

The associations of Amphipoda Hyperiidea with gelatinous zooplankton—I. Associations with Salpidae*

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Abstract—Collection of live planktonic animals by divers has confirmed that hyperiid amphipods in the genera *Vibilia* and *Lycaea* are specific and obligate symbionts of salps. Species in the genera *Brachyscelus*, *Parathemisto*, *Oxycephalus* and *Phronima* are also sometimes associated with salps. *Vibilia* feed preferentially on the particulate food collected by the salp, whilst *Lycaea* consume the salp tissue directly. There are further differences in the distribution and life cycle of the two genera on their hosts. Our collections indicate specific host-parasite relationships exist in at least two species of *Lycaea*.

INTRODUCTION

SYMBIOTIC relationships are common and diverse among benthic marine animals, but few have been reported from planktonic organisms, because conventional net collections do not preserve evidence of these symbioses. It is even difficult to infer associations because different groups of animals are generally examined by different specialists.

Yet symbiotic associations do exist in the plankton, many of them involving hyperiid amphipods. The best known of these relationships are those between *Hyperia* and large medusae (from STRØM, 1762, to WHITE and BONE, 1972). Two genera of hyperiids are frequently and specifically associated with salps, although these relationships are not apparent in net samples. Type specimens of the genera *Vibilia* (MILNE-EDWARDS, 1830) and *Lycaea* (DANA, 1852) were taken from salps. MARION (1874) described *Lycaea pulex* as a parasite of salps and provided a few details of its behavior, as well as further notes on *Vibilia jeangerardii*. However, most of the major expedition reports provide little additional information on associations of hyperiids, since the various groups were worked up separately. More recently, LAVAL (1963, 1965) has described the behavior and early developments of *Vibilia armata* and *V. propinqua* on salp hosts.

In this paper we describe the nature of the relationships between salps and six genera of hyperiid amphipods, *Lycaea*, *Vibilia*, *Brachyscelus*, *Parathemisto*, *Oxycephalus* and *Phronima*. Associations of other hyperiids with cnidarians, ctenophores, colonial radiolarians, pteropods and heteropods are reported by HARBISON, BIGGS and MADIN (1977).

METHODS

The organisms described here were all hand-collected in individual jars by SCUBA divers working in the top 30 m. Collections were made in the Straits of Florida, the Gulf of California, the North Atlantic and the Caribbean. Hyperiid amphipods were collected in

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Table 1. Station list for hyperiid amphipods collected from gelatinous zooplankton. 'Time' is beginning and end of dive at local time.

Station number	Latitude	Longitude	Year	Month	Day	Time
24	25°45'N	79°25'W	71	10	7	
42	"	"	71	11	20	1458-1548
56	"	"	72	2	7	1100-1135
58	"	"	72	2	9	
64	"	"	72	2	22	1446-1526
66	"	"	72	2	24	1430-1505
67	"	"	72	2	25	1400-1435
72	"	"	72	3	8	1515-1555
73	"	"	72	3	22	
76	"	"	72	3	29	1529-1609
77	"	"	72	4	3	1419-1452
78	"	"	72	4	5	1335-1410
79	"	"	72	4	6	0900-0945
80	"	"	72	4	21	1500-1535
81	"	"	72	5	1	1522-1602
83	"	"	72	5	2	0945-1035
84	"	"	72	5	3	
85	"	"	72	5	4	1420-1455
88	"	"	72	5	15	1530-1610
94	"	"	72	5	24	1420-1440
95	"	"	72	5	26	1500-1540
97	"	"	72	6	3	1400-1440
101	"	"	72	7	7	1400-1440
102	"	"	72	7	10	1400-1440
103	"	"	72	7	12	0900-0945
104	"	"	72	7	13	1400-1445
109	"	"	72	7	24	1400-1446
111	"	"	72	7	26	1400-1440
118	"	"	72	8	4	1400-1435
124	"	"	72	8	9	1400-1448
125	"	"	72	8	10	1400-1445
137	"	"	72	8	19	1400-1446
138	"	"	72	8	19	1500-1550
201	42°27'N	30°01'W	72	7	4	1600-1700
206	34°03'N	22°50'W	72	7	9	1358-1505
208	35°00'N	18°58'W	72	7	11	1425-1522
212	38°24'N	11°12'W	72	7	15	1430-1512
216	39°43'N	71°04'W	72	8	14	1330-1415
221	25°50'N	111°18'W	73	7	5	1330-1420
222	"	"	73	7	7	0840-0930
230	"	"	73	7	16	0935-1020
233	"	"	73	7	20	0900-0945
237	"	"	73	7	29	0905-0950
238	"	"	73	7	31	0950-1035
242	"	"	73	8	4	0925-1015
252	41°00'N	66°00'W	73	6	30	1500-1600
259	39°46'N	69°51'W	73	9	14	1545-1630
260	35°19'N	63°43'W	73	9	16	1430-1457
262	33°40'N	62°16'W	73	9	17	1415-1457
265	32°35'N	59°43'W	73	9	20	1000-1058
266	32°20'N	63°06'W	73	9	21	0900-0950
267	32°18'N	63°00'W	73	9	21	1530-1620
268	32°32'N	59°48'W	73	9	23	1000-1055
269	27°25'N	80°00'W	73	10	31	0945-1115
270	27°12'N	80°00'W	73	11	2	1030-1245
273	28°11'N	78°49'W	73	11	14	0928-1030
274	28°07'N	79°46'W	73	11	14	1355-1512
275	27°44'N	79°47'W	73	11	15	0930-1012
276	27°46'N	79°44'W	73	11	15	1330-1445
277	27°25'N	79°52'W	73	11	26	1520-1630
278	27°28'N	79°45'W	73	11	27	1015-1110
279	27°34'N	79°49'W	73	12	6	1249-1352
280	27°40'N	79°43'W	73	12	6	
281	27°34'N	79°49'W	74	1	7	1517-1631
282	27°53'N	79°08'W	74	1	8	1243-1349
285	26°53'N	79°42'W	74	1	10	1043-1143
286	27°25'N	80°13'W	74	5	8	0935-1130
289	27°25'N	80°13'W	74	5	21	
290	"	"	74	6	11	0955-1015
292	27°17'N	79°45'W	74	6	13	1006-1056
293	27°23'N	79°38'W	74	6	13	1410-1448
294	27°34'N	79°55'W	74	6	14	1220-1315
295	26°45'N	79°55'W	74	7	16	1405-1440
297	"	"	74	7	17	1547-1613
298	"	"	74	7	18	1131-1150
299	"	"	74	7	19	1058-1128
300	"	"	74	7	20	1130-1215
301	"	"	74	7	22	
302	"	"	74	7	23	1411-1432
303	13°40'N	62°21'W	74	8	8	1011-1051
304	13°39'N	65°55'W	74	8	9	0956-1016
305	15°13'N	68°05'W	74	8	10	1124-1146
309	21°03'N	67°44'W	74	8	12	1549-1625
310	23°01'N	67°42'W	74	8	13	1045-1122
312	28°31'N	67°38'W	74	8	15	1004-1034
313	29°10'N	67°41'W	74	8	15	1510-1636
314	31°40'N	67°43'W	74	8	16	1106-1145
315	31°41'N	67°43'W	74	8	16	1515-1545
316	31°41'N	67°43'W	74	8	16	2009-2103
317	32°48'N	67°48'W	74	8	17	1034-1103
318	33°54'N	67°48'W	74	8	17	2320-2359
320	36°37'N	68°23'W	74	8	20	1315-1440
321	37°39'N	70°52'W	74	8	21	1400-1443
322	31°08'N	62°10'W	74	9	27	1615-1655

Table 1 continued

Station number	Latitude	Longitude	Year	Month	Day	Time
323	30°39'N	62°17'W	74	9	27	2010-2016
324	26°30'N	62°18'W	74	9	28	2038-2131
325	25°29'N	62°21'W	74	9	29	1044-1123
326	25°16'N	62°20'W	74	10	1	1553-1629
328	25°16'N	62°25'W	74	10	2	1507-1538
330	28°31'N	62°30'W	74	10	3	1555-1638
331	29°57'N	63°45'W	74	10	4	1645-1655
332	30°32'N	64°11'W	74	10	7	1516-1539
333	18°59'N	63°32'W	75	1	30	1430-1505
335	18°58'N	58°41'W	75	2	1	0957-1024
336	19°01'N	56°16'W	75	2	2	1016-1033
337	19°00'N	55°50'W	75	2	2	1450-1516
338	18°59'N	53°47'W	75	2	3	1340-1407
339	18°58'N	52°28'W	75	2	4	1310-1350
340	18°56'N	52°09'W	75	2	4	1625-1733
341	19°02'N	50°01'W	75	2	5	1013-1046
342	19°22'N	50°00'W	75	2	5	1515-1555
346	16°53'N	54°53'W	75	2	7	1515-1554
348	16°12'N	56°15'W	75	2	8	1439-1512
349	15°17'N	58°50'W	75	2	9	1040-1105
350	15°17'N	58°50'W	75	2	9	1425-1507
351	15°22'N	58°56'W	75	2	9	1945-2025
352	14°44'N	60°01'W	75	2	10	1005-1045
353	14°44'N	60°01'W	75	2	10	1415-1452
354	12°09'N	61°21'W	75	2	11	1400-1433
355	34°16'N	10°47'W	75	5	24	1503-1533
356	32°41'N	13°53'W	75	5	25	0934-1003
357	30°34'N	17°57'W	75	5	26	0921-0955
358	30°20'N	18°30'W	75	5	26	1445-1515
363	29°28'N	30°13'W	75	5	29	0900-0921
364	29°28'N	30°13'W	75	5	29	0957-1030
365	29°25'N	30°36'W	75	5	29	1443-1513
366	29°28'N	34°20'W	75	5	30	0910-0940
367	28°31'N	34°53'W	75	5	30	0910-0940
368	29°30'N	38°26'W	75	5	31	0900-0940
369	29°33'N	39°00'W	75	5	31	1542-1612
370	29°29'N	42°03'W	75	6	1	0910-0940
371	29°31'N	42°47'W	75	6	1	1515-1547
372	29°30'N	46°22'W	75	6	2	0915-0945
373	29°31'N	46°50'W	75	6	2	1415-1450
374	29°28'N	51°25'W	75	6	3	1530-1605
375	29°30'N	54°30'W	75	6	4	0932-1002
377	29°30'N	58°37'W	75	7	5	0845-0917
380	30°38'N	61°49'W	75	6	6	0850-0930
381	31°01'N	62°29'W	75	6	6	1540-1610

association with salps on 89 out of 381 dives made between August 1971 and June 1975. Each dive is considered a station, and all stations where hyperiid amphipods were collected are listed in Table 1. The accompanying Fig. 1 shows the approximate location of stations in the Atlantic. This table and figure comprise all of the locations cited here and by HARBISON, BIGGS and MADIN (1977). Salps were collected during these dives for a variety of purposes; amphipods from almost all salps were routinely preserved. Thus salps with and without amphipods were collected, but the diving collections are not quantitative and do not provide numerical information on absolute density of animals, relative abundance of salp species or overall infestation rates of amphipods.

Living amphipods were visible through the transparent body walls of the hosts; observations and photographs of amphipods and hosts were made both underwater and in shipboard aquaria. All amphipod specimens were preserved with sodium borate buffered formalin (10%) for later counting, identification and measurement.

Identification of the amphipods was based largely on available taxonomic works. The confusion in the family Lycacidae, particularly with the *Lycae pulex* species group, has been discussed in two publications (HARBISON, 1976; HARBISON and MADIN, 1976), based on the same material considered here. There remain several uncertain forms in the genus *Lycaea*, and one in *Vibilia*, as noted below.

RESULTS

We have collected at least 18 species of hyperiid amphipods in six genera from salps. The distribution of these by sex and in relation to their host species is given in Tables 2, 3 and 4.

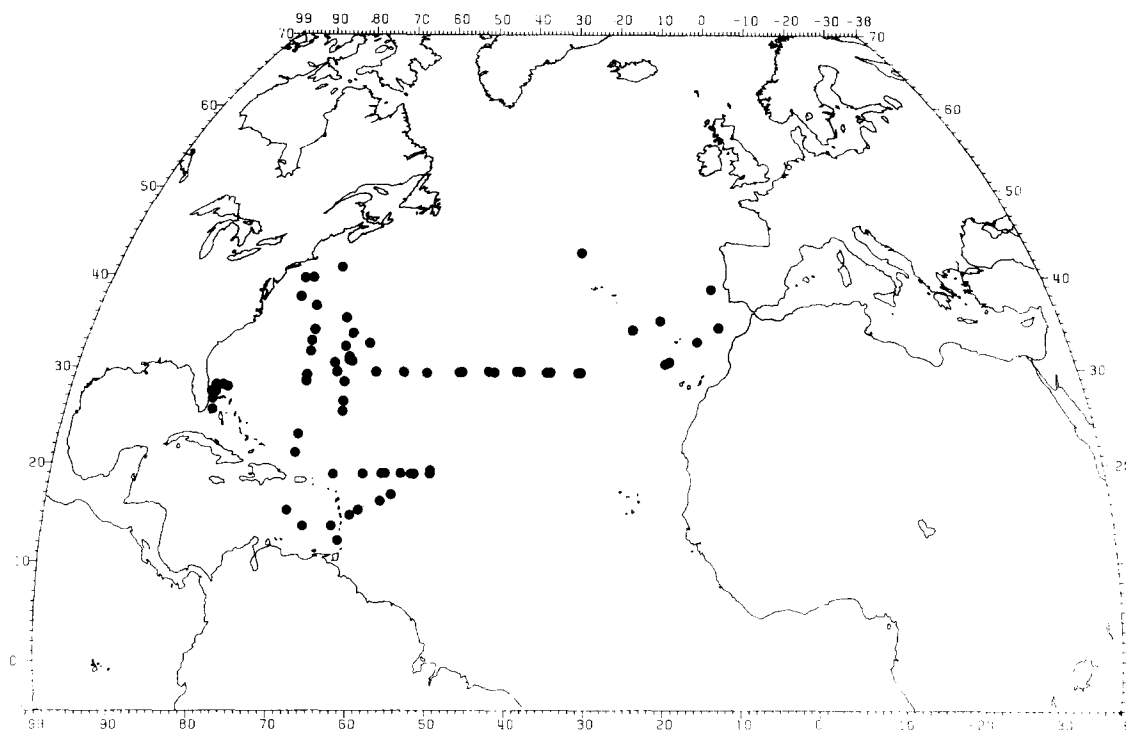


Fig. 1. Approximate locations where hyperiid amphipods were collected with gelatinous zooplankton. Stations so close together as to overlap are not included.

The tables also indicate the number of instances of association (I.A.) for each salp–amphipod species combination. An instance of association is defined as a single occurrence of an individual salp or chain of aggregated salps with one or more individuals of a single amphipod species. For example, a chain of five *Pegea confederata* which has on it two *Lycaea pulex* and one *Vibilia viatrix* represents two instances of association, one for each amphipod species. This index, while not strictly quantitative, indicates the relative abundance in our collection of different salp–amphipod combinations. Similarly, the I.A.s give some idea of which species of salp were commonest in the areas where we collected—usually these included *Pegea confederata*, *Salpa cylindrica*, *S. maxima*, *Cyclosalpa affinis* and *C. polae*. Amphipod infestation did not appear to be disproportionate on abundant or rare species of salps.

NOTES ON THE GENERA AND SPECIES

Genus *Vibilia* MILNE-EDWARDS, 1830

EIGHT SPECIES OF *Vibilia* were collected from salps (Table 2). We have identified seven of our eight species using the keys of BOVALLIUS (1887), BEHNING (1913) and HURLEY (1955). The eighth form, here called *Vibilia* sp. A, does not appear to fall into an established category. Juveniles are especially difficult, and rather than make guesses about their identity, we have combined them into a single category of unidentified juveniles in Table 2.

Table 2. Numbers of *Vibilia* associated with salps. Number of instances of association indicated in column I.A

Salp species	I.A.	<u>V. viatrix</u>		<u>V. propinqua</u>		<u>V. sp. A</u>	<u>V. pyripes</u>		<u>V. jeangerardi</u>		<u>V. stebbingi</u>	<u>V. chuni</u>	<u>V. kroyeri</u>	Unidentified juveniles
		M	F	M	F	F	M	F	M	F	F	F	F	
<u>Cyclosalpa affinis</u>	1			1										1
<u>Cyclosalpa polae</u>	2										1	1		
<u>Iasis zonaria</u>	2						3	1						7
<u>Pegea socia</u>	5		9			12								60
<u>Pegea bicaudata</u>	2													65
<u>Pegea confederata</u>	27	3	26	2	2	1								70
<u>Salpa cylindrica</u>	23	3	19		1	15								62
<u>Salpa fusiformis</u>	1										1			
<u>Salpa maxima</u>	10		4		3				1	3	1	1	1	7
Totals	73	6	58	2	7	28	3	1	1	3	3	2	1	272

Table 3. Numbers of *Lycaea* associated with salps. Numbers of instances of association indicated in column I.A

Salp species	IA	<u>L. pulex</u>			<u>L. vincentii</u>			<u>L. nasuta</u>			<u>L. sp. A</u>			<u>L. "bovallioides"</u>		
		M	F	J	M	F	J	M	F	J	M	F	J	M	F	J
<u>Cyclosalpa affinis</u>	25	4	9	1				52	60	37						
<u>Cyclosalpa bakeri</u>	1	1	1													
<u>Cyclosalpa pinnata</u>	7	37	52											1	2	
<u>Cyclosalpa polae</u>	12	11	9	10							1	1				
<u>Helicosalpa komaii</u>	1		1	4												
<u>Ihlea punctata</u>	1		1													
<u>Pegea socia</u>	2	11	26	1										1		
<u>Pegea bicaudata</u>	1	8	52	3												
<u>Pegea confederata</u>	8	4	2		1	1								1		
<u>Salpa cylindrica</u>	32	7	3	3	42	47					1			1	4	
<u>Salpa maxima</u>	13	14	55	14							1			1		
<u>Traustedtia multitentaculata</u>	1	1														
Totals	104	98	211	36	43	48		52	60	37	2	2		3	6	2

Table 4. Numbers of *Brachyscelus*, *Parathemisto* and *Oxycephalus* collected with salps. Numbers of instances of association indicated in column I.A.

Salp species	I.A.	<u>Brachyscelus</u> <u>crusculum</u>		<u>Parathemisto</u> <u>gaudichaudii</u>	<u>Oxycephalus</u> <u>clausi</u>	
		F	J	J	M	F
<u>Cyclosalpa</u> <u>affinis</u>	2	5	2			
<u>Iasis</u> <u>zonaria</u>	2	1		1		
<u>Pegea</u> <u>socia</u>	2	1				1
<u>Pegea</u> <u>bicaudata</u>	1			70		
<u>Salpa</u> <u>cylindrica</u>	2				3	1
<u>Salpa</u> <u>maxima</u>	2	5	1			
<u>Thalia</u> <u>democratica</u>	1	1				
Totals		12	3	71	3	2

Vibilia viatrix BOVALLIUS, 1887: 6 ♂, 5.0 to 8.0 mm; 58 ♀, 4.7 to 11.7 mm. This is the most widely distributed species of *Vibilia* (STEPHENSEN, 1925) and was the most commonly found species of salps. Probably most of the unidentified juveniles are *V. viatrix*.

Adults are a reddish-brown colour when alive, closely matching the colour of the gut nucleus of the *Pegea* spp. on which they were often found. The youngest juveniles are specialized larval forms, transparent and dorso-ventrally flattened.

Stations: 24, 58, 64, 67, 80, 84, 95, 103, 104, 201, 265, 266, 270, 274, 278, 279, 281, 285, 330, 333, 338, 339, 342, 346, 348, 349, 355, 363, 368, 380.

Vibilia propinqua STEBBING, 1888: 2 ♂, 5.5, 5.8 mm, 7 ♀, 4.2 to 8.6 mm. Specimens assigned to this species agree overall with STEBBING's (1888) description. The character used to distinguish *V. propinqua* in the keys (BEHNING, 1913; HURLEY, 1955) is the presence of minute teeth on the distal edges of the urosomites. This feature has not been illustrated by any of the authors who use it, and we have found it very difficult to evaluate. Colouration of the live animals is similar to *V. viatrix*.

Stations: 58, 76, 77, 97, 326, 328, 339.

Vibilia sp. A: 28 ♀, 3.5 to 10.8 mm. These specimens are generally similar to *V. viatrix* and *V. propinqua* but differ in the shape of the first antenna, the length of the dactyls and the length of the carpal process on pereopod 2.

Stations: 281, 300, 304, 320, 322, 330, 340, 356, 380.

Vibilia stebbingi BEHNING and WOLTERECK, 1912: 5 ♀, 3.7 to 8.0 mm.

Stations: 381, 324, 366, 380.

Vibilia chuni BEHNING and WOLTERECK, 1912: 2 ♀, 5.2, 6.3 mm. The larger one had ova in the marsupium.

Station: 316.

Vibilia pyripes BOVALLIUS, 1887: 3 ♂, 6.8, 8.4, 9.3 mm; 1 ♀, 6.7 mm.

Station: 212.

Vibilia jeangerardii LUCAS, 1845: 1 ♂, 11.7 mm; 3 ♀, 8.6, 8.8, 9.7 mm; 4 juv., 2.6 to 4.2 mm. Station: 355.

Vibilia kroyeri BOVALLIUS, 1887: 1 ♀, 15.3 mm. This female had larvae in the marsupium. Station: 355.

Behaviour of Vibilia

The feeding mechanism of salps consists of a continuously-moving mucous filter net. This net removes particulate material from the water passing through the cylindrical body of the salp. It is moved posteriorly by the force of the water passing through it, and rolled into a food strand by ciliary tracts along the gill bar. This strand enters the oesophagus (MADIN, 1974).

Species of *Vibilia* feed principally on the food-strand of the salp (Figs. 2 and 3). The amphipods cling with pereopods 3 to 6 to the gill bar or the funnel-shaped opening of the oesophagus. Their mouthparts are positioned close to the moving mucous strand, and the first two pereopods are used to divert part of the food-strand to the mouth. The remainder continues into the salp's oesophagus. This movement of particulate material into the amphipods can be seen by adding carmine suspension to the aquarium. The carmine is filtered out by the mucous net and incorporated into the food strand. The guts and faecal pellets of feeding amphipods are stained red in 10 to 20 min.

The first larval stages of *Vibilia* are deposited on salps by an adult female; according to LAVAL (1963) the larvae at first feed parasitically on the salp's tissues. By the time they have attained general adult morphology and an overall length of 1 to 1.5 mm they position themselves on the gill bar and feed on the food stand. A dozen may be lined up on a single salp (Fig. 2). Adults of *Vibilia* usually occur only one to a salp, (Fig. 3) and are nearly always positioned at the oesophagus with their head down in the opening.

Confinement of the salps in jars disrupts their continuous feeding and soon affects the behaviour of the amphipods, which leave the positions described above and move about the interior of the salp. They occasionally grasp at parts of the mucous net before it is rolled into a strand, and may also eat parts of the salp itself. Species of *Vibilia* rarely leave their hosts in the aquarium.

Genus *Lycaea* DANA, 1852

We have collected 3 distinct species of *Lycaea*, and several others which do not appear to fit any published description. Identifications were based on original descriptions and the keys of BARNARD (1930) and HARBISON and MADIN (1976). The occurrence of species of *Lycaea* on their hosts is listed in Table 3.

Lycaea pulex MARION, 1874: 98 ♂, 2.7 to 13.3 mm; 211 ♀, 2.9 to 10.8 mm; 36 juv., 1.5 to 3.3 mm. This species was the most abundant and the most broadly distributed, both geographically and among different host species (Table 3). Morphological characters which distinguish *L. pulex* from the similar *L. vincentii*, are given in HARBISON (1976).

Live *L. pulex* adults ranged from pinkish, through off white with dotted or reticulate brown pigmentation to an overall brown colour. This variation may reflect different degrees of chromatophore expansion. Sex was usually indeterminate in specimens smaller than 3.0 mm. Sexual maturity, indicated in males by hairs on the first antenna and in females by the presence of ova or a well-developed marsupium (HARBISON, 1976), was attained in the range of 7 to 9 mm. However, in several large collections of *L. pulex* from the vicinity of the Azores (Stas. 201, 208), the size at maturity was from 11.0 to 13.0 mm for males and 8.0 to 10.0 mm for females.

Stations: 42, 56, 66, 67, 73, 76, 77, 78, 79, 83, 94, 95, 97, 101, 102, 109, 118, 138, 201, 208, 221, 222, 237, 265, 274, 280, 281, 285, 286, 299, 315, 316, 320, 335, 338, 341, 355, 356, 357, 363, 369, 371, 380.

Lycaea vincentii STEBBING, 1888: 43 ♂, 2.7 to 9.5 mm; 48 ♀, 2.7 to 8.0 mm. *L. vincentii* is very similar to *L. pulex* and has been considered a synonym of that species (SHOEMAKER, 1945). HARBISON (1976) has shown that it is a separate species, distinguished from *L. pulex* by the relative length of the rami of uropod 1, presence of teeth on the propod of peraeopod 5 and the shape of the male first antenna. These characters are most distinct in mature amphipods; separation of immature *L. vincentii* from immature *L. pulex* is considerably less certain.

The amphipods have the same range of colouration as *L. pulex*. Some mature males have strikingly blue eyes. Mature males were 7.6 mm or larger, mature females 6.0 mm or larger.

Stations: 101, 102, 125, 137, 262, 266, 275, 279, 280, 281, 285, 294, 298, 300, 302, 304, 314, 320.

Lycaea nasuta CLAUS, 1887: 52 ♂, 2.6 to 8.3 mm; 60 ♀, 2.4 to 8.8 mm; 37 juv., 0.9 to 2.2 mm. This species is readily distinguished from all others in the genus by its characteristic urosome and second peraeopods (HARBISON and MADIN, 1976). All of the specimens in our collections have been associated with *Cyclosalpa affinis*.

Colouration of the live amphipods is similar to that described for *L. pulex*. Females commonly have red pigment spots, especially along the sides of the pleon and on the appendages. The larger males had prominent nose-like projections on the head, as described by CLAUS (1887), but none in our collection had hairs on the first antenna and so were probably not fully mature. Some 7.0-mm females had ova in the marsupium; other larger individuals were collected along with numerous juveniles in the same salp.

Stations: 56, 76, 81, 83, 88, 111, 262, 278, 279, 280, 281, 285, 310, 326, 336, 341.

Uncertain species

We have collected a few specimens of *Lycaea* which we cannot yet assign to species. As they constitute only 13 of 610 *Lycaea* reported here, they are considered only briefly.

Lycaea sp. A: 2 ♂, 9.2, 9.5 mm; 2 ♀, 3.4, 6.8 mm. These amphipods resemble *Lycaea bovallii* CHEVREUX, 1900, but they have dactyls almost as short as those of *L. nasuta*. These specimens may be the same as the female which BARNARD (1930) incorrectly identified as *L. nasuta* (see HARBISON and MADIN, 1976). Clarification of the position of these amphipods must await additional material.

Stations: 316, 322, 371.

Lycaea spp.: 3 ♂, 5.9, 6.9, 7.3 mm; 6 ♀, 4.7 to 6.6 mm. These specimens are similar in detail, but appear to fall into five groups. They all resemble *L. bovalliioides* STEPHENSEN, 1925, in having long dactyls, articulation of the outer ramus of uropod 2 and no teeth on the anterior margin of the propodus of peraeopod 5. Unfortunately, Stephensen's description of *L. bovalliioides* figures only the urosome, stating that the species is otherwise identical to *L. bovallii*. The differences among our specimens are more in their overall appearance than in detailed morphology, and final determination of these long-dactylled forms will require more material and a re-examination of the type specimens of *L. bovallii* and *L. bovalliioides*.

Stations: 95, 286, 300, 323, 330, 358, 374, 381.

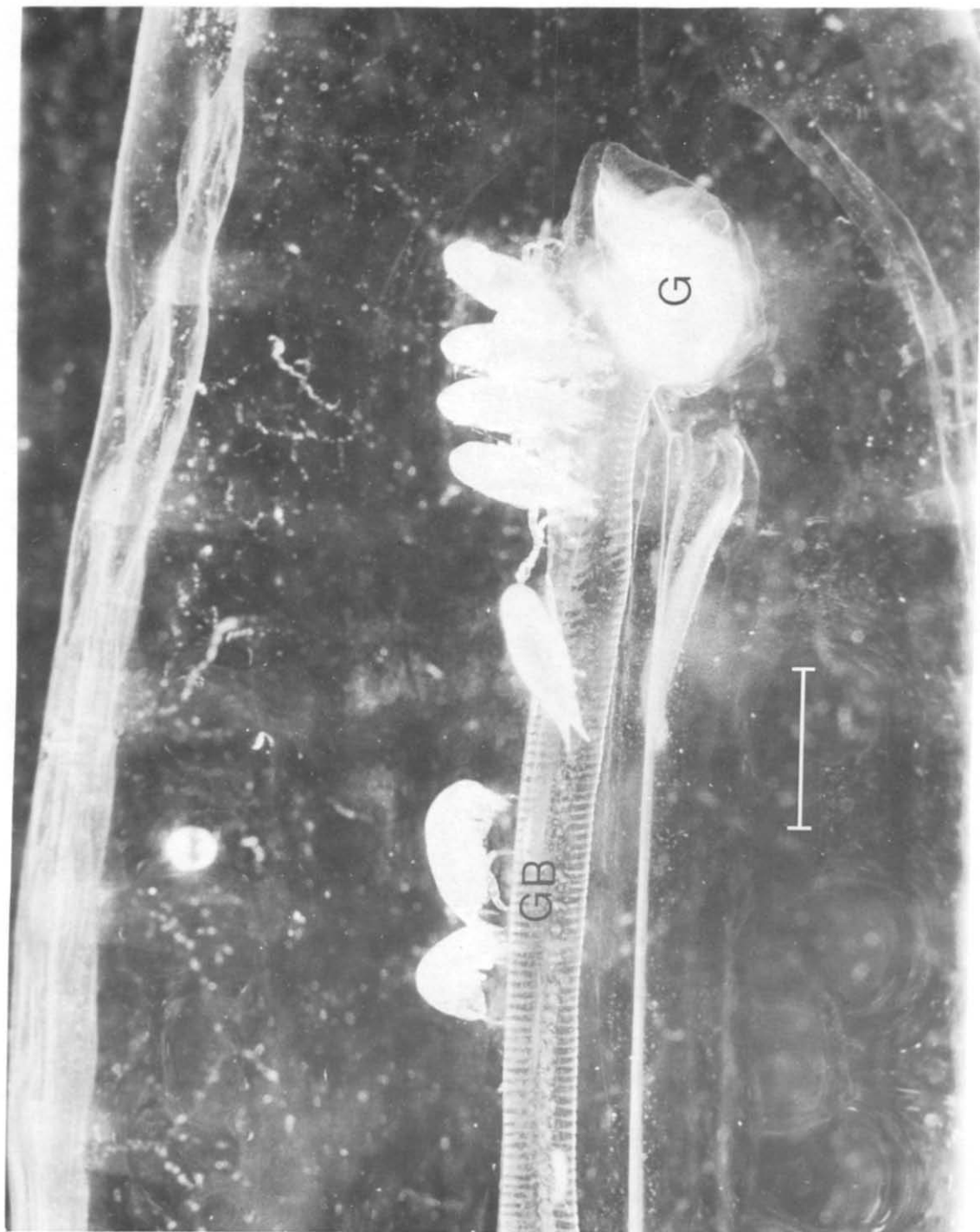


Fig. 2 *Vibilia* sp. juveniles clinging to the gill bar of a *Salpa cylindrica* solitary while feeding on the food strand of the salp (Sta. 67). G = gut. GB = gill bar. Scale line = 2 mm.

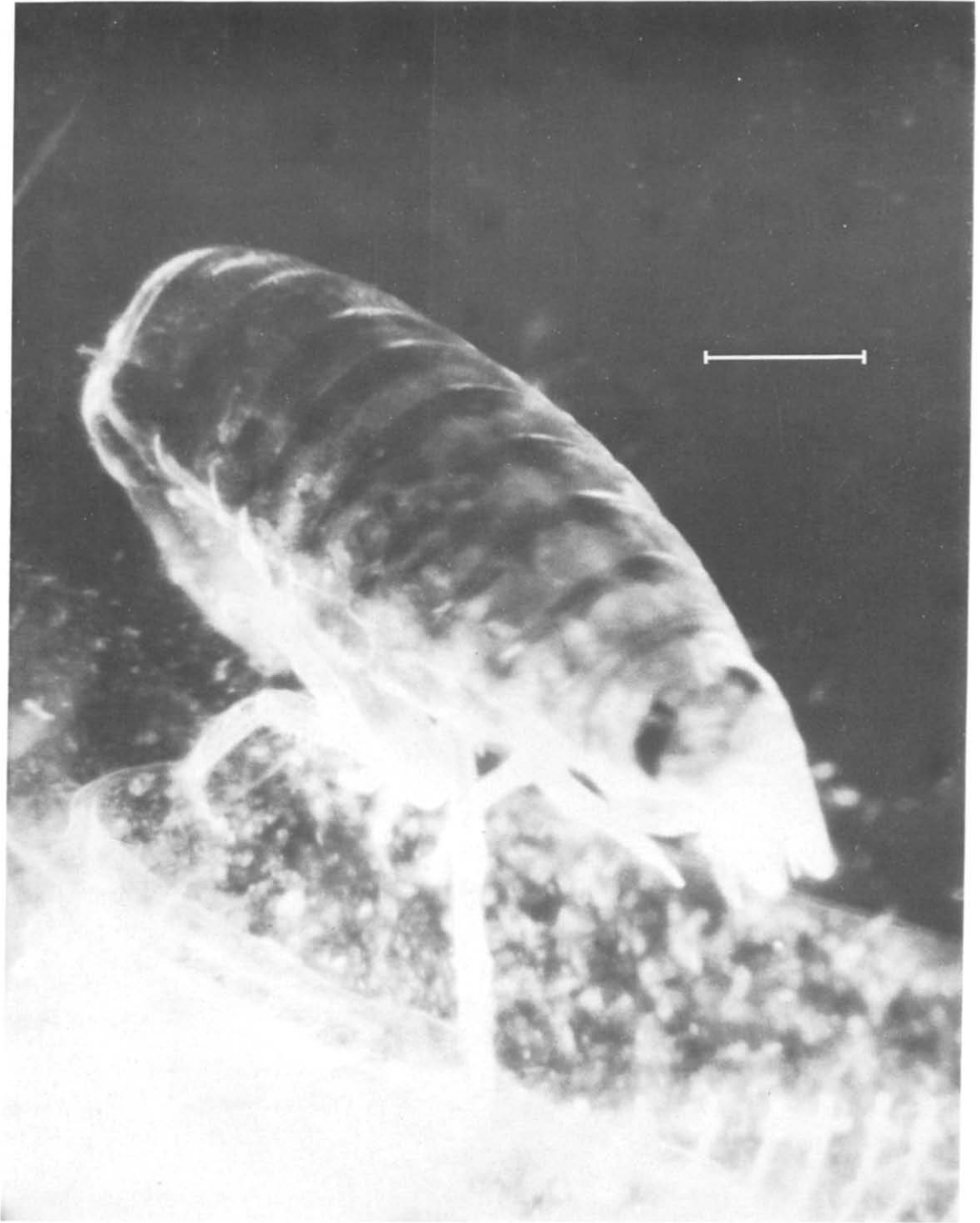


Fig. 3. Adult *Vibilia stebbingi* on the gill bar of *Pegea confederata* (aggregate generation). Figures 3 and 4 are from later stations than are recorded in this paper. Scale line = 1 mm.



Fig. 4. Juvenile *Lycaea pulex* eating the gill bar of a *Salpa maxima* aggregate. Scale line = 1 mm.

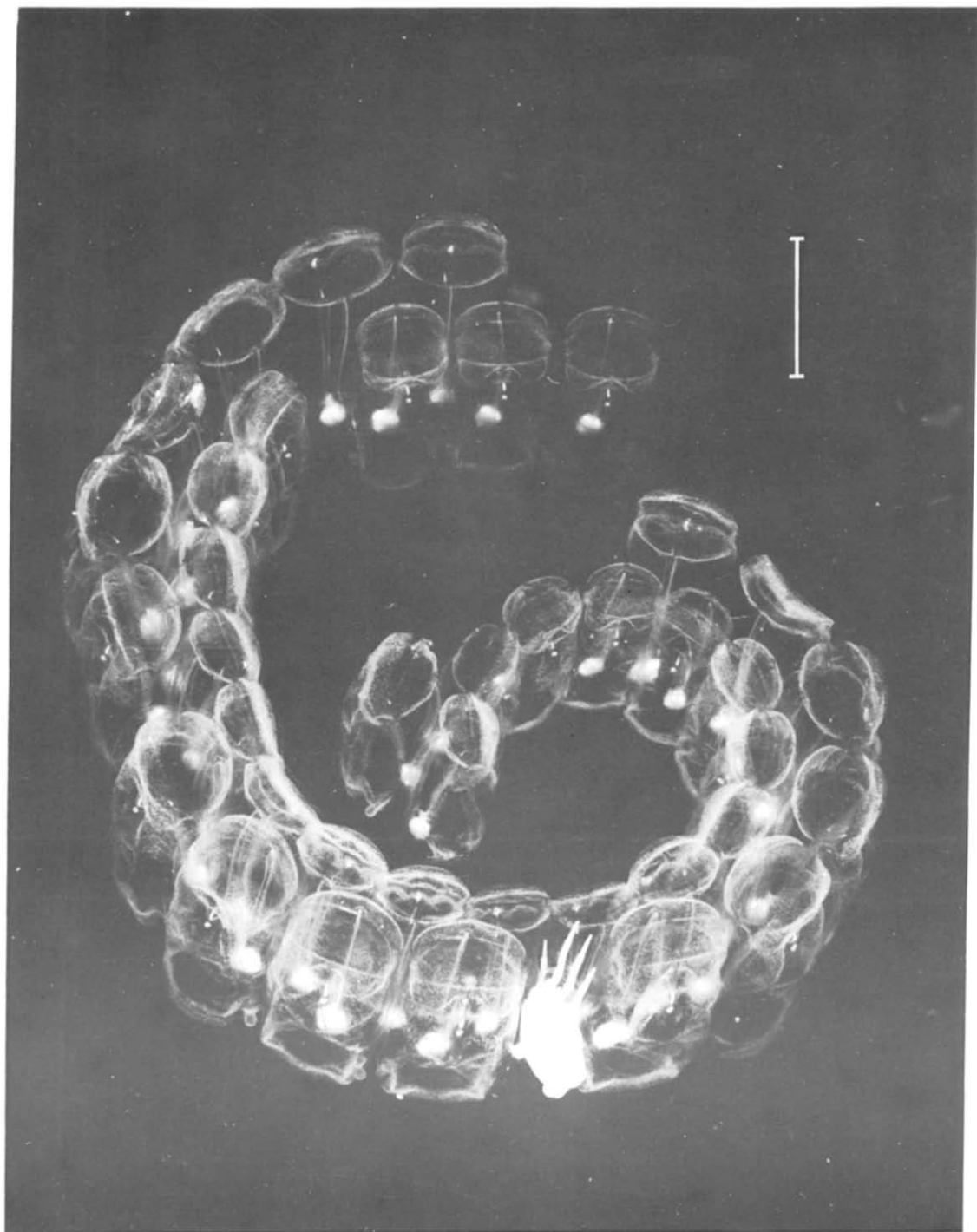


Fig. 5. *Planes minutus* on a chain of *Pegea socia* (Sta. 364). Scale line = 10 mm.

Behaviour of Lycaea

Members of the genus *Lycaea* feed on the tissues of their hosts. Feeding is more intermittent and variable than among the species of *Vibilia*. We have seen *Lycaea* grazing on the cilia rows of the gill bars, leaving bare patches (Fig. 4). They also chew at the interior body wall and consume developing embryos. On one occasion an amphipod grasped the mucous food strand, but we do not believe that this feeding mode is of much importance.

The *Lycaea* species are much more mobile around their hosts than members of *Vibilia*, moving from inside to outside, among salps in a chain and sometimes between unconnected salps. Some of this activity is probably due to confinement in the aquarium, but we have also seen them swim away from salps underwater. Once, several amphipods were seen to abandon a large salp that was caught in the tentacles of a medusa.

Genus *Brachyscelus* BATE, 1861

This genus is in a state of considerable taxonomic confusion. At least 17 species have been described, but without comparative and meristic characters. Many workers (SHOEMAKER, 1945; HURLEY, 1955; DICK, 1970) have ignored this plethora of nominal species, ascribing specimens to one of the few species that have been adequately described. We have been forced to continue this procedure for our few specimens, but hope that a revision of the genus will be undertaken soon. Identifications are based on the keys in DICK (1970) and original descriptions.

Brachyscelus cruscolum BATE, 1861: 13 ♀, 2.7 to 7.0 mm; 3 juv., 1.5, 2.4, 3.1 mm. Only a few of these amphipods were collected from salps; species in this genus were more frequently associated with medusae (HARBISON, BIGGS and MADIN, 1977). Six females were ovigerous. Occurrence is listed in Table 4.

Stations: 222, 286, 316, 321, 380, 381.

Genus *Parathemisto* BOECK, 1870

Specimens in this genus were identified using the key of SHEADER and EVANS (1974).

Parathemisto gaudichaudii (GUERIN-MENEVILLE, 1825): 71 juv., 1.8 to 4.6 mm. On a few occasions we have collected large numbers of juvenile *P. gaudichaudii* from *Pegea bicaudata* (Table 4). These amphipods closely resemble the 'short-legged' form of *P. gracilipes* described by STEPHENSEN (1925), but recently synonymized with *P. gaudichaudii* (SHEADER and EVANS, 1974). Our specimens are of the 'compressa' form (SHEADER and EVANS, 1974); they show no serrations on the inner side of the peduncle or inner ramus of the third uropod. All are less than 5 mm in overall length, corresponding to stages 4 to 8 as described by KANE (1963). No secondary sexual characteristics can be distinguished; the amphipods all appear to be juveniles recently released from the marsupia.

The *Parathemisto* were all situated on the outside of the salps. They held on with peracopods 5, 6 and 7, facing away from the salps, as described by SHEADER and EVANS (1975) for *P. gaudichaudii* on hydromedusae. None of the *Parathemisto* appeared to be eating the salp, and several of them swam away when salps were collected, suggesting their relationship with the salp is more tenuous than that of *Vibilia* or *Lycaea*.

While we have not often collected *P. gaudichaudii* from salps, they can be present in large numbers on individual hosts. Recent collections of *P. gaudichaudii* from *Pegea* spp. and *Salpa* spp. included more than 1200 juvenile amphipods on a chain of 13 salps. While these data have not yet been analyzed in detail and are not included in Table 4, the large numbers of

amphipods involved strongly suggest that the association with salps is a normal part of the life history of *P. gaudichaudii*.

Stations: 201, 212.

Genus *Oxycephalus* MILNE-EDWARDS, 1830

Members of this genus were identified using the key of PILLAI (1966).

Oxycephalus clausi BOVALLIUS, 1887: 3 ♂, 17.3, 20.5, 21.2 mm; 2 ♀, 24, 28.8 mm. These large amphipods were collected while clinging to or actively eating salps (Table 4). *Oxycephalus clausi* seems to be a generalized predator on gelatinous zooplankton (HARBISON, BIGGS and MADIN, 1977).

Stations: 67, 346, 369.

Genus *Phronima* LATREILLE, 1802

We have collected only two phronimids on salps. However, others found free-swimming were inside barrels which appeared to have been made from salp tests (HARBISON, BIGGS and MADIN, 1977). Although *Phronima* is a voracious predator on small salps (LAVAL, 1968), the two specimens listed here were not eating their hosts. Identifications were based on the key in SHIH (1969).

Phronima sedentaria (FORSKAL, 1775): 1 ♀, 19.5 mm. This ovigerous female was holding onto a chain of *Salpa maxima* aggregates.

Station: 369.

Phronima colleti BOVALLIUS, 1887: 1 ♀, 13.8 mm. This specimen was holding onto a *Salpa cylindrica* solitary.

Station: 330.

MISCELLANEOUS ASSOCIATIONS

We have collected several Sargassum crabs (*Planes minutus*) from chains of *Pegea socia* (Sta. 364) (Fig. 5) and portunid megalopa larvae from *Pegea confederata* aggregates in the Gulf of California (Sta. 224). The latter salps also harboured six unidentified fish 10 to 30 mm long. A few juveniles of *Caranx* sp. and other fishes have been found inside *Pegea* spp., *Salpa maxima*, and *Cyclosalpa pinnata* in several localities (Stas. 137, 355, 369, 380). The colour of the small jacks closely matched the colour of the *Pegea* gut nucleus.

FREQUENCY DISTRIBUTION, HOST SPECIFICITY AND CO-OCCURRENCE

The frequency of occurrence of different numbers of *Vibilia* spp. and *Lycaea* spp. per salp is given in Table 5. The Table summarizes instances from all stations in which the number of amphipods per salp was recorded, including observations made *in situ*. When only one

Table 5. Frequency of occurrence of different numbers of amphipods on salps. The table gives the number of instances of association and below it, the percentage of total instances

Amphipod	Number of individual amphipods per salp									
	1	2	3	4	5	6	7	8	9	10+
<i>Vibilia</i>	130 67%	42 22%	12 6%	3 1.5%	3 1.5%	1 0.5%	0 -	0 -	0 -	3 1.5%
<i>Lycaea</i>	72 47%	16 10.5%	44 29%	1 0.6%	5 3.2%	4 2.6%	1 0.6%	2 1.3%	6 3.9%	2 1.3%

amphipod was found on a chain or whorl of aggregate salps, the occurrence was recorded as one amphipod per salp. Both solitary and aggregate generation salps are included.

It can be seen that adult *Vibilia* spp. are most often present singly or in pairs (89% of all instances). Although a dozen or more juvenile *Vibilia* spp. were sometimes present in a single salp, these occurrences were not routinely recorded and so are not included in Table 5.

The distribution for *Lycaea* differs from that for *Vibilia*; greater numbers of amphipods per salp were common. *Lycaea* juveniles were rarely found without adults in the same salp, and presumably are not left on salps in the same way that *Vibilia* juveniles are.

Although most parasitized salps harbored only a few amphipods, we sometimes encountered heavy infestations. Chains of *Pegea* spp. for example, often had one or two *Vibilia* in each salp. One chain of *P. confederata* in the Florida Current held 80 adult *V. viatrix* in 71 salps; a chain of 256 *P. bicaudata* in the Azores held 56 *Vibilia* juveniles, 73 *Lycaea pulex*, and 59 *Parathemisto gaudichaudii*. A chain of 57 *Pegea socia* from the mid North Atlantic contained 77 *Vibilia viatrix* and *V. sp. A*, and 38 *Lycaea pulex*. Two whorls of 4 and 11 *Cyclosalpa pinnata* from the Azores harbored 28 and 35 *L. pulex*, respectively; three whorls of 6, 4 and 4 *C. affinis* from the Florida Current contained 49, 24 and 20 *L. nasuta*.

We can provide no estimates of overall infestation rates because quantitative samples of salp populations were not taken. Our subjective impression is that infestation is quite variable; during dives at some stations all the salps were parasitized, at other times few or none were. Generalizations about the infestation patterns require information on the distribution, abundance, and population dynamics of both salps and amphipods which we do not yet have.

Certain instances of host specificity are apparent from our observations. It can be seen from Table 2 that *Vibilia* spp. (mainly juvenile) occurred almost entirely on *Pegea socia*, *P. bicaudata*, *P. confederata*, and *Salpa cylindrica*. We do not yet have enough *Vibilia* of different species to analyse host specificity below the generic level. Among the species of *Lycaea*, there are two clear causes of specific associations. It is obvious from Table 3 that *Lycaea nasuta* is exclusively associated with *Cyclosalpa affinis*, and *L. vincentii* nearly exclusively with *Salpa cylindrica*. *L. pulex* is distributed among several hosts, but our data indicate a preponderance of associations with *Salpa maxima*, *Cyclosalpa pinnata*, and *C. polae*.

Until recently (HARBISON, 1976), *L. vincentii* was considered a synonym of *L. pulex*. This taxonomic error would certainly have obscured the host affinities of both species. We expect that future collections of the rarer forms will further clarify both systematics and host specificities.

There are 38 cases of associations in our collection in which a salp harboured several species of symbionts. In seven instances two or more species of *Lycaea* were present in the same salp, and in two cases there were two or more species of *Vibilia*. Species of *Lycaea* and *Vibilia* were found in the same salp in 17 instances. The copepod *Sapphirina* occurred together with *Lycaea* or *Vibilia* in 18 instances; other symbionts (*Parathemisto*, *Brachyscelus*, fishes) were found with *Lycaea* or *Vibilia* in three cases.

DISCUSSION

The two genera of hyperiid amphipods principally associated with salps, *Vibilia* and *Lycaea*, display distinctly different behavioural adaptations to their hosts, in their feeding biology and in their distribution on salps. However, we have seen no marked differences in behaviour among species within genera.

The early development of *Vibilia armata* and *V. propinqua* has been studied by LAVAL

(1963, 1965) who described two specialized larval stages. According to Laval, ovigerous females cling to a salp with peraeopods 3 to 6 during a 20-day period of incubation. When the first-stage embryos ('pantochelis' larva) hatch, the female deposits each on the surface of the salp with specialized 7th peraeopods. A few hours later the pantochelis larva moults to a 'protopleon' larva which persists through three stages, by the last of which rudimentary pleopods and uropods appear. In the next molt (4th) the larvae metamorphose to the adult morphology.

LAVAL noted (1963) that the larvae feed parasitically on the hosts. After deposition, they crawl around and into the interior of the salps, where they eat tissues in the vicinity of the branchial bar and the nucleus. Laval gave no evidence that these larvae fed on food collected by the salp; however, he did not state whether the salp was collecting food. Juvenile *Vibilia* spp. that we have seen feeding on the food strand are at least 1.0 mm long and have general adult morphology. While species of *Vibilia* may feed on the tissues of the salp through the first two larval stages, they feed preferentially on the food strand as postlarvae. This feeding behaviour is maintained through the adult stage, although intervals of tissue consumption may occur when food-collection by the salp is interrupted.

If the amphipods grow to maturity within a single host, they obviously must not kill it during that period, and salps infested with *Vibilia* spp. indeed showed no significant morphological damage. However, even if not causing acute physical damage or deprivation of food to the host, the amphipods most likely have long-term effects on growth, longevity or reproduction of salps.

LAVAL reported (1963) that there was usually a single *Vibilia armata* larva per salp. He inferred that adult females, after depositing a larva, moved to another salp. In contrast, we have frequently encountered ten or more identical juveniles in a single salp, presumably all deposited by the same female at the same time. However, we rarely found more than one or two adults per salp, and these were generally positioned with their heads down in the oesophagus rather than along the branchial bar. While the food collected by a single salp might support ten juveniles, it probably could not support more than one or two adults, especially if they competed for the oesophagus position. Although we have seldom seen specimens of *Vibilia* leave their salps, some of the juveniles must find other hosts as they grow older, perhaps moving to an adjacent salp in a chain or onto a developing embryo or stolon. The males may not stay with salps at all after a certain stage. We have found only 12 males out of 115 specimens of *Vibilia* that could be sexed. LAVAL (1974) contended that only the females of *V. armata* are associated with salps, and that the males are free-swimming predators.

Both juveniles and adults of *Lycaea* eat the tissues of their hosts, often producing visible damage (Fig. 4). The capacity of hosts to withstand this attack may vary from species to species and presumably depends on the size of the salp, the size and number of the amphipod parasites and whether or not they happen to feed on vital organs of the host. Small amphipods probably could not kill a salp immediately, but might shorten its life in other ways. For example, the grazing of cilia off the gill bar would interfere with food collection, chewing through blood vessels or nerves would cause general deterioration, and consumption of embryos or stolon would reduce or prevent reproduction. Apparently the salps' sole defence against these amphipods is their rapid rate of growth and reproduction. While we have no evidence for regenerative capacity, salps do show some toleration to physical damage. We have collected salps with gaping holes in the body wall or with guts completely bitten away, yet which were still swimming. Some large salps appeared healthy despite the

presence of 10 or 20 amphipods; others with heavy infestations had considerable damage and appeared moribund.

Over twice as many *L. pulex* females as males were found on salps, whereas approximately equal numbers of male and female *L. nasuta* and *L. vincentii* were collected. In all species there were very few fully adult males, but mature females with offspring were common. It seems likely that adult females and immature amphipods of both sexes spend their lives on salps, while adult males spend much of their time free-swimming. The greater development of the pleon and the elongate, streamlined shape of adult males of *L. pulex* and *L. vincentii* (HARBISON, 1976) support this hypothesis.

The occurrence of large numbers of *L. nasuta* juveniles in whorls of *Cyclosalpa affinis* (Table 3) suggests that these salps serve as brood chambers for the amphipods, and that ovigerous females remain in a salp at least long enough to release their young. Whorls of *Cyclosalpa* aggregates appear particularly well suited as sources of food and shelter for females and their young. Unlike linear chains of salps, the whorls contain maximum internal volume and surface area in minimum external dimensions. Thus developing amphipods have large resources of space and food within a compact volume.

The first stage after hatching of *L. pulex* (one-podomere stage) superficially resembles a protopleon larva (LAVAI, 1965), but probably does not leave the marsupium (HARBISON, 1976). By the four-podomere stage, the amphipod has essentially adult morphology. While we have no *in situ* observations of dispersal, possible mechanisms include deposition of young on salps by females, movement of amphipods into developing embryos or aggregate chains before their release from the parent salp, the breaking up of aggregate salp whorls or chains bearing amphipods, and free-swimming from one host to another.

Salps are probably only an occasional host for *Brachyscelus*, which is most often associated with hydromedusae (HARBISON, BIGGS and MADIN, 1977). To *Oxycephalus* they may be only one of many prey species, and to *Phronima* a source of food and barrels. *Parathemisto gaudichaudii* is thought to be a free-living species (SHEADER and EVANS, 1975), but juveniles do associate with salps. This relationship may be parasitic or simply phoretic, providing a substrate for young amphipods insufficiently developed to lead independent pelagic lives.

Salps would appear to be ideal hosts for hyperiid amphipods; they provide a large protected living space, ample food in the form of collected particulate material or their own tissue, opportunities for dispersal of amphipods with their chains or embryos, and seem to have no defensive mechanisms against parasites. The large numbers of *Lycaea* sometimes found on salps suggest that the hosts provide virtually unlimited resources to these parasites.

Vibilia and *Lycaea* almost certainly stem from different phyletic lines (PIRLOT, 1932) and have converged in their choice of a host. The differences in feeding behavior between the two genera may reduce competition for food when species of *Vibilia* and *Lycaea* share a host, unless the *Lycaea* kill the host, depriving the *Vibilia* of its food supply. Specificity for certain host species would further reduce competitive interactions, and there is clearly some specificity in the specimens discussed here. *Lycaea vincentii* and *L. nasuta* probably have the same feeding behaviour but no overlap in host species. *Lycaea pulex*, while widely distributed among salps, is rare in the hosts of *L. nasuta* and *L. vincentii*. The mechanisms for the specificity between particular species of salps and amphipods remain to be investigated. The large compound eyes in *Lycaea* tempt one to suppose that they might select their hosts visually; species of *Vibilia* lack large eyes but have remarkably developed first antennae, suggesting chemo- or rheo-reception for host location.

We conclude that the biology of juvenile and female amphipods in the genera *Lycaea* and *Vibilia* is an obligate symbiotic relationship with various species of salps. We have recovered only two *Lycaea pulex* from other hosts (HARBISON, BIGGS and MADIN, 1976) and expect that most specimens present in net tows were in fact associated with salps when collected (see also LAVAL, 1974). While adult males of both genera may be largely free-swimming, their biology also involves salps both as a food source during their development and as the abode of females of their species. The specific associations of species of *Vibilia* and *Lycaea* with salps mean that the distribution and population dynamics of these amphipods are dependent on the biology of their hosts. Conversely, as commensals and parasites on nearly all species of salps, amphipods may influence the growth and reproductive rate of their hosts. The extent of this interaction remains to be quantified. Recent studies of the feeding biology of salps (MADIN, 1974; HARBISON and GILMER, 1976) indicate that they may be much more important in oceanic and slope-water ecosystems than previously appreciated. Accordingly, an understanding of the role of their symbionts may take on commensurate importance.

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