
<i>Phronima sedentaria</i>	in barrel	-	1	-	354
<i>Phronima coletti</i>	in barrel	-	1	-	354
<i>Phronima atlantica</i>	in barrel	1	-	-	381
<b>Phrosinidae</b>					
<i>Anchylomera bloesvillei</i>	no host	1	2	-	316
<b>Lycaeopsidae</b>					
<i>Lycaeopsis themistoides</i>	<i>Diphyes dispar</i>	-	1	-	286
<i>L. themistoides</i>	<i>D. dispar</i>	-	-	1	294
<b>Lycaeidae</b>					
<i>Lycaea bovillioides?</i>	<i>Gerolla spectabilis</i>	-	2	-	-
<i>Lycaea serrata</i>	no host	-	1	-	266
<i>Lycaea</i> sp.	<i>Gleba cordata</i>	-	-	1	299
<i>Pseudolycaea variegata</i>	<i>Liriope tetrahylla</i>	-	1	-	238
<i>P. variegata</i>	<i>L. tetrahylla</i>	1	2	-	238
<i>P. variegata</i>	<i>L. tetrahylla</i>	-	-	12	238

\* Co-occurred on the same siphonophore with *Remaneopsis parva*.

## Family Phronimidae DANA, 1853 (Table 2)

### 6. Genus *Phronima* LATREILLE, 1802

Species in this genus were identified using the key and figures of SHIH (1969).

*Phronima coletti* BOVALLIUS, 1887: 4 ♀, 8.0 to 16.0 mm. The barrels in which these specimens were found all had ridges resembling those on the test of *Salpa aspera* CHAMISSO, 1819.

*Phronima pacifica* STREETS, 1877: 2 ♀, 7.8, 11.0 mm. The smaller specimen was in a barrel fashioned from the posterior nectophore of the siphonophore, *Abylopsis tetragona* (OTTO, 1823), while the barrel of the larger specimen resembled the test of *S. aspera*.

*Phronima sedentaria* (FORSKÅL, 1775): 2 ♀, 16.0, 17.0 mm.

*Phronima solitaria* GUÉRIN-MENEVILLE, 1836: 1 ♀, 17.3 mm.

*Phronima atlantica* GUÉRIN-MENEVILLE, 1836: 1 ♂, 8.9 mm. Although males are generally regarded as free-swimming predators (SHIH, 1969), this specimen was found in a barrel.

### 7. Genus *Phronimella* CLAUS, 1872

The synonymy and key of SHIH (1969) was used for the identification of the single species within this genus.

*Phronimella elongata* (CLAUS, 1862): 1 ♀, 16.0 mm; 13 juv., 3.8 to 4.5 mm.

Family Phrosinidae DANA, 1853 (*Table 2*)8. Genus *Anchylomera* MILNE-EDWARDS, 1830

This genus has been regarded as monotypic by all authors since BOVALLIUS (1889).

*Anchylomera blossevillei* MILNE-EDWARDS, 1830: 1 ♂, 8.7 mm; 2 ♀, 7.1, 8.2 mm. These specimens were collected at only one station, at night. On this occasion, amphipods were very abundant close to our surface lights. In fact, night-lighting seems to attract numerous hyperiid amphipods (e.g. SHOEMAKER, 1925; PIRLOT, 1932). Several large specimens of the physonect siphonophore, *Forskalia tholoides* HAECKEL, 1888, were also present and were feeding on them. The small number of amphipods in Table 2 reflects the difficulty of catching them in jars while diving, rather than their relative abundance.

Family Lycaeopsidae CHEVREUX, 1913 (*Table 2*)9. Genus *Lycaeopsis* CLAUS, 1879b

Specimens were identified to species on the basis of the synonymy proposed by BARNARD (1930).

*Lycaeopsis themistoides* CLAUS, 1879b: 1 ♀, 2.8 mm; 1 juv., 2.8 mm. Both specimens were found in excavations in superior nectophores of the siphonophore, *Diphyes dispar* CHAMISSE and EYSENHARDT, 1821. The burrows were U-shaped with two openings to the exterior, and reached to the level of the somatocyst. The diameter of one was only slightly greater than  $1\frac{1}{2}$  × that of the amphipod, while the second was about 3 × the size of the amphipod. In the latter (Sta. 294), the distal part of the somatocyst had been entirely eaten.

*Lycaeopsis themistoides* will leave its burrow when disturbed. It has bright red eyes and a bar of red-brown pigment along each body segment, making it readily visible inside its burrow.

Family Lycaeidae CLAUS, 1879b (*Table 2*)10. Genus *Lycaea* DANA, 1852

Identification to species is discussed in our previous papers (HARBISON and MADIN, 1976; MADIN and HARBISON, 1977). The majority of this genus are parasites on salps.

*Lycaea serrata* CLAUS, 1879b: 1 ♀, 12.7 mm.

*Lycaea* spp. cf. *bovalliioides* (see MADIN and HARBISON, 1977): 2 ♀, 4.0, 2.8 mm. No damage was visible to its host, the pseudothecosomatous pteropod, *Corolla spectabilis* DALL, 1872.

*Lycaea* sp.: 1 juv., 3.2 mm. No damage was visible to its host, the pseudothecosomatous pteropod, *Gleba cordata* FORSKÅL, 1775.

11. Genus *Pseudolycaea* CLAUS, 1879b

The genus is regarded as monotypic.

*Pseudolycaea pachypoda* CLAUS, 1879b: 1 ♂, 4.0 mm; 3 ♀, 3.5, 4.0, 4.0 mm; 12 juv., 0.9 to 1.1 mm. These amphipods were collected with the trachymedusa, *Liriope tetraphylla* CHAMISSE and EYSENHARDT, 1821. Most of the juveniles were sitting on the subumbrella and the upper peduncle, though one was found inside the gastric cavity above the gonad. There was no apparent damage to the medusa.

Family Brachyscelidae STEPHENSEN, 1923 (*Table 3*)12. Genus *Brachyscelus* BATE, 1861

We have discussed the problems of identification within this genus in a previous paper

Table 3. Associations of the family Brachyscelidae with gelatinous zooplankton other than salps

Amphipod species	Host species	Number of amphipods (m) (f) (j)			Station number
<i>Brachyscelus rapacoides</i>	hydromedusa	1	-	-	85
<i>B. rapacoides</i>	cornaria larva	1	-	-	86
<i>B. rapacoides</i>	cornaria larva	1	-	1	87
<i>B. rapacoides</i>	<i>Aequorea</i> sp.	-	1	-	128
<i>B. rapacoides</i>	<i>Aequorea</i> sp.	17	19	-	128
* <i>B. rapacoides</i>	<i>Aequorea</i> sp.	-	-	1	276
* <i>B. rapacoides</i>	<i>Aequorea</i> sp.	-	-	2	277
* <i>B. rapacoides</i>	<i>Aequorea</i> sp.	-	-	1	277
<i>B. rapacoides</i>	<i>Aequorea</i> sp.	1	2	3	277
<i>B. rapacoides</i>	<i>Orchestoma</i> sp.	1	-	-	279
<i>B. rapacoides</i>	<i>Aequorea</i> sp.	1	3	6	292
<i>B. rapacoides</i>	<i>Aequorea</i> sp.	-	1	3	293
<i>B. rapacoides</i>	<i>Aequorea</i> sp.	-	1	-	294
* <i>B. rapacoides</i>	<i>Aequorea</i> sp.	1	-	-	294
<i>B. rapacoides</i>	<i>Aequorea</i> sp.	1	-	2	295
<i>B. rapacoides</i>	<i>Aequorea</i> sp.	-	1	1	302
<i>B. rapacoides</i>	<i>Cavolinia longirostris</i>	-	1	-	303
<i>B. rapacoides</i>	<i>Leuckartiara</i> sp.	-	1	-	317
<i>B. rapacoides</i>	<i>Leuckartiara</i> sp.	-	1	-	320
<i>Brachyscelus</i> sp.	<i>Orchestoma</i> sp.	-	-	1	269
<i>Brachyscelus</i> sp.	<i>Aequorea</i> sp.	-	-	2	270
<i>Brachyscelus</i> sp.	<i>Aequorea</i> sp.	-	-	1	273
* <i>Brachyscelus</i> sp.	<i>Aequorea</i> sp.	-	-	1	274
<i>Brachyscelus</i> sp.	<i>Aequorea</i> sp.	-	-	2	277
<i>Brachyscelus</i> sp.	<i>Aequorea</i> sp.	-	-	1	281
* <i>Brachyscelus</i> sp.	<i>Aequorea</i> sp.	-	-	7	281
* <i>Brachyscelus</i> sp.	<i>Aequorea</i> sp.	-	-	2	292
<i>Brachyscelus</i> sp.	<i>Aequorea</i> sp.	-	-	1	301
<i>Brachyscelus</i> sp.	<i>Aequorea</i> sp.	-	-	3	302
<i>Brachyscelus</i> sp.	leptomedusa	-	1	-	304
<i>Brachyscelus crusculum</i>	leptomedusa	1	-	-	252
<i>B. crusculum</i>	<i>Aequorea</i> sp.	1	-	-	321
<i>B. crusculum</i>	<i>Pterotrachea</i> sp.	-	1	-	377
<i>Thamneus platyrhynchus</i>	<i>Pelagia noctiluca</i>	-	1	-	206
<i>T. platyrhynchus</i>	<i>P. noctiluca</i>	1	-	-	216

\* Co-occurred with *Lestrigonus schizogeneios* and *Lestrigonus* sp. on the same medusa.

\*\* Co-occurred with encysted juvenile Pionidae on the same medusa.

(MADIN and HARBISON, 1977). We have distinguished the two species listed below on the basis of the patterns of serration of pereopods 1 and 2 and the shape of the telson (see DICK, 1970).

*Brachyscelus rapacoides* STEPHENSEN, 1925 (Fig. 1): 25 ♂, 1.3 to 5.3 mm; 35 ♀, 1.2 to 4.2 mm; 20 juv., 0.8 to 2.0 mm.

*Brachyscelus* sp.: 1 ♀, 2.4 mm; 21 juv., 0.8 to 2.1 mm. *Brachyscelus rapacoides* seems to be preferentially associated with medusae, although specimens have been collected with enteropneust larvae and a pteropod. It is likely that the majority of the specimens termed *Brachyscelus* sp. belong to this species, although without knowledge of the development of *B. rapacoides* it is impossible to say. As with *Lestrigonus schizogeneios*, juveniles may be burrowed into the mesogloea of jellyfish. *Brachyscelus rapacoides* and *Brachyscelus* sp. co-occur on individuals of *Aequorea* sp. with *L. schizogeneios* and *Lestrigonus* sp. (compare Tables 1 and 3), much as do *Lycaea* and *Vibilia* on salps (MADIN and HARBISON, 1977). It appears that *Lestrigonus* may preferentially consume the food of the medusa, much as does *Vibilia*, while *Brachyscelus* consumes the tissues of the host, much as with *Lycaea*. Specimens of *B. rapacoides* (2.3 and 3.7 mm) from the small hydromedusa *Leuckartiara* sp. were almost as large as the host (ca. 4 mm). Their colouration was very similar to the yellow-brown of the medusa.

*Brachyscelus crusculum* BATE, 1861: 2 ♂, 6.6, 13.7 mm; 1 ♀, 7.0 mm. This species has also been found on salps (MADIN and HARBISON, 1977). Both medusae collected with *B. crusculum* had signs of damage to the subumbrella and system of radial canals. The heteropod, *Pterotrachea* sp., and the amphipod were seen swimming around one another, so this relationship is not clear. Since *B. crusculum* occurs with salps, medusae, and perhaps even heteropods, it may be a general predator or parasite on gelatinous zooplankton. Alternatively, this apparently broad specificity may be due to misidentification, since the bulk of nominal species are included in the *B. crusculum* group.

### 13. Genus *Thamneus* BOVALLIUS, 1887

Most recent authors regard this genus as monotypic.

*Thamneus platyrrhynchus* STEBBING, 1888: 1 ♂, 7.1 mm; 1 ♀, 9.1 mm. This species has been collected twice in the temperate North Atlantic, both times with *Pelagia noctiluca*. *Lestrigonus crucipes*, another parasite of *P. noctiluca*, was collected in the Florida Current (Table 1). As yet, we have not found these two species of hyperiid amphipods living together.

Table 4. Associations of the family Pronoidae with siphonophores

Amphipod species	Host species	Number of amphipods			Station number
		(m)	(f)	(j)	
<i>Paralycaea newtoniana</i>	<i>Sulculeolaria monoica</i>	-	~	3	298
<i>P. newtoniana</i>	<i>Sulculeolaria ohumi</i>	-	1	-	372
<i>P. newtoniana</i>	<i>Sulculeolaria</i> sp. (host escaped)	-	1	11	373
<i>P. newtoniana</i>	<i>S. quadrivalvis</i>	-	1	-	380
<i>Paralycaea hoylei</i>	<i>Sulculeolaria</i> sp. (host escaped)	-	1	-	371
<i>P. hoylei</i>	<i>S. quadrivalvis</i>	1	-	-	377
<i>P. hoylei</i>	<i>Nanomia bijuga</i>	1	~	-	381
<i>Paralycaea gracilis</i>	<i>Sulculeolaria ohumi</i>	-	-	4	294
<i>P. gracilis</i>	<i>S. monoica</i>	-	2	4	318
<i>P. gracilis</i>	<i>Agalma clausi</i>	1	-	-	352
<i>Sympronee parva</i>	<i>Fosacea cymbiformis</i>	1	-	-	314
* <i>S. parva</i>	<i>F. cymbiformis</i>	-	1	1	321
<i>S. parva</i>	<i>F. cymbiformis</i>	2	-	-	346
<i>Sympronee</i> sp.	<i>F. cymbiformis</i>	-	-	1	351
<i>S. parva</i>	<i>F. cymbiformis</i>	2	-	-	353
<i>S. parva</i>	<i>F. cymbiformis</i>	-	1	-	353
* <i>Eupronoe minuta</i>	<i>Agalma elegans</i>	1	-	-	351
<i>Eupronoe armata</i>	free-swimming	-	1	-	368

\*Co-occurred on the same siphonophore with *Amphithyrus bispinosus* and *A. glaber*.

\*\*Co-occurred on the same siphonophore with *Paraphronima crassipes*.

### Family Pronoidae CLAUS, 1879a (Table 4)

We have found members of this family solely on siphonophores. Our collections include specimens of three of the five genera.

### 14. Genus *Paralycaea* CLAUS, 1879b

The three species within the genus *Paralycaea* have been synonymized as *P. gracilis* CLAUS, 1879b, by PIRLOT (1930) and HURLEY (1955). While we have inadequate material to judge the



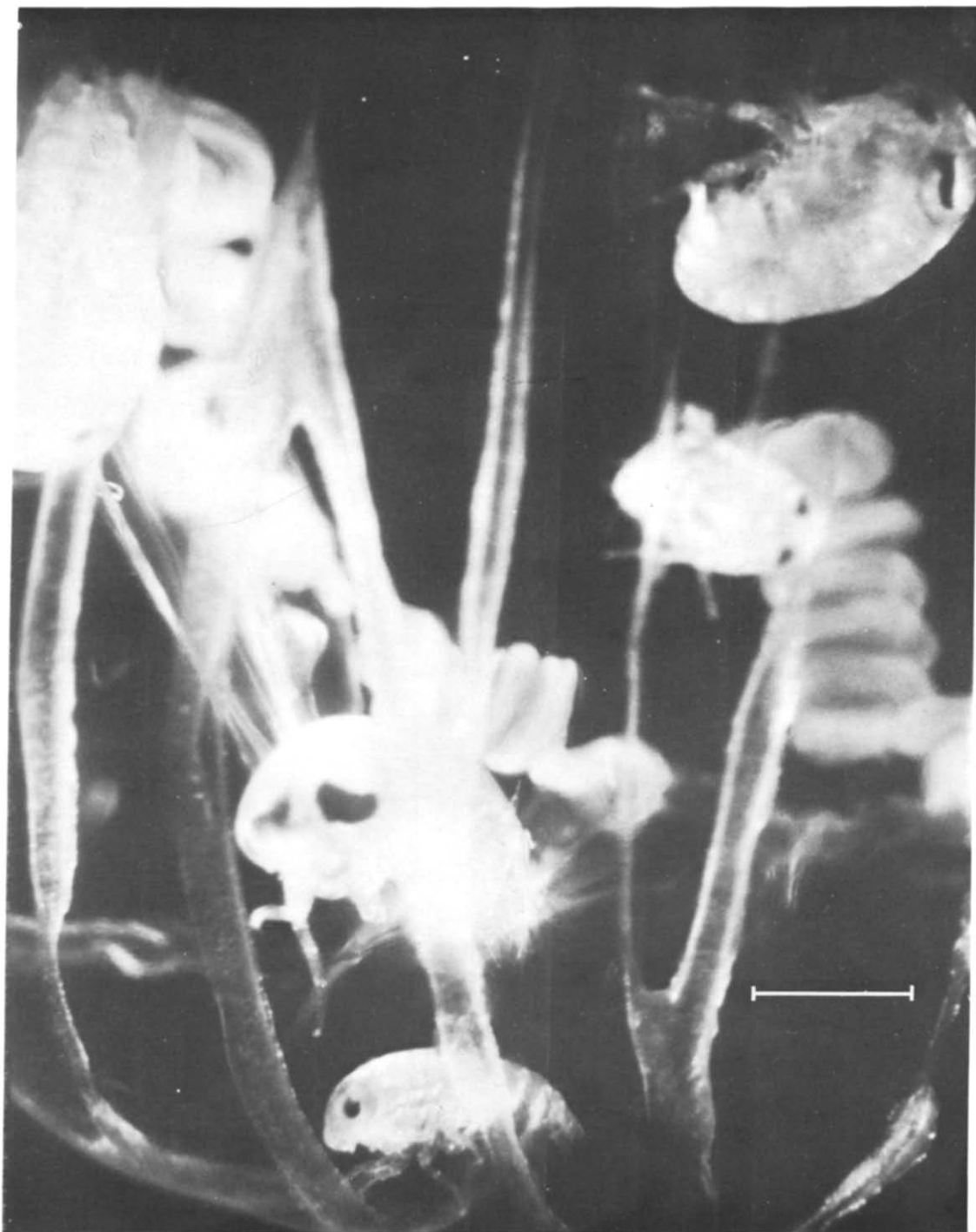


Fig. 1. A group of *Brachyscelus rapacoides* on a medusa, *Aequorea* sp. This picture and other photographs of living animals are from later stations than are recorded in this paper.  
Scale line = 1 mm.

[facing p. 472]

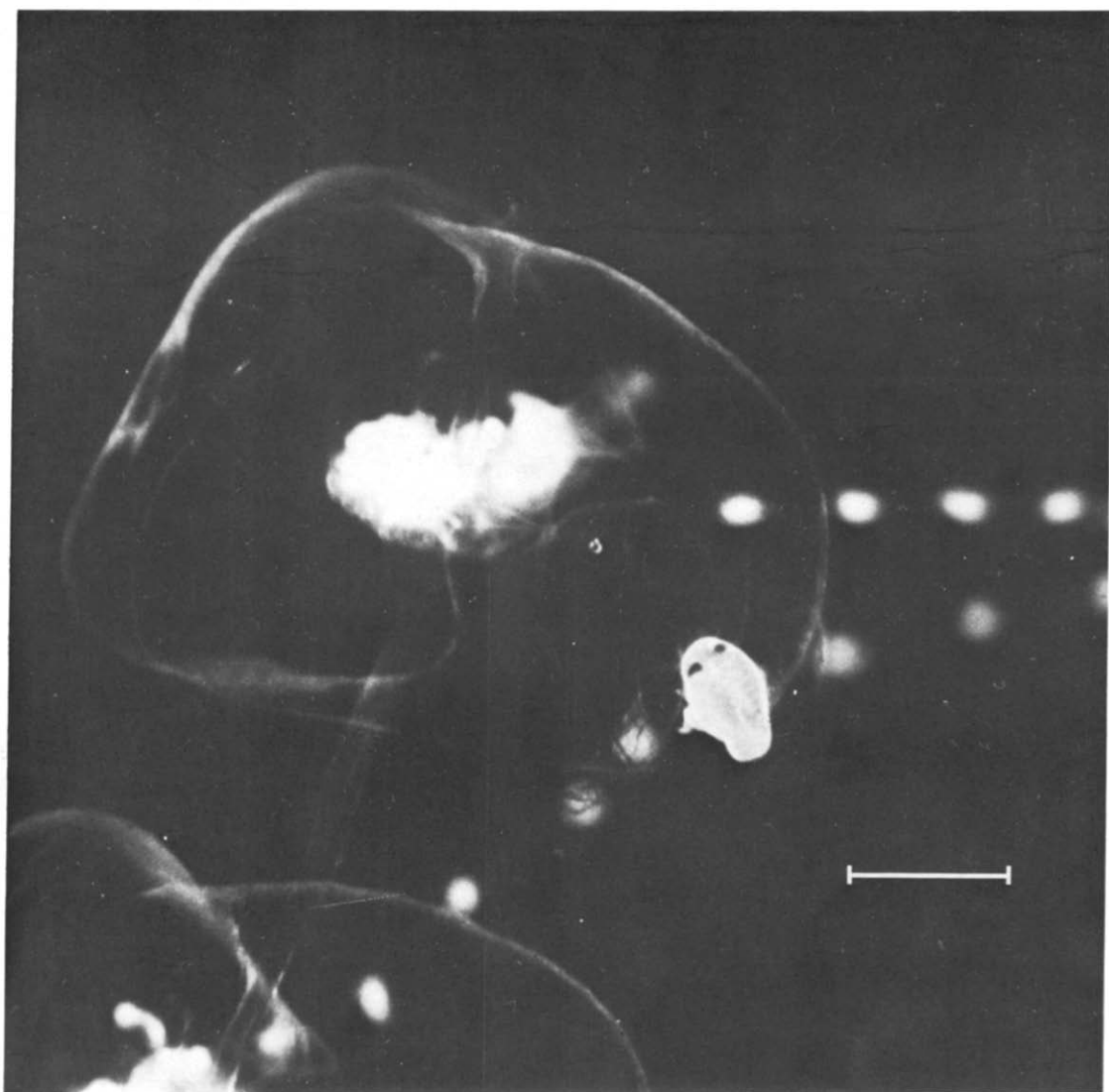


Fig. 2. A juvenile *Symprone parva* on the siphonophore, *Rosacea cymbiformis*. Scale line = 1 mm.



Fig. 3. An encysted juvenile *Eupromoe* sp. in a nectophore of *Agalmia clausi* (Sta. 351). The nectophore and encysted juvenile are preserved in formalin and have been stained with rose bengal to heighten the contrast. Scale line = 1 mm.

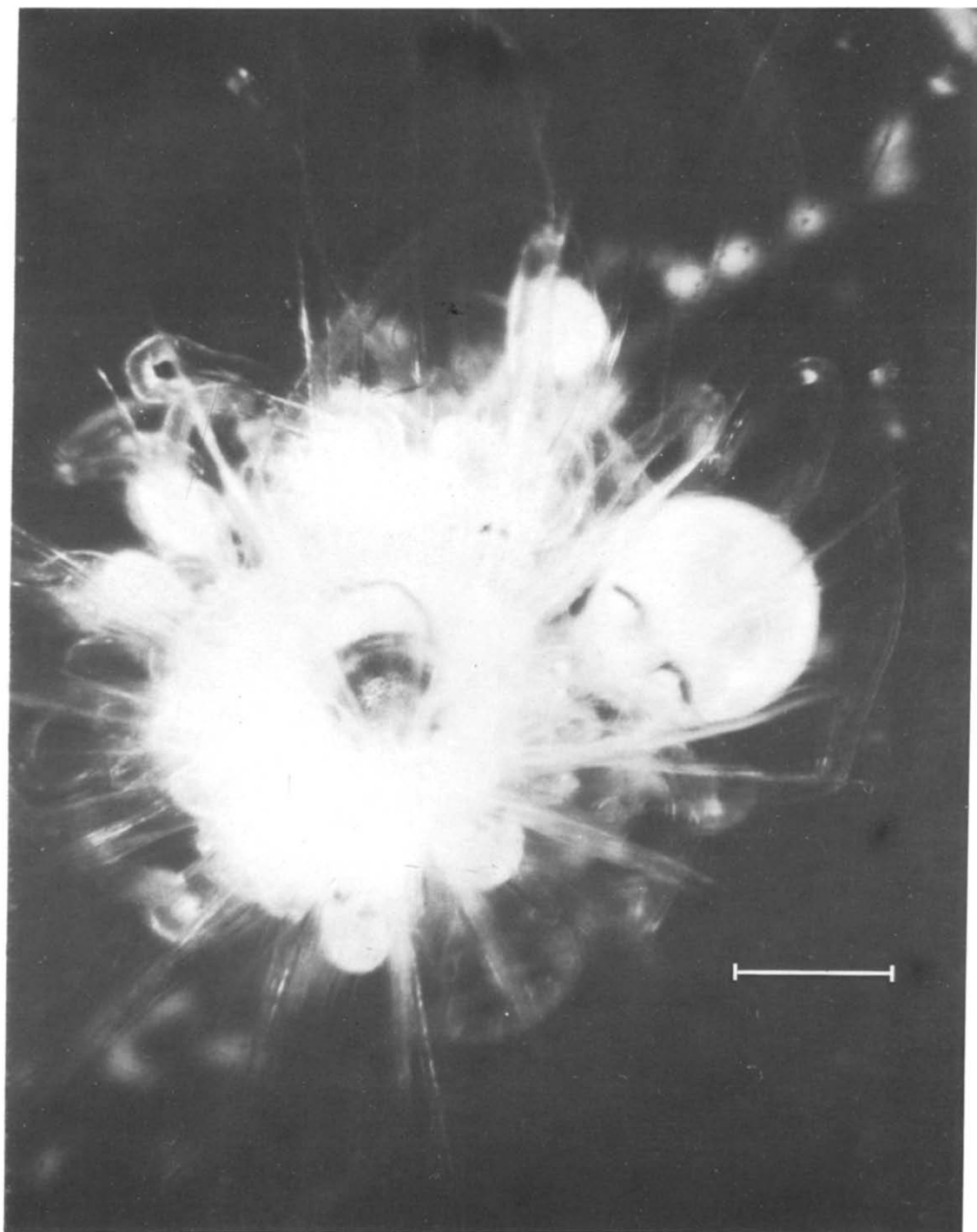


Fig. 7. A female and several juvenile *Thyropus similis* on the siphonophore, *Athorybia rosacea*.  
Scale line = 1 mm.

validity of their synonymies, there are such great differences between some of our specimens that we regard all of the nominal species as tentatively valid. *Paralycaea newtoniana* BOVALLIUS, 1887, has an oval head, and the inner ramus of uropod 2 is articulated with the peduncle. The merus does not overlap the carpus of pereopod 6. Red pigment densely covers the basis of pereopod 6, and also covers the dorsal surface of the animal, with greatest intensity on the pleon and urosome. *Paralycaea hoylei* STEBBING, 1888, closely resembles *P. newtoniana* except that the merus overlaps the carpus of pereopod 6. PIRLOT (1930) may have been correct in considering this species to be synonymous with *P. newtoniana*. *Paralycaea gracilis* has a round head and the inner ramus of uropod 2 is fused with the peduncle. The animal is uniformly pigmented.

*Paralycaea newtoniana*: 3 ♀, 2.8, 3.7, 3.8 mm; 14 juv., 1.2 to 2.5 mm.

*Paralycaea hoylei*: 2 ♂, 3.5, 4.3 mm; 1 ♀, 4.1 mm.

*Paralycaea gracilis*: 1 ♂, 2.4 mm; 2 ♀, 4.5, 6.2 mm; 8 juv., 1.3 to 2.5 mm. This species has been collected with *Sulculeolaria monoica* (CHUN, 1888), *Sulculeolaria chuni* (LENS and VAN RIEMSDIJK, 1908) and *Agalma clausi* BEDOT, 1888. The three smallest juveniles from *S. monoica* were sitting on the nectosac of the posterior swimming bell, while the other juveniles and females were sitting on exumbrellar surfaces of the bells and on the bracts surrounding the stem. The amphipod captured with *A. clausi* was sitting on the nectosac of one of the swimming bells but left the siphonophore when collected, as do the other species within the genus. The juveniles taken with *S. chuni* were eating the orange-coloured gonophores of this siphonophore.

#### 15. Genus *Sympronoë* STEBBING, 1888

All of the specimens we have collected were densely covered with pigment spots, as described for *S. propinqua* STEBBING, 1888, but the shape of the telson agrees better with the description of *S. anomala* SHOEMAKER, 1925. An immature male from Sta. 346 had a seven-articulated pereopod 7, while an adult male from the same siphonophore had a two-articulated pereopod 7. BARNARD (1932) regards both of these species as junior synonyms of *S. parva* CLAUS, 1879b, however, and our collections do not contradict this view.

*Sympronoë parva* (Fig. 2): 5 ♂, 3.9 to 7.4 mm; 2 ♀, 9.5, 7.0 mm; 2 juv., 1.9, 2.7 mm. This species has been collected only with the siphonophore, *Rosacea cymbiformis*. There was no apparent damage to the host specimens we examined, and none of these amphipods was found burrowed into the swimming bells or bracts. As with species of *Paralycaea*, *S. parva* readily quits its host when disturbed. Eight juveniles of *Paraphronima crassipes* were collected with two *S. parva* on a *R. cymbiformis* from Sta. 321 (Table 2).

#### 16. Genus *Eupronoe* CLAUS, 1879b

We have collected adult specimens of *Eupronoe* on but two occasions. Neither specimen, however, is easily ascribable to species. The specimen from Sta. 351 most closely resembles the figures of CLAUS (1887) for *E. minuta* CLAUS, 1879b, but does not resemble the descriptions given by STEPHENSEN (1925) and DICK (1970) for *E. minuta*, particularly with regard to the shape of pereopod 1. The specimen from Sta. 368 does not resemble any described species, although it appears to be mature. Aside from the dactyls of pereopods 3, 4, 5, and 6, which are as long as the propodi, this specimen most closely approximates *E. armata* CLAUS, 1879b, although it is much smaller.

*Eupronoe minuta*: 1 ♂, 5.9 mm. Co-occurred on the siphonophore, *Agalma elegans* (SARS, 1846) FEWKES, 1880, with *Amphithyrus bispinosus* CLAUS, 1879b, and *Amphithyrus glaber* SPANDL, 1924 (Tables 4 and 6).

*Eupronoe armata*: 1 ♀, 3.2 mm.

Table 5. Associations of encysted juvenile Pronoidae with siphonophores

Host species	Number of amphipods	Station number
<i>*Forskalia tholoides</i>	20	267
<i>Forskalia</i> sp.	1	267
<i>Forskalia</i> sp.	1	267
<i>*Forskalia edwardsi</i>	21	270
<i>Forskalia edwardsi</i>	6	300
<i>Forskalia tholoides</i>	60	316
<i>Forskalia tholoides</i>	3	320
<i>Forskalia edwardsi</i>	4	352
<i>Agalma clausi</i>	8	281
<i>Agalma clausi</i>	5	303
<i>Agalma okeni</i>	5	309
<i>*Agalma okeni</i>	1	313
<i>Agalma okeni</i>	4	325
<i>Agalma okeni</i>	7	326
<i>Agalma okeni</i>	1	326
<i>Agalma okeni</i>	15	346
<i>**Agalma clausi</i>	7	351
<i>Athorybia rosacea</i>	1	372
<i>Athorybia rosacea</i>	1	374

\* Co-occurred with *Thyropus* on the same siphonophore.

\*\* Co-occurred with *Tetrathyrus* on the same siphonophore.

#### Family Pronoidae—encysted juveniles (Table 5)

At least one species of juvenile amphipod was found encysted in the mesogloea of nectophores and bracts of five species of physonect siphonophores (Fig. 3). The burrows of these juveniles are no larger than  $1\frac{1}{2}$  times the dimensions of the amphipod and have no visible connection with the exterior. These juveniles have dark brown pigmentation on the peraeon and are easily visible in mesogloea.

We have found examples of three developmental stages in a single *Agalma okeni* (Sta. 346), which we describe below. The developmental stages of several species of hyperiid amphipods have been shown to be related to the number of podomeres on the exopodite and endopodite of the pleopods (KANE, 1964; EVANS, 1968; HARBISON, 1976). We will use the developmental stage nomenclature of HARBISON (1976).

Stage I (Fig. 4)—much inflated, peraeon with dorsal sutures only. All peraeopods simple, peraeopod 7 with all segments present. Pleopods without setae. Urosome extremely reduced; telson not fused with double urosomite. Eyes poorly developed, lacking pigment.

Stage II—not found on this colony, but resembles Stage I.

Stage III (Fig. 5)—peraeon still inflated. Peraeopod 1 simple, peraeopod 2 bluntly chelate, basis of peraeopods 5 and 6 slightly inflated, peraeopod 7 with 4 segments present. Pleopods with setae. Rami of uropods articulated with peduncles; telson about two-thirds length of double urosomite.

Stage IV (Fig. 6)—peraeon not inflated, perhaps resembling adult. Peraeopod 1 simple,

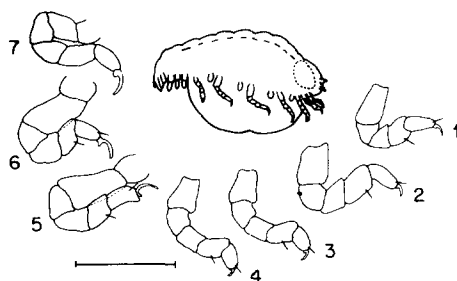


Fig. 4. One-podomere stage of *Eupronoe* sp. This amphipod and those in Figs. 5 and 6 were found encysted in the nectophores and bracts of a single specimen of *Agalma okeni* (Sta. 346). Scale line for Figs. 4, 5 and 6 = 0.1 mm for pereopods, 0.65 mm for amphipod.

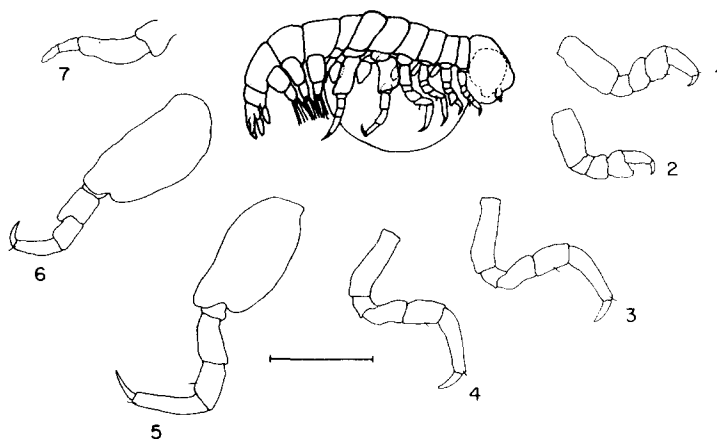


Fig. 5. Three-podomere stage of *Eupronoe* sp.

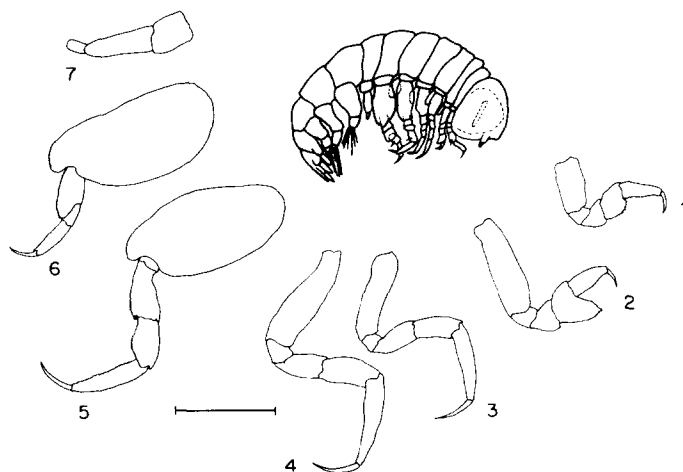


Fig. 6. Four-podomere stage of *Eupronoe* sp.

peraeopod 2 chelate, carpus with minute serrations, peraeopods 3 and 4 simple, bases of peraeopods 5 and 6 inflated, peraeopod 7 with three segments. Rami of uropods articulated with peduncles; telson triangular, not fused with double urosomite, about two-thirds length of double urosomite, and extends only two-thirds length of uropod 3.

We have not found encysted juveniles beyond stage IV. If the oldest juveniles resemble the adults, they belong to the Pronoidae. Within the Pronoidae, all genera save *Eupronoe* and *Sympronoe* must be excluded, since peraeopod 1 is simple and peraeopod 2 is chelate. *Parapronoe* also has this condition, but the carpus of peraeopod 1 is concave, as is the carpal process of peraeopod 2, which does not resemble our specimens. We believe that the stage IV juveniles belong to *Eupronoe*, rather than *Sympronoe*, primarily on the basis of the shape and dimensions of the telson and uropods. Furthermore, *Sympronoe*, which is well-represented in our collections (Table 4), has been collected only with *R. cymbiformis*, which we have not found to harbour encysted amphipods. *Eupronoe*, which has been collected only twice, occurred once with a physonect siphonophore (Table 4), several species of which we have found with encysted amphipods.

We also found a stage III amphipod on *Stephanophyes superba* CHUN, 1888 from Sta. 282 whose size (1.8 mm) and morphology closely resemble a stage IV individual. Though this specimen was not encysted, it closely resembles the encysted forms. We also found six amphipods resembling stage I encysted juveniles in the gut of a specimen of *Aequorea* sp. from Sta. 292, which also had two juvenile *Brachyscelus* sp. on the exumbrella (Table 3).

Stage I and Stage II juveniles: 89 specimens, 0.7 to 1.6 mm.

Stage III juveniles: 12 specimens, 1.1 to 2.3 mm.

Stage IV juveniles: 5 specimens, 1.5 to 2.4 mm.

Table 6. Associations of the family Platyscelidae with siphonophores

Amphipod species	Host species	Number of amphipods			Station number
		(m)	(f)	(j)	
* <i>Amphithyrus biepinosus</i>	<i>Agalma elegans</i>	1	-	-	351
* <i>Amphithyrus glaber</i>	<i>Agalma elegans</i>	1	-	-	351
<i>Amphithyrus similis</i>	<i>Chelophyes appendiculata</i>	-	1	3	356
** <i>Tetrathyrus forcipatus</i>	<i>Agalma clausi</i>	1	-	-	351
<i>Tetrathyrus forcipatus</i>	<i>Nanomia bijuga</i>	-	-	23	289
<i>Tetrathyrus</i> sp.	<i>Nanomia bijuga</i>	-	-	7	268
<i>Tetrathyrus</i> sp.	<i>Nanomia bijuga</i>	-	-	4	290
<i>Hemityphis rapax</i>	Captured by <i>Forskalia tholoides</i>	1	-	-	316

\* Co-occurred with *Eupronoe minuta* and a second species of *Amphithyrus* on the same siphonophore.

\*\* Co-occurred with encysted Pronoidae on the same siphonophore.

#### Family Platyscelidae BATE, 1862 (Table 6)

This is the fourth of five families which we have found only on siphonophores. We have collected three of five genera.



17. Genus *Amphithyrus* CLAUS, 1879b

Species within this group were identified using DICK's (1970) key and the original descriptions. Although we have only three adult specimens, it is clear that there are problems within this genus.

*Amphithyrus bispinosus* CLAUS, 1879b: 1 ♂, 4.8 mm.

*Amphithyrus glaber* SPANDL, 1924: 1 ♂, 5.1 mm.

*Amphithyrus similis* CLAUS, 1879b: 1 ♀, 2.9 mm, 3 juv., ca. 0.9 mm. These amphipods were all sitting on the upper region of the stem of a specimen of the siphonophore, *Chelophyes appendiculata* (ESCHSCHOLTZ, 1829). The three juveniles were transparent, while the female was brown with red-orange eye pigment. Chromatophores were most concentrated on the dorsal surface of the pereon. No damage to the siphonophore was apparent.

18. Genus *Tetrathyrus* CLAUS, 1879b

PIRLOT (1930) considers this genus to be monotypic, and since we have so few specimens, we must concur. The juveniles from Sta. 289 resemble *T. moncoeuri* STEBBING, 1888 in that pereopod 7 is 5-segmented. A number of authors have criticized the use of a reduced appendage for taxonomic purposes (SPANDL, 1927, for example) however. The amphipods from Stas. 268 and 290 are too small for identification to species.

*Tetrathyrus forcipatus* CLAUS, 1879b: 1 ♂, 4.6 mm, 34 juv., 0.9 to 2.0 mm.

19. Genus *Hemityphis* CLAUS, 1879b

All of the nominal species in this genus have been synonymized with *H. rapax* (MILNE-EDWARDS, 1830) by SHOEMAKER (1945) and his predecessors. SPANDL (1927), however, saw differences between two of the nominal species. Our specimen resembles Spandl's figures for *H. tenuimanus* CLAUS, 1879b, rather than his figures of *H. crustulum* CLAUS, 1879b. STEPHENSEN (1925) has shown that *H. tenuimanus* is a junior synonym of *H. rapax*.

*Hemityphis rapax*: 1 ♂ 5.8 mm. This specimen was found inside a gastrozoid of a colony of *Forskalia tholoides*. It was not appreciably digested, and so may have been recently captured and ingested. This siphonophore was also feeding on *Anchylomera blossevillei* at this station (Table 2).

## Family Parascelidae BOVALLIUS, 1887 (Table 7)

This is the fifth of five families we have found associated only with siphonophores. We have collected two of the three genera. We have already discussed the association between *Schizoscelus ornatus* CLAUS, 1879b, and *Bathyphysa sibogae* LENS and VAN RIEMSDIJK, 1908, in a previous paper (BIGGS and HARBISON, 1976), but we also include these data here for the sake of completeness.

20. Genus *Schizoscelus* CLAUS, 1879b

The genus is monotypic.

*Schizoscelus ornatus*: 3 ♂, 3.4 to 6.2 mm; 5 ♀, 3.5 to 5.4 mm.

Table 7. Associations of the family Parascelidae with siphonophores

Amphipod species	Host species	Number of amphipods (m) (f) (j)			Station number
<i>Schizoscelus ornatus</i>	<i>Bathypphysa sibogae</i>	-	1	-	312
<i>S. ornatus</i>	<i>B. sibogae</i>	-	1	-	313
<i>S. ornatus</i>	<i>B. sibogae</i>	-	1	-	313
<i>S. ornatus</i>	<i>B. sibogae</i>	3	1	-	315
<i>S. ornatus</i>	<i>B. sibogae</i>	-	1	-	331
<i>Thyropus edwardsii</i>	<i>Agalma okeni</i>	-	1	4	260
* <i>T. edwardsii</i>	<i>Forskalia tholoides</i>	-	2	-	267
<i>T. edwardsii</i>	<i>A. okeni</i>	1	-	-	285
<i>T. edwardsii</i>	<i>A. okeni</i>	1	-	-	285
<i>T. edwardsii</i>	<i>A. okeni</i>	1	-	-	292
<i>T. edwardsii</i>	<i>A. okeni</i>	1	-	-	292
<i>T. edwardsii</i>	<i>A. okeni</i>	-	1	-	292
<i>T. edwardsii</i>	<i>A. okeni</i>	1	-	-	297
<i>T. edwardsii</i>	<i>Diphyes dispar</i>	-	1	-	303
<i>T. edwardsii</i>	<i>A. okeni</i>	1	-	-	314
<i>T. edwardsii</i>	<i>Bathypphysa sibogae</i>	1	-	-	314
<i>T. edwardsii</i>	<i>A. okeni</i>	-	1	-	316
<i>Thyropus sphaeroma</i>	<i>Stephanophyes superba</i>	-	1	-	340
* <i>Thyropus similis</i>	<i>Agalma okeni</i>	-	1	-	313
<i>T. similis</i>	<i>Athorybia rosacea</i>	1	-	-	321
<i>T. similis</i>	<i>Athorybia rosacea</i>	-	1	1	350
<i>T. similis</i>	<i>Athorybia</i> sp.	-	1	-	369
<i>T. similis</i>	<i>Athorybia</i> sp.	-	1	-	372
<i>T. similis</i>	<i>Athorybia</i> sp.	-	2	-	372
<i>T. similis</i>	<i>Athorybia</i> sp.	-	1	-	375
<i>Thyropus</i> sp.	<i>Agalma okeni</i>	-	-	2	267
<i>Thyropus</i> sp.	<i>Agalma okeni</i>	-	-	4	267
<i>Thyropus</i> sp.	<i>Agalma okeni</i>	-	-	2	269
<i>Thyropus</i> sp.	<i>Stephanophyes superba</i>	-	-	1	269
<i>Thyropus</i> sp.	<i>Agalma okeni</i>	-	-	2	270
* <i>Thyropus</i> sp.	<i>Forskalia edwardsi</i>	-	-	2	270
<i>Thyropus</i> sp.	<i>Stephanophyes superba</i>	-	-	1	277
<i>Thyropus</i> sp.	<i>Forskalia</i> sp.	-	-	1	278
<i>Thyropus</i> sp.	<i>Agalma okeni</i>	-	-	1	285
<i>Thyropus</i> sp.	<i>Agalma okeni</i>	-	-	1	285
<i>Thyropus</i> sp.	<i>Diphyes dispar</i>	-	-	3	294
<i>Thyropus</i> sp.	<i>Agalma okeni</i>	-	-	1	297
<i>Thyropus</i> sp.	<i>Agalma okeni</i>	-	-	1	297
<i>Thyropus</i> sp.	<i>Stephanophyes superba</i>	-	-	2	298
<i>Thyropus</i> sp.	<i>Stephanophyes superba</i>	-	-	2	298
<i>Thyropus</i> sp.	<i>Alyia</i> sp.	-	-	1	305
<i>Thyropus</i> sp.	<i>Stephanophyes superba</i>	-	-	3	350
<i>Thyropus</i> sp.	<i>Stephanophyes superba</i>	-	-	2	351
<i>Thyropus</i> sp.	<i>Stephanophyes superba</i>	-	-	1	351
<i>Thyropus</i> sp.	<i>Athorybia</i> sp.	-	-	14	367
<i>Thyropus</i> sp.	<i>Athorybia rosacea</i>	-	-	8	371

\* Co-occurred with encysted Pronomidae on the same siphonophore.

## 21. Genus *Thyropus* DANA, 1852

We agree with STEPHENSEN's (1925) suggestion (acted upon by BOWMAN and GRUNER, 1973) that *Parascelus* should be considered a junior synonym of *Thyropus*.

We have found at least three species of the genus *Thyropus* on siphonophores of seven different families. It is apparent from our collections that the genus is in considerable need of revision. Based on previous synonymies (PIRLOT, 1939; SHOEMAKER, 1945), we recognize five of the ten nominal species listed by STEPHENSEN (1925).

We present below a provisional key to the genus *Thyropus*, based on the literature and our own collections. We regard *T. diaphanus* DANA, 1852, *T. atlanticus* BOVALLIUS, 1887, *T. danae* STEBBING, 1888 and *T. nasutus* (BOVALLIUS, 1887) as insufficiently described for identification. *Thyropus zebu* (STEBBING, 1888) has been synonymized with *T. edwardsii* (CLAUS, 1879b) by both PIRLOT (1939) and SHOEMAKER (1945).

A provisional key to the species of *Thyropus* follows:

- |  |                     |
|--|---------------------|
| 1. Peraeopod 6 with fissure in basis                                 | 2                   |
| Peraeopod 6 without fissure in basis                                 | 3                   |
| 2. Peraeopod 6, basis tapers greatly, merus does not overhang carpus | <i>T. sphaeroma</i> |
| Peraeopod 6, basis not tapered, merus overhangs carpus               | <i>T. similis</i>   |
| 3. Peraeopod 6, basis tapers greatly                                 | <i>T. edwardsii</i> |
| Peraeopod 6, basis not tapered                                       | 4                   |
| 4. Carpus of peraeopods 1 and 2 serrated                             | <i>T. parvus</i>    |
| Carpus of peraeopods 1 and 2 smooth                                  | <i>T. typhoides</i> |

*Thyropus edwardsii*: 7 ♂, 6.0 to 8.2 mm; 6 ♀, 3.4 to 7.0 mm; 5 juv., ca. 2.9 mm. *Thyropus edwardsii* appears to have a broad host specificity, since it has been found to occur on all three suborders of siphonophores.

*Thyropus sphaeroma* CLAUS, 1879b: 1 ♀, 4.9 mm. This specimen resembles *T. sphaeroma* ♂ of SPANDL (1927).

*Thyropus similis* (STEPHENSON, 1925) (Fig. 7): 1 ♂, 5.8 mm; 7 ♀, 3.7 to 6.2 mm; 1 juv., 1.9 mm. This species has been found on *Agalma okeni* and *Athorybia rosacea* (FORSKAL, 1775). *Thyropus similis* was also found associated with a species of *Athorybia* different from that discussed by TOTTON (1965). Two females from Sta. 372 began consuming the tentacles of this siphonophore after a short period in the laboratory. *Thyropus similis* is colourless except for a crescent of black eye pigment in each eye, four to six internal dark pigment spots in the peraeon, and one or two rows of black pigment spots on the posterior margin of the basis of peraeopod 6.

*Thyropus* sp.: 55 juv., 0.8 to 3.7 mm. By far the greater portion of our *Thyropus* material consists of juveniles too small to identify to species. On several occasions species of *Thyropus* co-occurred with encysted juvenile Pronoidae (Table 5), as was the case with *Tetrathyrus forcipatus*.

Table 8. Associations of the family Oxycephalidae with gelatinous zooplankton

Amphipod species	Host species	Number of amphipods			Station number
		(m)	(f)	(j)	
<i>Cranocephalus scleroticus</i>	<i>Pleurobrachia</i> sp.	1	-	-	230
<i>C. scleroticus</i>	<i>Pleurobrachia</i> sp.	1	-	-	233
<i>C. scleroticus</i>	<i>Pleurobrachia</i> sp.	-	1	1	242
<i>Glossoccephalus milne-edwardsii</i>	<i>Bolinopsis vitrea</i>	1	-	-	279
<i>G. milne-edwardsii</i>	<i>B. vitrea</i>	1	-	-	279
<i>G. milne-edwardsii</i>	<i>B. vitrea</i>	-	-	1	279
<i>Oxycephalus clausi</i>	no host	1	-	-	332
<i>O. clausi</i>	no host	-	1	-	354
<i>O. clausi</i>	<i>Ocyropsis maculata</i>	-	1	-	354
<i>O. clausi</i>	<i>Pterotrachea hippo-campus</i>	1	-	-	366
<i>O. clausi</i>	siphonophore fragments	-	1	-	377
<i>Streetsia porcella</i>	radiolarian colony	-	1	-	295
<i>S. porcella</i>	<i>Leurothea</i> sp.	1	9	-	302
<i>S. porcella</i>	no host	-	1	-	341
<i>S. porcella</i>	marine snow	1	-	-	366

### Family Oxycephalidae BATE, 1862 (Table 8)

Oxycephalids were identified to species using the synonymies of FAGE (1960), upon which PILLAI (1966) based his key. Four different genera have been collected, all with ctenophores, although some have also been found either free-swimming or on other substrates.

#### 22. Genus *Streetsia* STEBBING, 1888

*Streetsia porcella* (CLAUS, 1879b): 2 ♂, 3.5, 15.0 mm; 11 ♀, 3.3 to 16.6 mm. This species has been collected with a polycystine radiolarian colony, as well as with the ctenophore, *Leucothea* sp. The ctenophore was extremely fragile, fragmenting in the course of collection, so that damage caused by the amphipod could not be determined.

#### 23. Genus *Glossoccephalus* BOVALLIUS, 1887

*Glossoccephalus milne-edwardsii* BOVALLIUS, 1887: 2 ♂, 2.7, 5.3 mm; 1 juv., 1.7 mm. This species has been collected only at Sta. 279. No damage was apparent to the ctenophore, *Bolinopsis vitrea* (AGASSIZ, 1860) that could be ascribed to these amphipods. At this station, the ctenophores were quite heavily infested with this species, but the amphipods were extremely difficult to collect.

#### 24. Genus *Cranocephalus* BOVALLIUS, 1890

*Cranocephalus scleroticus* (STREETS, 1878): 2 ♂, 7.7, 8.5 mm; 1 ♀, 6.6 mm; 1 juv., 1.7 mm. The ctenophore with the female *C. scleroticus* had damaged ctene rows, and a juvenile was found embedded in the mesogloea of the ctenophore, much as with the juveniles of *Hyperoche medusarum* in *Pleurobrachia* (BRUSCA, 1970).

#### 25. Genus *Oxycephalus* MILNE-EDWARDS, 1830

*Oxycephalus clausi* BOVALLIUS, 1887: 2 ♂, 23.8, 29.0 mm; 3 ♀, 15.8, 25.5, 29.0 mm. This species seems to be predatory in behaviour, at least as an adult. The female collected at Sta. 354 had reduced a ctenophore, *Ocyropsis* sp., to small fragments within a few minutes. This amphipod also devours salps (MADIN and HARBISON, 1977), both in the field and under laboratory conditions. Since *O. clausi* is a large amphipod, differences between predation and parasitism may be based solely on size in relation to a given gelatinous zooplankton. We have not observed such voracious behaviour in *Streetsia porcella*, which has been found on almost as wide a variety of substrates. *Streetsia porcella* is considerably smaller than *O. clausi*, however.

### DISCUSSION

From our work and that of others (Table 9), it is clear that many hyperiid amphipods are intimately associated with gelatinous zooplankton during part or all of their lives. Table 9 lists previous observations made of associations between gelatinous zooplankton and hyperiid amphipods between 1762 and 1975. Seventy per cent of these previous records have been made on amphipods of the family Hyperiididae, many members of which are found close to shore. A comparison of Table 9 with Tables 1 to 8 reveals that, using Scuba diving techniques, we have observed the associations of more genera of hyperiid amphipods with gelatinous zooplankton in four years than were observed in all of the reports listed in Table 9, which spans over 200 years.

We have observed interactions between hyperiids and gelatinous zooplankton in 12 of the 22 families of Hyperiididae. These 12 families comprise the overwhelming bulk of hyperiid

amphipods living close to the surface in warmer waters (see STEPHENSEN, 1925). In only one of the families containing 'proper surface species' (STEPHENSEN, 1925), the Phrosinidae, have we failed to collect amphipods and gelatinous zooplankton together. Including *Parathemisto* and *Vibilia* (MADIN and HARBISON, 1977), of 48 'proper surface genera', we have collected 27; twelve of these genera have not been previously reported as forming associations with gelatinous zooplankton. If we add *Hyperia*, *Bougisia* and *Anchylomera* from Table 9, the total number of genera known to be associated with gelatinous zooplankton is increased to 30. We have no doubt that as future collections are made, we will observe many new associations. Indeed, in recent collections (not treated in this paper), we have found *Scina* sp. living on siphonophores, although previous authors (STEPHENSEN, 1918; PIRLOT, 1932) have considered this genus to be free-living.

Of the seven genera which STEPHENSEN (1925) lists as forming 'small shoals', we have collected all; of those he lists as forming larger shoals we have collected 9 of 21 genera. 'Shoaling' in hyperiid amphipods may thus reflect a multitude of amphipods on individual zooplankters, or a proliferation of hosts with a few amphipods on each. Of course, some hyperiids may indeed form free-living shoals. When working from net collections it is impossible to choose between these alternatives, especially when taxonomic groups are worked up without reference to one another. Our method of collecting gelatinous zooplankton leaves no doubt as to the nature of their symbionts. Collecting in jars has the further advantage of permitting observations of biological interactions between host and symbiont, and consequent evaluation of the nature of the associations. At this time, we cannot prove that any hyperiid amphipod is an obligate parasite on any gelatinous zooplankter. However, we do have strong evidence supporting this hypothesis (for example, the encysted *Eupronoe* spp. juveniles). Further, the high degree of specificity we have seen in a number of cases (species of *Lycaea* and *Vibilia* on salps, species of *Symprone*, *Paralycaea* and *Thyropus* on siphonophores, and species of *Lestrigonus* and *Thamneus* on medusae) add confirming evidence. If hyperiid amphipods are obliged to form associations with gelatinous zooplankton, then the distribution of their hosts must be the major factor determining both the horizontal and vertical distribution of the amphipods. To our minds, little information of ecological value can be gained from treating hyperiid amphipods as if they were free-living, totally planktonic organisms.

From our results, it is clear that the behaviour of the amphipod is usually flexible, and affected by the nutritional circumstances of the host. Many hyperiids will eat the host's food or the host's tissue, depending on availability. This study and LAVAL's (1972) studies of *L. schizogeneios* show that the 'normal' existence of hyperiid amphipods is essentially opportunistic. MANSUETI (1963) reports similar opportunism of feeding behaviour in fishes associated with scyphomedusae.

Females are more numerous than males in our collections. PIRLOT (1932) suggested that male hyperiids were free-swimming and only the females parasitic. This he inferred from the higher proportion of males in electric light collections. SHOEMAKER (1925), who made several electric light collections in the Gulf of California, did not report on the relative abundance of males and females, but he did collect species belonging to nine genera, all of which are now proved to be associated with gelatinous zooplankton. We have made night dives with electric lights at five stations, collecting free-swimming males and females of *Anchylomera blossevillei* at Sta. 316. The differences in composition of the gelatinous zooplankton seen on night dives suggests that Scuba divers will be able to collect many new amphipods that come near the surface with their migrating hosts.

Table 9. Reports on the associations of hyperiid amphipods and gelatinous zooplankton

Hyperiid amphipods	Host	Author
<b>Lanceolidae</b>		
<i>Lanceola sayana</i> (Lanceolidae) (Lanceolidae)	<i>Pelagia</i> coelenterates coelenterates	Chevreaux, 1900 Woltereck, 1927 Vinogradov, 1957
<b>Vibiliidae</b>		
<i>Vibilia borealis</i>	medusae	Bate & Westwood, 1868
<i>V. jeangerardi</i>	<i>Salpa maxima</i>	Marion, 1874
<i>V. jeangerardi</i>	<i>Salpa maxima</i>	Chevreaux, 1892, 1900
<i>V. robusta</i>	salps	Stephensen, 1918
<i>V. viatrix</i>	salps	Chevreaux & Fage, 1925
<i>V. armata</i> , <i>V. propinqua</i>	salps	Laval, 1963
<i>V. armata</i>	salps	Irie, 1967
<b>Hyperiididae</b>		
<i>Hyperoche kroyeri</i>	medusae	Sars, 1895
<i>H. mediterranea</i>	<i>Beroe forskali</i>	Steuer, 1911
<i>H. medusarum</i>	<i>B. forskali</i> , <i>A. aurita</i> , medusae	Stephensen, 1923
<i>H. medusarum</i>	<i>A. aurita</i> ,	Schellenberg, 1942
<i>H. medusarum</i>	<i>Tima formosa</i> , <i>Cyanea capillata</i>	Bowman <i>et al.</i> , 1963
<i>H. medusarum</i>	<i>Pleurobrachia bachei</i>	Brusca, 1970
<i>H. medusarum</i>	<i>Pleurobrachia pileus</i>	Evans & Sheader, 1972
<i>H. kroyeri</i>	<i>Beroe cucumis</i> , <i>Pleurobrachia pileus</i>	Sheader, 1973
<i>H. medusarum</i> , <i>H. mediterranea</i>	<i>Pleurobrachia bachei</i>	Flores & Brusca, 1975
<i>Hyperia agilis</i>	salps	Dana, 1853
<i>H. galba</i>	medusae	Gould, 1841
<i>H. galba</i>	<i>Rhizostoma cuvieri</i>	Thompson, 1847
<i>H. galba</i>	medusae	Gosse, 1853
<i>H. galba</i>	<i>Rhizostoma cuvieri</i>	Bate, 1862
<i>H. galba</i>	<i>Rhizostoma</i> , other medusae	Bate & Westwood, 1868
<i>H. galba</i>	<i>Aurelia aurita</i>	Romanes, 1877
<i>H. galba</i>	<i>Cyanea capillata</i>	Meinert, 1890
<i>H. galba</i>	<i>Aurelia</i>	Sars, 1895
<i>H. galba</i>	<i>Pelagia perla</i> , <i>Aurelia aurita</i> , <i>Chrysaora isosceles</i>	Tattersall, 1906
<i>H. galba</i>	<i>Tima batrati</i>	Evans & Ashworth, 1909
<i>H. galba</i>	<i>Melicerium</i> , <i>Leukartiara</i>	Tesch, 1911
<i>H. galba</i>	<i>Beroe</i>	Stephensen, 1923
<i>H. galba</i>	<i>Pelagia</i> , <i>Aurelia</i> , <i>Chrysaora</i> , <i>Rhizostoma</i>	Chevreaux & Fage, 1925
<i>H. galba</i>	<i>Rhizostoma</i>	Pirlot, 1932
<i>H. galba</i>	<i>Pelagia</i>	Pirlot, 1939
<i>H. galba</i>	<i>Beroe</i> , <i>Meliceridium octocostatum</i>	Schellenberg, 1942
<i>H. galba</i>	<i>Rhizostoma octopus</i>	Hollowday, 1947
<i>H. galba</i>	<i>Chrysaora hyoscella</i>	Alvarado, 1955
<i>H. galba</i>	<i>Cyanea capillata</i>	Dahl, 1959a, 1959b
<i>H. galba</i>	<i>Aurelia aurita</i> , <i>Cyanea capillata</i>	Bowman <i>et al.</i> , 1963
<i>H. galba</i>	<i>Rhizostoma octopus</i> , <i>Chrysaora hyoscella</i>	Dales, 1966
<i>H. galba</i>	medusae	Agrawal, 1967
<i>H. galba</i>	<i>Aurelia aurita</i>	Metz, 1967
<i>H. galba</i>	<i>Rhizostoma</i>	Russell, 1970
<i>H. galba</i>	<i>Aurelia</i> , <i>Cyanea</i>	Evans & Sheader, 1972
<i>H. galba</i>	<i>Cyanea capillata</i> , <i>C. Lemarki</i> , <i>A. aurita</i>	Sheader, 1973
<i>Hyperia macrocephala</i>	medusae	Dana, 1853
<i>H. macrocephala</i>	<i>Desmonema gaudichaudii</i>	White & Bone, 1972
<i>H. macrocephala</i>	medusae	Bowman, 1973
<i>Hyperia medusarum</i>	medusae	Strom, 1762
<i>H. medusarum</i>	<i>Rhizostoma cuvieri</i>	Thompson, 1847
<i>H. medusarum</i>	<i>Eucharis</i>	Chun, 1880
<i>H. medusarum</i>	<i>Aurelia</i> , <i>Cyanea</i>	Sars, 1895
<i>H. medusarum</i>	<i>Thaumantias</i>	Stephensen, 1923
<i>H. medusarum</i>	<i>Cyanea capillata</i>	Bowman <i>et al.</i> , 1963
<i>H. medusarum</i>	<i>Rhizostoma pulmo</i>	Dales, 1966
<i>Hyperia</i> sp.	<i>Aurelia</i> , <i>Cyanea</i>	Lambert, 1936
<i>Hyperia</i> sp.	medusae	Edward, 1868

Our observations suggest that the electric light induces a frenzied swarming, much as with insects. It may well be that males outnumber females in these collections because they are better swimmers and approach the light more rapidly. It is clear that white light induces behavioural modifications, perhaps causing the amphipods to quit their hosts. While our collections, and the morphology of the two sexes, suggest that males may indeed spend a greater portion of their lives freely swimming, the biology of the males is still connected with gelatinous zooplankton, to the extent that they must locate females on gelatinous hosts in order to reproduce.

Table 9 (Continued)

Hyperiid amphipods	Host	Author
<b>Hyperiidae (Continued)</b>		
<i>Lestrigonus schisogenetos</i>	<i>Lampetia pancerina</i> , <i>Chrysaora hyoscella</i>	Alvarado, 1955
<i>L. schisogenetos</i>	<i>Phialidium</i>	Laval, 1968a
<i>L. schisogenetos</i>	<i>Phialidium</i> , <i>Liriope tetraphylla</i> , <i>Leuckartiara nobilis</i>	Laval, 1972
<i>Bougisia ornata</i>	<i>Phialidium</i>	Laval, 1966
<i>Parathemisto gracilipes</i> (= <i>P. abyssorum</i> ?)	<i>Aurelia</i>	Norman, 1869
<i>Parathemisto compressa</i>	<i>Umbrosa lobata</i>	Tregouboff & Rose, 1957
<i>Parathemisto pacifica</i>	<i>Calycopsis nematophora</i>	Renshaw, 1965
<b>Phronimidae</b>		
<i>Phronima sentinella</i>	<i>Aequorea</i> , <i>Geronies</i>	Risso, 1816
<i>P. sedentaria</i>	<i>Pyrosoma</i> , <i>Beroe</i>	Risso, 1816
<i>P. custos</i>	medusae	Desmarest, 1823
<i>P. sedentaria</i>	<i>Pyrosoma</i> , <i>Beroe</i>	Desmarest, 1823
<i>P. curvipes</i>	<i>Abylopsis</i>	Laval, 1968b
<i>Phronima</i> (females)	<i>Pyrosoma</i>	Pirlot, 1932
<i>Phronima</i> (larvae)	<i>Acanthephyra</i> eggs	Gordon, 1968
<b>Phrosinidae</b>		
<i>Anohylomera macrophthalmia</i>	<i>Pyrosoma elegans</i>	Carus, 1885
<b>Lycaeopsidae</b>		
<i>Lycaeopsis themistoides</i>	<i>Monophyes</i> ( <i>Diphyes</i> )	Stephensen, 1925
<i>L. themistoides</i>	<i>Chelophyes appendiculata</i>	Laval, 1965
<b>Pronoidae</b>		
<i>Paralycaea gracilis</i>	medusae ( <i>Aglantha</i> ?)	Stephensen, 1925
<b>Lycaeidae</b>		
<i>Lycaea ochracea</i>	salps	Dana, 1853
<i>L. pulex</i>	<i>Salpa maxima</i>	Marion, 1874
<i>L. pulex</i>	<i>S. maxima</i> , <i>Pyrosoma</i>	Chevreaux, 1900
<i>L. pulex</i>	<i>S. maxima</i> , <i>Pyrosoma</i>	Chevreaux & Fage, 1925
<i>Pseudolycaea pachypoda</i>	salps, <i>Pyrosoma</i>	Chevreaux, 1900
<i>Pseudolycaea pachypoda</i>	salps, <i>Pyrosoma</i>	Chevreaux & Fage, 1925
<b>Brachyscelidae</b>		
<i>Brachyscelus crusciculum</i>	salps	Stephensen, 1925
<i>Brachyscelus</i> sp.	<i>Bolina</i>	Chun, 1888
<i>Thamneus platyrrhynchus</i>	medusae	Stephensen, 1925
<i>Thamneus</i> ( <i>Daira</i> ) <i>debilis</i>	medusae	Dana, 1853
<i>Thamneus recurvirostris</i>	<i>Pelagia</i>	Chevreaux, 1900
<i>Thamneus platyrrhynchus</i>	<i>Pelagia</i>	Pirlot, 1939
<b>Platyscelidae</b>		
<i>Platyscelus ovoidea</i>	<i>Aequorea</i>	Risso, 1816
<b>Oxycephalidae</b>		
<i>Oxycephalus piscator</i>	<i>Eucharis multicornis</i>	Chun, 1889
<i>Glosscephalus milne-edwardsii</i>	<i>Detoea</i>	Steuer, 1911
<i>Glosscephalus</i> sp.	<i>Bolithopsis vitrea</i>	Swanberg, 1974

One generalization that is immediately apparent from our data is that species within a given genus often are restricted to a particular type of host. For example, *Lestrigonus* and *Hyperia* have been found almost exclusively on medusae, by us and others. *Lestrigonus crucipes* in our collections has been found only with *Pelagia*. *Lycaea* and *Vibilia* are restricted to salps, with highly specific associations (MADIN and HARBISON, 1977). We have collected members of the families Paraphronimidae, Lycaeopsidae, Pronoidae, Platyscelidae and Parascelidae only with siphonophores. *Brachyscelus* appears to have a wide range of hosts, but is usually found on *Aequorea*. Undoubtedly, future collections will improve our knowledge of amphipod systematics and hence of detailed host specificity.

In order to understand the evolution of hyperiid amphipods, one must also understand the evolution of their hosts. PIRLOT (1932) and LAVAL (1965) have discussed this relationship at some length, but their ideas have received little attention. It is equally obvious that in order to

understand the distribution of hyperiid amphipods one must know the distribution of their hosts. One cannot separate the two components of the system, treating one without reference to the other.

It is possible at this point to consider a few morphological aspects of hyperiids which may have specific adaptive functions in relation to their feeding biology or host specificity. Species within the two families (Platyscelidae and Parascelidae) that are capable of rolling up into a ball (conglobation) have been collected only on siphonophores. It is reasonable to suppose that their ability to roll into a tight ball is related to their lives on siphonophores. We have seen that some of these species are stung and eaten by siphonophores when their freedom of movement is restricted in an aquarium (BIGGS and HARBISON, 1976). This is in contrast to members of the Hyperiidae, which seem to be immune to the stings of medusae, and even eat the tentacles. Possibly the Platyscelidae and Parascelidae shield themselves from the nematocysts of their hosts by rolling up; the specialized morphology of the basis of pereopods 5 and 6 produces a tight shield over the amphipod's venter. The conglobate species are commonly found in the nectophores, suggesting that their globular shape might have evolved in response to the architecture of siphonophore colonies, which have numerous small openings into internal cavities. The broad side wings of *Amphithyrus hispinosus* may be a further means of holding on within the nectophores or hydroecium.

Endoparasitic juveniles of the family Hyperiidae feed by sucking liquids from the radial canals of their medusan hosts (WHITE and BONE, 1972). The radial canals of physonect bells and bracts communicate with the gastrovascular cavity of the siphonophore and may provide pre-digested food for developing *Eupronoe* juveniles in a similar manner. Structural damage to the radial canals is never obvious and must be minimal, since the parts of the siphonophore which are parasitized do not atrophy or autotomize. Multiple infestations of juveniles on siphonophores are the rule, and often more than one juvenile is present in the same bell or bract. Most likely these encysted juveniles cannot swim, so the host provides protection from both predation and sinking.

Development of the urosome and pleopods, presumably reflecting swimming ability, is quite variable among hyperiids. The species capable of conglobation have a weakly-developed pleon and urosome and swim poorly. In these species there is little sexual dimorphism, whereas in *Lycaea* the males are long and thin with strong urosomes, and are probably largely free-swimming. Amphipods with a predatory feeding biology, such as *Oxycephalus*, have even greater development of the pleon and urosome and swim very rapidly. The oxycephalids also show extreme development of the rostrum; the length of the rostrum almost exactly parallels the degree of elongation of the uropods and telson in each species, ranging from *Simorhynchotus* to *Rhabdosoma*. This tendency to form a rostrum is present in the Lycaeidae and Pronoidae, where the rostrum is always more pronounced in males than in females. It is tempting to speculate that, since males swim more than females, the rostrum serves for streamlining, to enhance swimming speed, or for manoeuvrability. Clearly, more details of the host specificity and feeding behaviour of hyperiid amphipods will contribute greatly to knowledge of their functional morphology.

We feel that our results have given credence to the speculation that dates back to 1840, when MILNE-EDWARDS stated "les Hyperines...sont pour la plupart plus ou moins parasites: les unes se fixent sur les poissons, d'autres sur les meduses". Others, such as BATE (1861), PIRLOT (1932) and BOWMAN and GRUNER (1973), have reiterated this theme, primarily based on morphological studies, since few cases of association were known in detail. We have now added so many new examples of associations between hyperiids and



gelatinous zooplankton that this mode of behaviour may be accepted as the rule, rather than the exception. In fact, we believe that there are essentially no exceptions. We would be rather surprised if a totally free-living existence were demonstrated for any hyperiid amphipod. Even *Parathemisto gaudichaudii*, thought to be a free-living raptorial species (KANE, 1964; EVANS, 1968; SHEADER and EVANS, 1975) is associated with salps during its juvenile stage (MADIN and HARBISON, 1977). When our collection techniques develop to the point where we can obtain appropriate samples from the deeper reaches of the ocean, we expect to see associations of the remaining genera of hyperiid amphipods with gelatinous zooplankton.

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