

# Symbiotic associations between crustaceans and gelatinous zooplankton in deep and surface waters off California

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**Abstract** Using a remotely operated submersible (ROV) in the sea off Monterey, California, we collected deep-living zooplankton and observed their associations with crustacean symbionts. Little is known about the nature of these symbioses. Among the most interesting findings was the description of a previously unknown modality of symbiosis of the deep-living copepod *Pseudolubbockia dilatata* Sars. It was recorded within the subumbrellar cavity of three specimens of the bathypelagic hydromedusa *Aegina citrea* Eschscholtz at depths of 606–1,098 m. One of these medusae hosted a mating pair of adult copepods along with the remains of their molts corresponding to copepodid stages CV of the female and CII, CIII, CIV, and CV of the male; another medusa had an adult female, and molts of a female CV and of male CIII, CIV and CV copepodids. Our data indicate that the medusae were occupied first by an early male copepodid, and then the female joined as a CV. The presence of an adult female alone with its CV molt in a third medusa suggests that females invade the host regardless of the presence of the male in it. The medusa represents a protected environment for these copepods during vulnerable stages or processes

(molting and mating). We also observed 13 new associations between hyperiid amphipods and gelatinous zooplankton at different depths. These involve four new records among members of the Infraorder Physosomata, for which only six other associations were known, and five species of amphipods and six hosts among the gelatinous zooplankton not previously recorded as symbionts. Data are provided on three families of Hyperiidea for which symbiotic associations were hitherto unknown. The ROV represents a valuable tool for the observation and sampling of these associations, whose existence has been known for a long time, but which are still poorly understood.

## Introduction

The Monterey Canyon, located in the Eastern Pacific off the coast of central California, is about 160 km long, with water depths reaching more than 2,700 m. This system has been investigated recently using a remotely operated vehicle (ROV) that allows in situ observations and sampling of the deep-sea fauna. Recent surveys of the deep-living gelatinous zooplankton of this area have yielded new, interesting information on the biology and ecology of different groups of gelatinous zooplankton (i.e., siphonophores, medusae, ctenophores, salps) (Robison 2004).

Among the most recently explored topics from deep ROVs is the biology of the symbiotic associations between the planktonic jellies and crustaceans (mainly hyperiid amphipods) (Gasca and Haddock 2004). Most of the available data about these relationships refer mainly to epipelagic species (Madin and Harbison 1977; Laval 1980). Deep-water collections have recently

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yielded new, stimulating data on the nature of these symbioses (Gasca and Haddock 2004).

Copepods are known to be associated with all the major groups of marine vertebrates and invertebrates. Their associations with cnidarians are among the best studied, although most of these copepods are symbiotic on benthic forms (i.e., Alcyonacea, Actiniaria, and Gorgonacea, among others) (Humes 1985). There are only a few isolated records of copepods associated with epipelagic scyphomedusae, and all of these refer to strictly associated, non-planktonic forms (Boxshall and Halsey 2004); before now, no records of planktonic copepods symbiotic on hydromedusae are known.

In this contribution we report and analyze the unique presence of a deep-living planktonic copepod as a symbiont of a deep sea hydromedusa. We also report new associations of deep-living and epipelagic gelatinous zooplankton with hyperiid amphipods, from in and around the Monterey Canyon, CA.

## Materials and methods

The planktonic fauna of Monterey Bay and Monterey Canyon off central California were surveyed during two oceanographic cruises carried out aboard the R/V Western Flyer in 21–28 May 2004 and 5–11 April 2005, and the R/V Point Lobos in 12–16 December 2005 and 9–12 January 2006, both ships of the Monterey Bay Aquarium Research Institute (MBARI).

We used blue-water SCUBA diving (Haddock and Heine 2005) to survey the upper 20 m and a remotely operated submersible (ROV) to sample the zooplankton fauna between 200 and 3,000 m. An additional record is from a cruise of the R/V Ventana carried out in May 2003 in the same area. Specimens of gelatinous zooplankton (medusae, siphonophores, ctenophores, salps) were captured together with their associated crustacean fauna and brought on board the ship, where both the host and crustacean guest species were examined. After an initial manipulation and observation *in vivo*, all specimens were fixed in 4% formaldehyde and preserved in a solution of propylene glycol 4.5%, propylene phenoxetol (0.5%), and sea water (95%) for further taxonomic examination. Adult copepods and several copepodid exuviae were extracted from the subumbrellar cavity of three medusan specimens harboring copepods; specimens were then transferred to 70% ethanol for taxonomical examination. Voucher specimens of both copepods and hyperiids were deposited in the collection of zooplankton at El Colegio de la Frontera Sur, Unidad Chetumal, in Chetumal, Quintana Roo, Mexico (ECO-CH-Z).

## Results and discussion

### Copepoda

Order: Cyclopoida

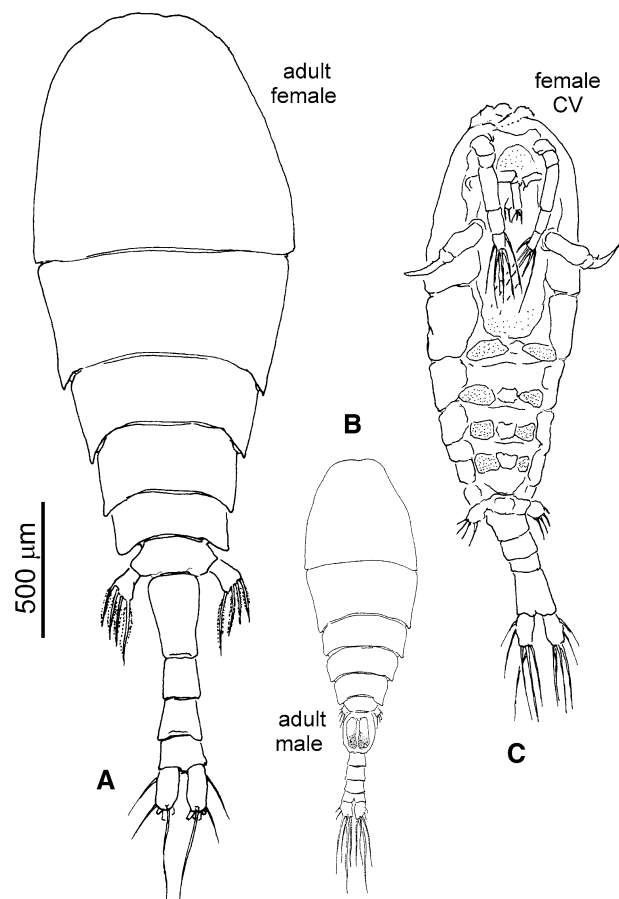
Family: Lubbockiidae Huys and Böttger-Schnack, 1997

*Pseudolubbockia dilatata* Sars, 1909

(Figs. 1, 2)

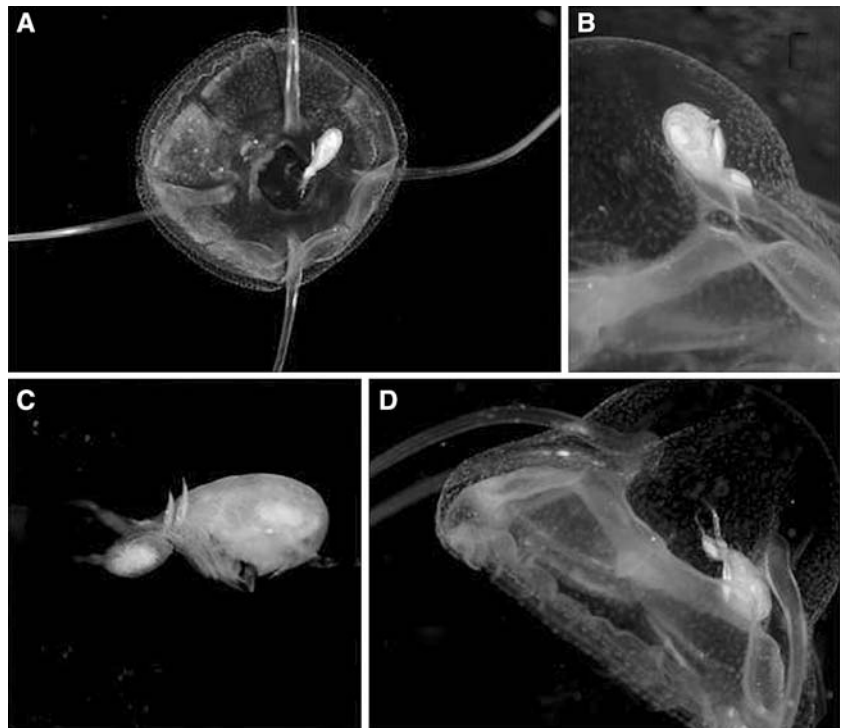
### Material examined

Three adult females, undissected, ethanol-preserved, vials deposited in ECO-CH-Z-02769. Specimens collected 28 May 2004, ROV dive 682 at 1,098 m deep (36°41.75'N, 122°5.02'W); 15 December 2005, ROV dive 553 at 791 m deep; 11 January 2006, ROV dive 559 at 606 m deep, respectively. Each of three specimens in subumbrellar cavity of three individuals of the hydromedusa *Aegina citrea* Eschscholtz, 1929. One

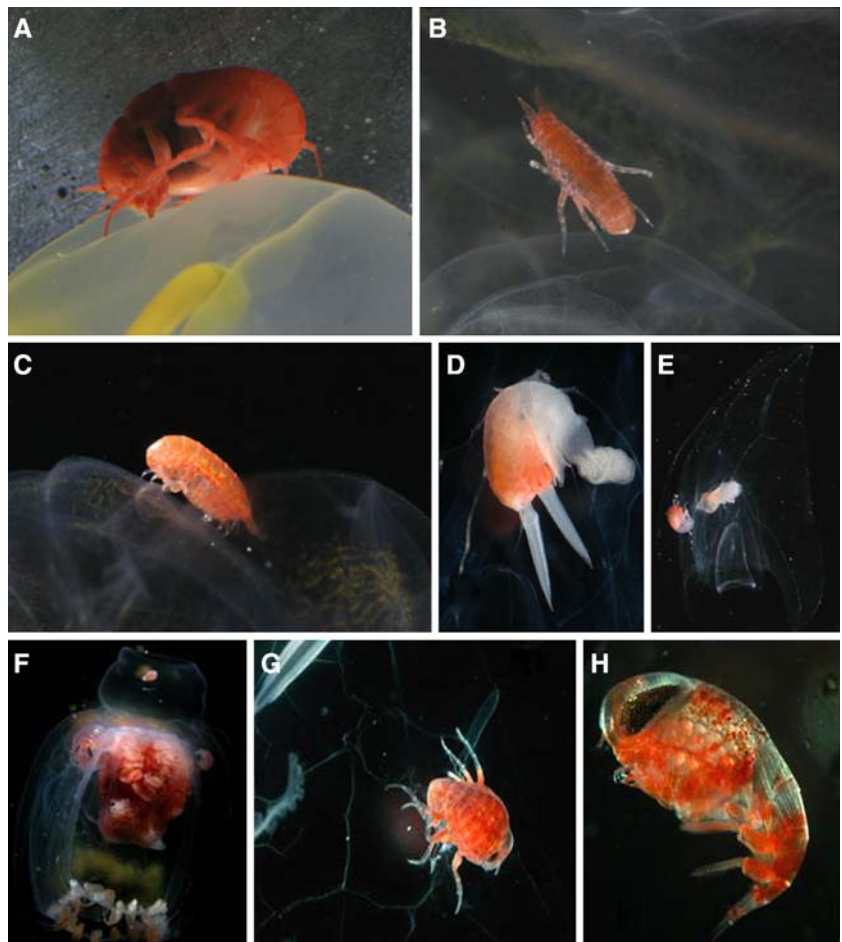


**Fig. 1** *Pseudolubbockia dilatata* Sars, 1909 from Monterey Bay, California. **a** Adult female, habitus, dorsal view; **b** Adult male, habitus, dorsal view; **c** CV (fifth copepodid stage) of female. Figure shows overall comparative sizes between male and female of this species

**Fig. 2** *Pseudolubbockia dilatata* Sars, 1909 in the medusa *Aegina citrea* from Monterey Bay, California. **a** aboral view of medusa with copepods; **b** view of the medusa showing position of copepods near base of tentacles; **c** lateral view of *P. dilatata* showing large female with male clinging to ventral surface of urosome; **d** view of position of mating copepods from different angle



**Fig. 3** Gelatinous zooplankters hosting hyperiid amphipods in waters off California, as observed during this survey. **a** *Aegina citrea* with *Lanceola pacifica*; **b** *Salpa aspera* with *Vibilia propinqua*; **c** *Pegea socia* with *Vibilia viatrix*; **d** *Nectadamas diomedea* with *Mimonectes sphaericus*; **e** *Nectadamas diomedea* with *Proscina stephensi*; **f** *Leuckartiara zaca* with *Hyperia medusarum*; **g** *Mitrocoma cellularia* with *Hyperoche medusarum*; **h** *Tryphana malmi*, found in *Mitrocoma cellularia* and *Solmissus incisa*. Amphipods size ranges 5–8 mm (**b, c, e–h**) and 10–15 mm (**a, d**)



adult male, specimen undissected (ECO-CH-Z-02769), plus male CII, CIII, CIV, and CV exuvia, undissected, semi-permanent slides (ECO-CH-Z-02880) found in medusa collected at 1,098 m; male CIII, CIV, CV exuviae found in medusa collected at 791 m. Three female CV (copepodid stage V) exuvia, partially dissected, semi-permanent slides, each on one of the three medusae examined (ECO-CH-Z-02879).

#### Host

The host is the meso- to bathypelagic hydromedusa *A. citrea*; this species, a member of the narcomedusan family Aeginidae, has a cosmopolitan distribution and has been recorded commonly in the Eastern Pacific and the Californian region (Wrobel and Mills 1998). Early observations (Mayer 1910) and subsequent data (Kramp 1965; Thurston 1977) define this species as a deep-living form (700–3,000 m) although it can be recorded occasionally in the epipelagic layer as a result of extensive vertical migrations.

#### Remarks

The cyclopoid family Lubbockiidae (see, Boxshall and Halsey 2004), which contains planktonic oceanic forms, was created recently by Huys and Böttger-Schnack (1997) to recognize differences between these forms and the Oncaidae, in which they were previously included. Currently, seven genera of this family are known (Boxshall and Halsey 2004); *Pseudolubbockia* is a monotypic genus described by Sars (1909) from specimens caught in the Eastern Atlantic. The copepod species found as a symbiont of *A. citrea* in Monterey Bay was identified as *Pseudolubbockia dilatata* Sars, 1909. The morphology of this species was studied by Heron and Damkaer (1969) and Heron and Bradford-Grieve (1995).

The morphology of our adult male and female specimens is identical in most respects to the profusely illustrated description by Heron and Damkaer (1969) from material collected in deep waters (600–1,275 m) of the Gulf of Alaska. The size of the Alaskan specimens (female 2.30–3.02 mm; male 1.35–1.40 mm) is similar to that recorded in the Californian individuals (female 2.93–3 mm, caudal rami included; male 1.26 mm); the adult male recorded here is smaller than any published size record of this species.

#### Development

Aside from the fact that this copepod is a deep-living oceanic form (Heron and Damkaer 1969; Razouls

1996), little is known about its biology and development (Gardner and Szabo 1982). Heron and Damkaer (1969) reported the occurrence of this species in 18 samples in the Gulf of Alaska (79 specimens), but they did not find copepodids, which were hitherto unknown. The exuvia of *P. dilatata* found in the Californian medusae were in good condition, thus allowing a general morphological examination. These molts correspond to three female CVs (Fig. 1) and a series of CII–CV of the male. The stage to which each exuvium belonged was determined following the criteria of Izawa (1991) for the development of cyclopoid copepods and complemented by data provided by Heron and Damkaer (1978) on the copepodid stages of the related genus *Lubbockia*. The sexes of the molts were established based on their relative size, as the adult female is nearly 2.5 times larger than the adult male (Fig. 1a, b). Therefore, the largest exuvia (CV's measuring 1.83–1.91 mm, caudal rami included) were assigned to the female (Fig. 1c) and the remaining, smaller ones (CII 0.69 mm; CIII 0.76 mm; CIV 0.91 mm; CV 1.3 mm) were regarded as males.

The progression of the copepodid stages observed is clearly marked by the increase of one urosomite at each succeeding stage between CI and CIV. This is the usual pattern known in other cyclopoid copepods (Izawa 1991). Also, it was noted that maturation of the male of *P. dilatata* includes the formation of the genital complex during the last molt, adding one urosomite between the CV and the CVI (adult). This pattern agrees with that found in the genus *Lubbockia* (Heron and Damkaer 1978). This is the first information on the development of this deep-living species.

#### Distribution

*Pseudolubbockia dilatata* has been known to be distributed in the Eastern Tropical Atlantic (Azores), the Sargasso Sea, off Gibraltar, and the Gulf of Alaska (Razouls 1996). The finding of this bathypelagic copepod species in the area of California is a significant latitudinal range extension of this species into the Eastern Pacific.

#### Biology and behavior

The existing information on the biology of the family Lubbockiidae suggests that they are loosely associated with other zooplanktonic forms (Heron and Damkaer 1969, 1978, Huys and Böttger-Schnack 1997). The invasion of the hydromedusa *A. citrea* by the copepod *P. dilatata* implies interesting topics that are discussed herein.

### Relation of copepods with host

There was no evidence that the copepods fed upon the host medusae during development, no damage was observed on the host surface tissues; most probably, they act as commensals. Direct observation would be required in order to determine the source of food during the symbiosis. This association, however, implies some kind of initial contact, probably related to a loose relationship involving a phoretic behavior as that observed in the Oncaeidae, a group of copepods closely related to the Lubbockiidae. Oncaeids attach themselves to the outer surface of gelatinous zooplankton (mainly appendicularians and salps) for transport or to feed upon them, but only as adults, not as copepodids (Go et al. 1998). The grasping structure of the maxilliped in lubbockiids, similar to that found in oncaeids, suggests this kind of behavior. In a completely dark environment, detection of the medusan host by the copepod might even be related to a distinct bioluminescent pattern emitted by the host, and luminescence is present in *Aegina citrea* (Haddock, personal observation). It is not known if this symbiosis is species specific, but the available data suggest that the copepod is linked to this medusan species, which in turn can host at least another crustacean species (see, Table 2).

### Detection and invasion of the host in the water column

Invasion of the host by males and females of this copepod appears to be the result of separate events. The males probably invade the medusae as an early copepodid and the female joins the male or occupies the medusa later on as a pre-adult (CV) copepodid.

Male copepods are commonly attracted to the female by the pheromones (Lonsdale et al. 1997); some of our data suggest a reverse pattern as it is presumed that early males invaded the medusa before the females. Attraction of females by male exudates is rare (Lonsdale et al. 1997; Van Duren and Videler 1996). However, the finding of one medusa harboring only a female, without evidence of males, weakens this pheromone-related hypothesis. Hence, bioluminescence of the medusa could be advanced as a potential factor allowing host recognition by these copepods, either males or females.

### Mating

Our data suggest that both the male and the female CVs of *P. dilatata* molted into the adult stage within

one of the host medusae, in which these adult copepods were found during mating (Fig. 2). The position of the male attached ventrally to the fourth legs of the female is the usual copulatory position in many cyclopoid copepods (Boxshall 1990). The fact that this position was established between adult male and female indicates true copulation but does not exclude a precopulatory mate guarding behavior, in which the juvenile female is clasped by the adult male (Boxshall 1990).

### Copepod symbiosis in the plankton

Other copepods have been recorded as symbionts of medusae, scyphomedusae only, and most of them members of the cyclopoid family Macrochironidae. This group is well known for its associations with benthic cnidarians (Boxshall and Halsey 2004) with only a few species known from medusae (Reddiah 1968, 1969). Large numbers (>1,000) of the harpacticoid *Nitocra medusaea* Humes were found as ectosymbionts of a scyphomedusa (Table 1). There are, however, striking differences between these associations and the one recorded here. The Lubbockiidae is a group in which all species are planktonic, oceanic, free-living forms (Boxshall and Halsey 2004); hence, this kind of association would not be expected in this group of copepods. Also, there is no evidence that the macrochironids found associated with medusae use them as reproductive sites, which is clearly what the evidence presented herein shows for *P. dilatata*. It is probable that this association evolved from a loose commensal behavior, present in other related planktonic forms (i.e., Oncaeidae), to a much closer symbiosis in which the copepod obtains a safe place to develop, find a partner, and mate in a challenging environment. All other records of *P. dilatata* refer to free-living adult specimens; it is probable that this commensal relationship is not isolated to the Californian population and it is expected that focused samplings will reveal a wider occurrence of this behavior. Finally, this peculiar association of a deep-living planktonic copepod using a hydromedusa as a molting and mating site represents an unprecedented type of symbiosis in the deep sea.

### Amphipoda

Hyperiid amphipods are frequently found as symbionts of gelatinous zooplankton and have a wide vertical distribution in the oceans (Vinogradov et al. 1996; Vinogradov 1999). Information about 16 associations obtained during this survey is presented in Table 2. Overall, we report 13 new associations; these include also the first data available on the symbiotic relations

**Table 1** Records of associated copepods of the orders Harpacticoida and Cyclopoida found in medusae with data on the nature of the association and hosts

Species	Reference	Host	Geographic location	Habitat	Symbiosis
Order Harpacticoida					
Family Ameiridae					
<i>Nitocra medusaea</i>	Humes (1953)	<i>Aurelia</i> sp. (S)	New Hampshire	Nearshore	Ectoparasitic
Order Cyclopoida					
Family Macrochironidae					
<i>Paramacrochiron ennorensis</i>	Reddiah (1968)	Unidentified medusa	India	Bay	Commensal
<i>P. sewelli</i>	Reddiah (1968)	<i>Lychnorhyza malayensis</i> (S)	India	Nearshore	Commensal
<i>P. rhizostomae</i>	Reddiah (1968)	<i>Rhizostoma</i> sp. (S)	India	Nearshore	Commensal
<i>Pseudomacrochiron stocki</i>	Reddiah (1969)	<i>Dactylometra quinquecirrha</i> (S)	India	Nearshore	Commensal
<i>Sewelochiron fidens</i>	Humes (1969)	<i>Cassiopea xamachana</i> (S)	Puerto Rico	Shallow bottom	Commensal
Family Lubbockiidae					
<i>Pseudolubbockia dilatata</i>	This survey	<i>Aegina citrea</i> (H)	California	Deep-water	Reproduction site, refuge

H Hydromedusa, S Scyphomedusa

within the hyperiid families Mimonectidae, Prosciniidae, and Anapronoidae, belonging to the Infraorder Physosomata. New information is provided about five amphipod species and six species of gelatinous zooplankton not previously recorded as symbionts. Two of the symbioses presented involve undescribed species of a siphonophore and a medusa (Table 2). The table includes also data on the egg number and size of some species of hyperiid amphipods; this information is useful to infer the reproductive strategies in this environment.

Shih and Cheng (1995) state that reports on the associations of amphipods of the infraorder Physosomata are scarce when compared with those of the Infraorder Physocephalata; it was unknown if this difference was related to distinct life habits or to collection methods. Our results, adding four records of associations of physosomatous amphipods to the six previously known, suggests that ROVs are effective in surveying aspects of the life history and biology of this group of hyperiids that otherwise, would remain unveiled because these forms are distributed mainly in deep water, below 1,000 m. Symbiosis among the Physosomata could be more common than previously thought.

An overall account of the known associations between hyperiid amphipods and gelatinous zooplankton was published by Laval (1980); more than two decades after this work, the advances in this topic have been relatively scarce and focused on specific geographic areas. The only previous survey in the

Californian region is that by Gasca and Haddock (2004); they provided data of 14 symbiotic associations recorded in deep and shallow waters of the Gulf of California.

Members of the amphipod families Hyperiididae and Lestrigonidae have a wide variety of hosts among the gelatinous zooplankters (Laval 1980; Buecher et al. 2001); our results support this finding. They also confirm the preference of some families (i.e., Vibiliidae) or genus (i.e., *Paralycaea*) to associate with a single group of gelatinous zooplankton, salps and siphonophores, respectively (Harbison et al. 1977).

## Conclusion

Novel and interesting associations among deep-sea zooplankton are readily discovered using technologically advanced methods. Both blue-water diving and the ROV represent valuable tools to provide in situ information about these associations. These were only guessed as net plankton samples have been proved as a source of artificial data on these relations by putting together species that were not in fact symbionts but fortuitously found inside gelatinous zooplankters (De Lima and Valentin 2001). Furthermore, direct observations of these biological interactions have the additional advantage of allowing observations on general behavior and use of the host by these crustaceans, including different degrees of parental care (Gasca and Haddock 2004).

**Table 2** Symbiotic relations between hyperiid amphipods and gelatinous zooplankton found during this survey

Hyperiid symbionts	Data of symbiont	Host	Date	lat. N	long. W	Depth (m)	Sampler	Observations
Infraorder Physosomata Family Lanceolidae <i>Lanceola pacifica</i> Stebbing, 1888	One male	Family Aeginidae <i>Aegina citrea</i> Eschscholtz, 1929	6 April 2005	35°38'	129°52'	1322	ROV dive 841	First record of symbiosis of <i>L. pacifica</i> (Fig. 3a)
Family Mimonectidae <i>Mimonectes sphaericus</i> Bovallius, 1885	One male	Family Prayidae <i>Nectadamas diomedea</i> (Bigelow, 1911)	7 April 2005	35°30'	123°52'	1082	ROV dive 842	First observation of symbiosis in both species (Fig. 3d)
Family Proscimidae <i>Proscima stephensi</i> (Pirlot, 1929)	One female	Family Prayidae <i>Nectadamas diomedea</i> (Bigelow, 1911)	5 May 2003	36°68.5'	122°06.3'	392	ROV dive 843	First observation of symbiosis in the Proscimidae (Fig. 3e)
Family Scinidae <i>Scina spinosa</i> Vosseler, 1901	One male	Family Halicreatidae <i>Haliscera bigelowi</i> (Kramp, 1947)	7 April 2005	35°30'	123°52'	394	ROV dive 843	First observation of <i>S. spinosa</i> as a symbiont
Infraorder Physocephalata Family Vibiliidae <i>Vibilia viatrix</i> Bovallius, 1887	One adult + six female juveniles	Family Salpidae <i>Pegea socia</i> (Bosc, 1802)	6 April 2005	35°30'	123°52'	10	Blue-water diving	Hyperiid species only found on salpids (Fig. 3c)
<i>Vibilia propinqua</i> Stebbing, 1888	One female juvenile	Family Salpidae <i>Salpa aspera</i> Chamisso, 1819	6 April 2005	35°30'	123°52'	308	ROV dive 841	Hyperiid not previously found in <i>S. aspera</i> , but in other salpids (Fig. 3b)
Family Hyperiididae <i>Hyperia medusarum</i> (Müller, 1776)	Three adult females 5.5–7.2 mm; 34 juv. 2–3 mm	Family Pandeidae <i>Leuckartiara zacae</i> Bigelow, 1840 four specimens	23, 25 May 2004	35°28'	123°52'	10	Blue water diving	One of few confirmed records of <i>H. medusarum</i> as a symbiont of a medusa (Fig. 3f)
Family Hyperiididae <i>Hyperia medusarum</i> (Müller, 1776)	One egg-carrying adult female 14.2 mm; plus one juvenile (4 mm)	Family Pandeidae <i>Neoturris</i> sp. Hartlaub, 1914	26 May 2004	36°34.09'	122°31.3'	237	ROV dive 680	Female with 398 eggs (mean diameter: 307 µm). The medusa is an undescribed species
Family Hyperiididae <i>Hyperoche medusarum</i> (Kröyer, 1838)	12 juveniles and 6 adult females (5.8–6.3)	Family Mitrocomidae <i>Mitrocoma cellularia</i> (Agassiz, 1865) Six medusan	27 May 2004	36°34.09'	122°31.3'	10	Blue water diving	Ovigerous females with 25–83 eggs (158–236 µm) within the host cavity. First record of <i>H. medusarum</i> in this medusa (Fig. 3g)

Table 2 continued

Hyperiid symbionts	Data of symbiont	Host	Date	lat. N	long. W	Depth (m)	Sampler	Observations
Family Lestrigonidae <i>Hyperietta stephenseni</i> Bowman, 1973	One egg-carrying female	Family Salpidae <i>Iasis zonaria</i> (Pallas, 1974)	24 May 2004	34°44.9'	124°34.3'	5–15	Blue water diving	First observation of symbiosis between these two species
Family Lestrigonidae <i>Lestrigonus schizogenetos</i> (Stebbing, 1888)	One juvenile female	Family Pandeidae <i>Leuckartiara zacaë</i> Bigelow, 1840	26 May 2004	35°28.8'	123°52.7'	5–15	Blue water diving	First observation of symbiosis between these two species
Family Pronoidea <i>Paralycaea hoylei</i> Stebbing, 1888	Two juvenile females	Family Diphyidae <i>Chelophyes appendiculata</i> (Eschscholtz, 1829)	25 May 2004	35°28'	123°52.7'	5–15	Blue water diving	First observation of symbiosis between these two species
Family Anapronoidea <i>Anapronoe reinhardtii</i> Stephensen, 1925	Juvenile male	undescribed physonect siphonophore	11 April 2005	36°41'	122°3.36'	200	ROV dive 847	First observation of symbiosis in the genus <i>Anapronoe</i>
Family Tryphanidae <i>Tryphana malmi</i> Boeck, 1870	One juvenile female	Family <i>Mitrocomia cellularia</i> (Agassiz, 1865)	27 May 2004	36°34'	122°31.3'	5–15	Blue water dive	First observation of symbiosis between these two species (Fig. 3h)
Family Tryphanidae <i>Tryphana malmi</i> Boeck, 1870	Three adult females	<i>Solmissus incisa</i> (Fewkes, 1886)	21 May 2004	36°41'	122°4.96'	458	ROV dive 673	First observation of this symbiosis (Fig. 3H)
Family Brachyscelidae <i>Euthamneus rostratus</i> (Bovallius, 1887)	One specimen	<i>Solmissus incisa</i> (Fewkes, 1886)	7 April 2005	35°05'	123°52'	243	ROV dive 843	First observation of <i>E. rostratus</i> as a symbiont of this medusa



The presence of a mating pair of copepods within a hydromedusa is a peculiar and previously unknown form of symbiosis that reflects the complexity of the biological interactions in the deep sea. The nature of the known but still poorly understood associations between the hyperiid amphipods and the gelatinous zooplankters has been a matter of discussion for decades; in the literature opinions are divergent. Some authors consider these associations as a strict parasitism and others define these symbioses as a diverse array with different degrees of commensalism, including ecto and endo commensalism, protection, and micropredation (see, Gasca and Haddock 2004). The mechanism by which these crustacean symbionts do not become a prey of their gelatinous host also remains unanswered. According to Hay et al. (2004), many aquatic biological interactions fall within the limits of mutualism as a dynamic reciprocal association shifting from positive to negative depending on the context. From this controversy and our findings, it is clear that our knowledge of the nature and dynamics of these associations in the deep sea is still largely incomplete and should be investigated in more detail emphasizing their behavioral aspects.

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