



Associations between gelatinous zooplankton and hyperiid amphipods (Crustacea: Peracarida) in the Gulf of California

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Abstract

Hyperiid amphipods are pelagic crustaceans that live associated with gelatinous zooplankton including medusae, ctenophores, siphonophores, and salps. Standard plankton sampling disrupts natural associations, so the most reliable way to determine an association is through direct observation of the organisms in their environment. The planktonic fauna of the Gulf of California dwelling between 10 and 3000 m was surveyed using SCUBA diving and a remotely operated submersible (ROV) during March 2003. Here we report our observations on a total of 14 symbiotic associations found between the hyperiid amphipods and various taxa of gelatinous zooplankton. We found parental care behavior in a group of amphipods (Oxycephalidae) in which this phenomenon has not been previously reported. For two hyperiid species, *Euthamneus rostratus* and *Vibilia australis*, we present the first information on their symbiotic relations. Additional hosts were discovered for other well-known and widely distributed hyperiid species (i.e. *Brachyscelus crusculum*, *Hyperoche medusarum*). Photographic evidence of some of these interactions is included in this contribution. This is the first survey of these relationships in the Gulf of California, and many aspects of the ecology and biology of these symbioses remain to be studied.

Introduction

Hyperiid amphipods have been advanced as a polyphyletic group (Bowman & Gruner, 1973), bringing together the descendants of different lineages of benthic forms that have developed a benthic-like existence on the pelagic substratum provided by gelatinous zooplankton (Laval, 1980). The relatively low host specificity and the morphological evidence provided by the analysis of the mouthparts suggest that parasitism in hyperiid amphipods has evolved only recently (Dittrich, 1988, 1992). Hyperiids are associated with different kinds of gelatinous zooplankton at the onset of their existence, when they are assumed to be strict parasites (Dittrich, 1987, 1992); the duration of the

association depends on the hyperiid species and varies according to biological and ecological factors. The relationship is nearly always detrimental to the host, although Vader (1983) categorized the different types of hyperiid relations as ectocommensalism, endocommensalism, protection, and micropredation, while hyperiids also obtain buoyancy and transportation. It is assumed that most hyperiid amphipods are not biologically suited to a pelagic free-living existence (Laval, 1980).

Some genera and even families appear to be restricted to associations with certain host groups, but we are far from being able to know the mechanisms or specificity for host selection. The juveniles expelled from the pouch, in many cases

without swimming appendages (Dittrich, 1992), would have a very little likelihood of encountering a host by themselves. The adult female does not produce a large number of eggs to compensate for this low probability of host encounter; therefore, she is responsible for the dissemination of her limited progeny, seeking the correct hosts and demersupiating on them.

Prior works have described some of these peculiar symbiotic interactions (Madin & Harbison, 1977; Thurston, 1977; Laval, 1980). In this contribution, we report our observations on the interaction of hyperiids with different gelatinous zooplankton obtained during surveys of the water column between the surface and 3000 m in four different areas of the Gulf of California.

Methods

The planktonic fauna of the Gulf of California was surveyed during an oceanographic cruise carried out aboard the R/V *Western Flyer* of the Monterey Bay Aquarium Research Institute (MBARI). The cruise took place between March 12 and 31, 2003, and included sampling stations in

Guaymas, Pescadero, and Farallon Basins and Alarcón seamount of the southern Gulf of California (Fig. 1). We used blue-water SCUBA diving to survey the upper 20 m, and a remotely operated submersible (ROV) to sample the zooplankton fauna between 200 and 3000 m depths. Specimens were captured together with their associated hyperiids in glass jars on SCUBA dives, or using 'detritus samplers' described by Youngbluth (1984) for the ROV samples. In short, the samplers are acrylic cylinders with hydraulically actuated lids on the top and bottom. These slide closed to seal the vessel when the animal has been maneuvered into the chamber. Once brought on board the ship, the host species and its associated copepods and amphiods were examined and identified. After this initial manipulation *in vivo*, the 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. The identification of the hyperiid amphipods was made using the keys, illustrations, and descriptions of Zeidler (1992, 1998), Shih & Chen (1995), and Vinogradov et al. (1996). The hydromedusa described herein as *Aequorea coerulescens* was called *A. macrodactyla*

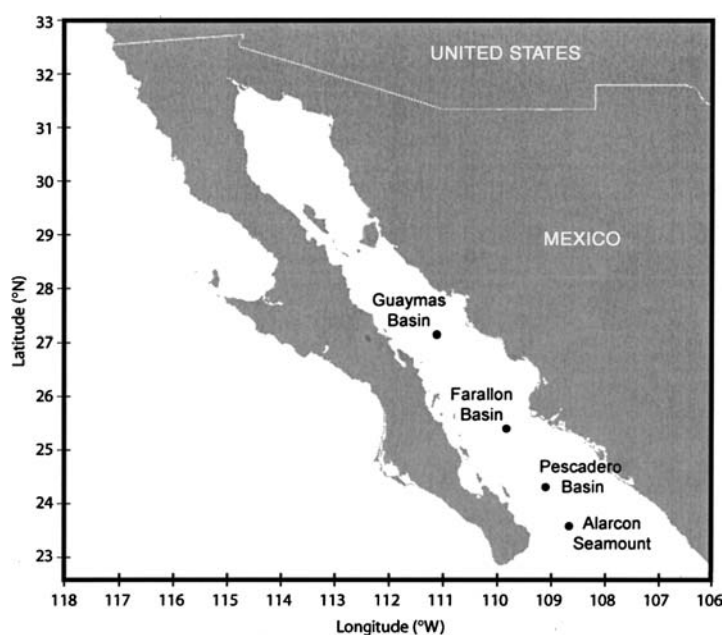


Figure 1. The Gulf of California region showing the stations where ROV and blue-water SCUBA dives were conducted.

by Stretch & King (1980) during their study of the region.

Results and discussion

We identified the following gelatinous organisms carrying hyperiid amphipods: two species of

hydromedusae, and one each of scyphomedusa, siphonophore, salp, heteropod mollusc, and ctenophore (Fig. 2). Up to six species of hyperiids were recorded in association with these animals (Table 1). Previous faunistic work in the Gulf (Siegel-Causey, 1982; Brinton et al., 1986) has reported on the composition and distribution of the hyperiid fauna, but not in relation with their hosts.

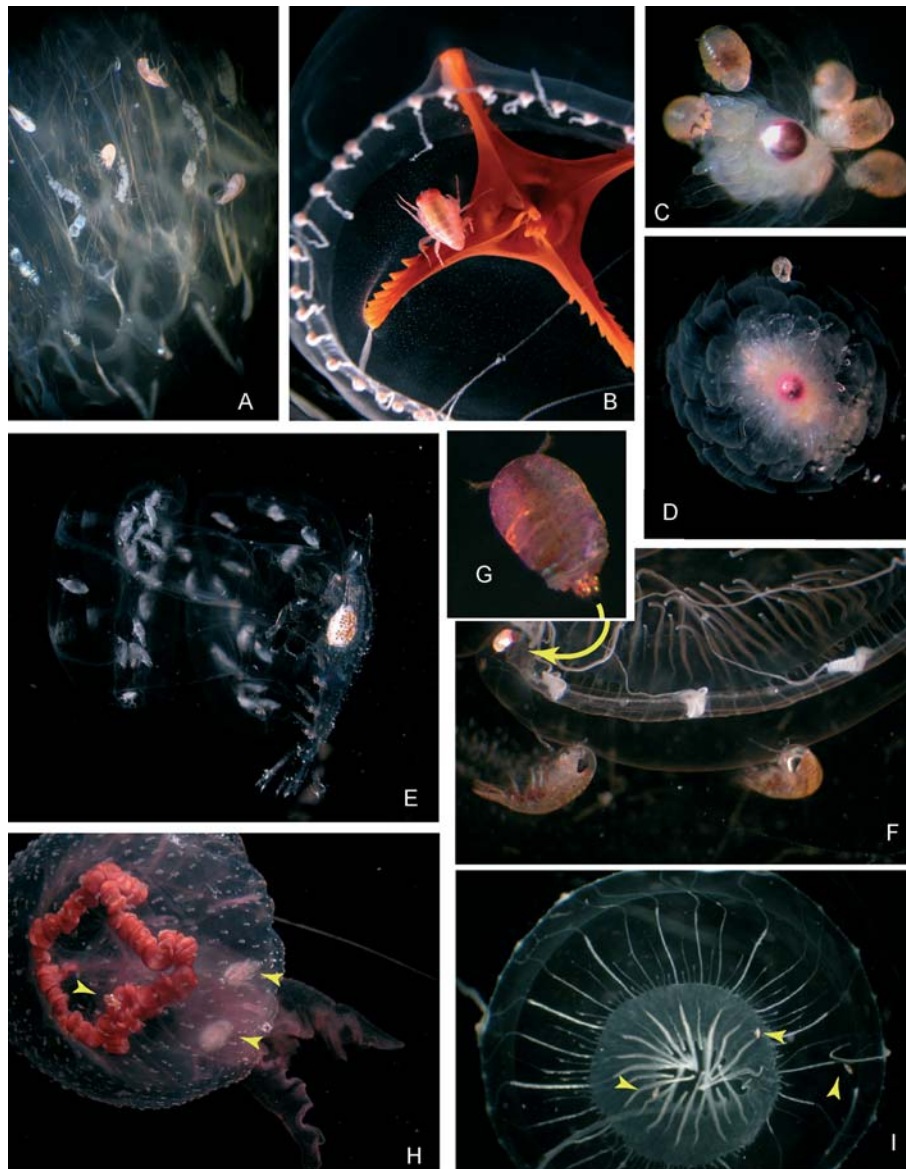


Figure 2. Amphipods and their gelatinous hosts. (A) *Vibia australis* on *Cyclosalpa bakeri*. (B) *Hyperoche medusarum* on *Chromatonema erythrogonon*. (C, D) *Parascelus typhoides* on *Athorybia rosacea*. (E) *Oxycephalus clausi* female and juveniles on *Ocyropsis crystallina crystallina*. (F) *Brachyscelus crusculum* and (G) *Sapphirina nigromaculata* on *Aequorea coerulescens*. (H) *Euthamneus rostratus* on *Pelagia noctiluca*. (I) *Euthamneus rostratus* juveniles on *Aequorea coerulescens*.

Table 1. Amphipods (A) and copepods (Co) associated with different gelatinous taxa (M = medusae; S = siphonophores; Ct = ctenophores; H = heteropod) collected in the Gulf of California at different depths (in m) during the survey period

Associated crustacean	Host	Locality	Depth (m)	Dive
<i>Hyperoche medusarum</i> (Kröyer, 1838) (A) w/eggs	<i>Chromatonema erythrogonon</i> (Bigelow, 1909) (M)	Carmen Basin	1100	ROV 546
<i>Vibilia australis</i> Stebbing, 1888 (A)	<i>Cyclosalpa bakeri</i> Ritter, 1905 (Salp)	Alarcón Seamount	244	ROV 547
<i>Brachyscelus cruscum</i> (A) w/larvae in marsupium	<i>Pterotrachea hippocampus</i> Philippi, 1836 (H)	Pescadero Basin	15	BW9
<i>Brachyscelus cruscum</i> Bate, 1861 (A)	<i>Aequorea coerulescens</i> (Brandt, 1838) (M)	Isla Cerralvo	10	BW1
<i>Brachyscelus cruscum</i> (A) with eggs	<i>Aequorea coerulescens</i> (M)	Farallon Basin	15	BW3
<i>Brachyscelus cruscum</i> (A) & <i>Sapphirina</i>	<i>Aequorea coerulescens</i> (M)	Guaymas Basin	10	BW4
<i>nigromaculata</i> Claus, 1863 (Co)				
<i>Brachyscelus cruscum</i> juv. male (A) &	<i>Aequorea coerulescens</i> (M)	Alarcón Seamount	10	BW10
<i>Sapphirina nigromaculata</i> (Co)				
<i>Brachyscelid</i> (A) unidentifiable juv.	<i>Aequorea coerulescens</i> (M)	Pescadero Basin	10	BW8
<i>Euthamneus rostratus</i> (A) adult and juv.	<i>Pelagia noctiluca</i> (Forskål, 1775)(M)	Pescadero Basin	10	BW8
<i>Euthamneus rostratus</i> (Bovallius, 1887) (A) juv.	<i>Aequorea coerulescens</i> (M)	Farallon Basin	10	BW3
<i>Oxycephalus clausi</i> Bovallius, 1887 (A) and juv.	<i>Ocyropsis crystallina crystallina</i> (Rang, 1826) (Ct)	Pescadero Basin	10	BW2
<i>Oxycephalus clausi</i> Bovallius, 1887 (A) and juvs.	<i>Ocyropsis crystallina crystallina</i> (Ct)	Farallon Basin	10	BW5
<i>Parascelus typhoides</i> Claus, 1879 (A)	<i>Athorybia rosacea</i> (Forskål, 1775) (S)	Isla Cerralvo	10	BW1
<i>Parascelus typhoides</i> (A)	<i>Athorybia rosacea</i> (S)	Pescadero Basin	10	BW8

Parental care

Many benthic amphipods have shown different degrees of parental care (Thiel, 1997; Thiel et al., 1997), whereas this phenomenon seems to be quite unusual (or unknown) in the planktonic forms. Members of the hyperiid family Phronimidae are the only hyperiid crustaceans for which maternal care has been reported (Thiel, 1976, 2000). In this family, the mother feeds and keep the larvae within barrel-shaped salp tests after demarsupiation. In our study, a female of *Oxycephalus clausi*, a member of the family Oxycephalidae, was observed taking care of the juveniles demarsupiated into the ctenophore *Ocyropsis crystallina*; the female was keeping the young individuals (ca. 30 juveniles) on the surface of the ctenophore, where they were randomly distributed across the host. The female, using her pereopods, kept the juvenile-carrying ctenophore in constant motion and swam about in different directions without losing contact with the ctenophore (Fig. 2E). This behavior persisted for several hours after the time of collection. This is the first report of maternal care in this hyperiid family; further studies could elucidate if, as reported for the Phronimidae, the oxycephaliids also feed their larvae or if they feed directly on the ctenophore tissues. Demarsupiation is yet another interesting process by which the females expells the larvae from her pouch to the host surface where they can feed upon the host tissues (Laval, 1980). This phenomenon was not observed in the specimens examined herein.

Remarks on the species

Shih & Chen (1995) stated that most of the associations reported in the literature involve amphipods of the families of the Infraorder Physocephalata (except for some *Scina*); all the species recorded herein belong to this taxon.

Euthamneus rostratus is a relatively rare species, but it is widely distributed; it has been known to occur in tropical as well as temperate areas. It was found at a depth of 10 m associated with the scyphomedusa *Pelagia noctiluca* (Fig. 2H) and the hydromedusa *Aequorea coerulescens* (Fig. 2I), both of which are known to host a wide variety of hyperiids (Laval, 1980). However, there are no previous records of symbiosis of this hyperiid.

Vibilia australis is a species widely distributed in the surface waters of the tropical latitudes of the oceans. This genus is said to be restricted to salps (see Madin & Harbison, 1977), and in our case it was recovered from *Cyclosalpa bakeri* collected with the ROV. However, as noted for *E. rostratus*, this is the first information about the symbiotic relation of this hyperiid species.

Parascelus typhoides dwells in the upper 200 m layer. It is a relatively rare species distributed in tropical and temperate regions. The females of this species were recently synonymized under *P. edwardsi* Claus, 1879, by Zeidler (1998). This species has been found in the siphonophore *Forskalia ?edwardsi* K  lliker, 1853 (Laval, 1980), and in our surveys two females of this species were recorded at a depth of 10 m in association with another siphonophore, *Athorybia rosacea* (Fig. 2C and D).

Brachyscelus cruscolum is a common epipelagic form, widely distributed in the oceans. This species has been found in symbiosis with several groups of pelagic organisms, mainly with salps (*Salpa fusiformis* Cuvier, 1804, *Salpa maxima* Forsk  l, 1775, *Thalia democratica* (Forsk  l, 1775)) but also with medusae (*Aequorea* spp.) and heteropod molluscs (*Pterotrachea* spp.) (see Laval, 1980). On several occasions, we found this species associated with the hydromedusa *Aequorea coerulescens* (Fig. 2F) and with the heteropod *Pterotrachea hippocampus*. The only male specimen in any of our samples was a juvenile of this species associated with *A. coerulescens*.

Hyperoche medusarum is considered to be a bipolar form; it was recorded at 1100 m depth in the Gulf of California. This amphipod has been found in symbiosis with a wide variety of pelagic coelenterates, including six species of medusae, and six ctenophores (see Laval, 1980). The finding of this species with the medusa *Chromatonema erythrogonon* has not been reported before and adds this species to the host list of *H. medusarum* (Fig. 2B). (The specimens referred to herein as *H. medusarum* show some morphological differences from previous descriptions. Hence, if the taxonomic status of these specimens changes, this record could reflect to a new association.)

Oxycephalus clausi (Fig. 2E) has been found more frequently in ctenophores such as *Eurhamphaea vexilligera* Gegenbaur, 1856, *Mnemiopsis mccradyi* Mayer, 1900, *Bolinopsis vitrea* (L. Agassiz,

1860), and *Ocyropsis maculata* (Rang, 1826), among others (Harbison et al., 1978); the list includes also *Ocyropsis crystallina crystallina* on which it was found during this survey. It has also been found associated with the heteropod mollusc *Pterotrachea hippocampus* and with the tunicates *Pegea socia* and *Salpa cylindrica* (Madin & Harbison, 1977).

General remarks

There is still much to be studied with respect to these biological interactions. Some authors suggest that hyperiids associate with hosts only intermittently for food, transportation, or protection (Vader, 1983; Dittrich, 1992). Others argue that these crustaceans are mostly free-living forms (Evans & Sheader, 1972; Westernhagen, 1976), while a third view is that they are obligate symbionts of their hosts and that they are not able to survive independently (Laval, 1980). The range of behavior within these associations is very wide: some species show a parasitoid behavior, leaving their offspring in the host, while other species have a marked and relatively prolonged parental care. Another interesting issue yet to be studied is whether males are more independent from hosts than females. Males are not usually found on the hosts and some hyperiid males even remain unknown (Laval, 1980). We found only one juvenile male (*B. cruscolum*) associated with the gelatinous zooplankton examined herein. New investigative efforts could be directed to find out if these symbiotic relations are species-specific or are established between well-defined taxa. This could lead to an improved understanding of the degree of co-evolution of hyperiids with their hosts (see Dittrich, 1992). Many unanswered questions remain concerning reproduction and development, fertility, and the impact of parental care on the species success-survival. Further *in situ* observations and direct collections will improve our understanding of these complex and fascinating interactions between phyla.

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