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New symbiotic associations of hyperiid amphipods (Peracarida) with gelatinous zooplankton in deep waters off California

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Hyperiid amphipods are holoplanktonic marine crustaceans that are known as temporary symbionts of different groups of gelatinous zooplankton. The nature and dynamics of these associations are still poorly understood, particularly in deep waters. The mesopelagic and deep-living planktonic fauna off Monterey Bay, California (down to 4000 m) was surveyed using a remotely operated submersible (ROV) and blue-water diving (BWD) between September 2005 and January 2008. In this work we report our observations on a total of 51 symbiotic associations observed in situ *(not from zooplankton samples), between hyperiid amphipods and various taxa of gelatinous zooplankton. We present the first information on the symbiotic relations of the hyperiid* Vibilia caeca*, and we provide data of 34 previously unknown symbiotic associations. The host range was expanded for several widely distributed hyperiid species. These findings suggest that the symbiotic associations between hyperiid amphipods and gelatinous zooplankton in deep waters deserve further study worldwide.*

Keywords: symbiotic associations, deep-living zooplankton, crustaceans, gelatinous zooplankton, hyperiid amphipods, symbiosis, plankton, siphonophores, medusae, ctenophores

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INTRODUCTION

Hyperiids represent a remarkable lineage of amphipods that are adapted to live as holoplanktonic forms from primitive benthic forms. The life cycle of most species of hyperiids involves a symbiotic association with other pelagic organisms, mainly gelatinous zooplankters, which are used as a substratum (Laval, 1980). The duration and nature of the symbiosis depends on the hyperiid species and varies according to factors including season, abundance and size of hosts, development of host's gonads and water temperature (Dittrich, 1987, 1992). The ways in which hyperiids are associated with the gelatinous zooplankton are quite variable (Vader, 1983) and in most cases, the biological details of these symbioses remain unstudied. Some hyperiid taxa appear to be restricted to associations with certain host groups, but the mechanisms for host selection are yet to be studied. In general, it is assumed that most hyperiid amphipods depend on the symbiosis to complete their life cycle (Laval, 1980), but the scant evidence is still inconclusive.

Previous studies have documented the composition and distribution of these symbiotic interactions in different geographic areas and environments (Madin & Harbison, 1977; Thurston, 1977; Laval, 1980). These data are mainly from surveys in the epipelagic layers; hence, the amphipod fauna of deep waters is still poorly known, along with its associated host species. Some recent efforts have explored this interesting phenomenon at meso- and bathypelagic depths (Gasca & Haddock, 2004; Gasca, 2005; Gasca *et al.*, 2007). In this contribution we report new observations on the interaction of hyperiids with different groups of gelatinous zooplankton observed (and collected) *in vivo* during surveys of the water column between the surface and 4000 m in four different areas of the Pacific Ocean.

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MATERIALS AND METHODS

The planktonic fauna of Monterey Bay, California, was surveyed during several oceanographic cruises carried out on board the R/V Western Flyer of the Monterey Bay Aquarium Research Institute (MBARI). The cruises took place between 2006 and 2008. A remotely operated submersible (ROV) was used to sample the zooplankton at depths between 200 and 3000 m. Specimens of different groups of gelatinous zooplankton were individually captured together with their associated hyperiids and brought on board the ship where the host species and symbiotic amphipods 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 seawater (95%) for further taxonomic examination. The identification of the hyperiid amphipods followed Shih & Chen (1995), Vinogradov *et al.* (1996) and Zeidler (1992, 1998, 2003, 2004). The gelatinous zooplankton was identified following mainly Totton (1965), Mills (1987), Godeaux (1998) and Mills & Haddock (2007).

To examine broader questions of the depth distribution of hyperiid amphipods in association with cnidarians and ctenophores, we used the MBARI's 25-year record of ROV dives.

Each dive is annotated by experts and entered in the VARS (Video annotation and retrieval system) database (Schlining & Jacobsen Stout, 2006). Using a custom script to generate database searches (vars_retrieve_concept.py, available at http://bitbucket.org/mbari/database/), we queried this database for records of hyperiid amphipods and for amphipods in association with each species of cnidarian and ctenophore that has been entered into the database. These datasets were filtered using Unix commands cut, sort, and uniq, and histograms were generated using R version 3.0.1.

RESULTS

We collected amphipods associated with eight species of ctenophores, eight of medusae, four siphonophores, five salps and one mollusc (Table 1). Up to 23 species of hyperiid amphipods were recorded in association with these gelatinous organisms. Overall, 34 new associations of hyperiid species with gelatinous zooplankters were recorded (marked with * in Table 1). In addition, we recorded and confirmed a total of 12 associations that were reported in other works (Gasca & Haddock, 2004; Gasca, 2005; Gasca et al., 2007) and documented some of these prior associations in the Monterey Bay area. Details of the new symbioses discovered during this survey, including data on the hosts and biological remarks, are provided below and in Table 1.

The database searches for Hyperiid amphipods retrieved 11,292 annotations of hyperiids spanning the years 1989 to 2014, and with depths from the surface to a maximum of 3980 m. These records were not necessarily associated with hosts and not necessarily identified to species. We searched for records of hydrozoan, scyphozoan and ctenophore hosts associated with amphipods, with the command 'vars_retrieve_concept.py -a Hydrozoa, Scyphozoa, Ctenophora + Amphipod'. This search process used hosts concepts from 309 hydrozoans, 57 scyphozoans and 85 classifications of Ctenophora, along with 40 concepts (genera, species) for amphipods. Total amphipods were found frequently to the deepest depths that MBARI's ROVs can operate (Figure 3A). The records with specific associations between amphipods and hosts ranged as deep as 3493 m, with the deepest host being the scyphomedusa *Poralia* sp. (Table 2).

Infraorder PHYSOSOMATA
Family LANCEOLIDAE
Lanceola clausi clausi Bovallius, 1885

Remarks: This is the first record of a species of *Lanceola* as a symbiont of a larvacean. The juvenile female observed was crawling outside the larvacean house. Hitherto, the known associations involving members of this family are those of *Lanceola sayana* with *Pelagia* sp., *L. pacifica* found as a symbiont of the medusa *Aegina citrea* Eschscholtz, 1829 (Gasca et al., 2007), and *Lanceola loveni* with the hydromedusae *Solmissus* sp. (Zeidler, 2012).

Family MIMONECTIDAE
Mimonectes gaussi (Woltereck, 1904)

Remarks: We are not completely sure of the identification of this species because all the specimens collected were juveniles. This species has been previously recorded from a lobate ctenophore and *Bolinopsis* sp. (Zeidler, 2012). During this survey it was found as a symbiont of the lobate ctenophores *Bathocyroe fosteri* Madin & Harbison, 1978 (Figure 1), *Deiopea kaloktenota* Chun, 1879, and *Kiyohimea usagi* Matsumoto & Robison, 1992. This genus appears to have a wide host range among lobate ctenophores.

Mimonectes sphaericus Bovallius, 1885

Remarks: This hyperiid, recorded herein in association with the siphonophore *Nectadamas diomedeae* (Bigelow, 1911) was previously found from the same host in the Monterey Bay area by Gasca et al. (2007). In the same work it was recorded as *Proscina stephenseni* from the same host (see Zeidler, 2012). It is here reported in association with an unidentified medusa of the genus *Bythotiara* hosting a single male juvenile at a depth of 690 m. Zeidler (2012) reported it previously on the medusae *Bythotiara* sp. and *Solmissus* sp. This amphipod is widely distributed in the world oceans and has been observed in different regions of the Pacific Ocean (Vinogradov et al., 1996). Young specimens are commonly found in the water column between 200 and 2000 m but mature females have been recorded near the surface (Vinogradov et al., 1996).

Family SCINIDAE
Scina spinosa Vosseler, 1901

Remarks: The specimen reported herein was identified as *S. spinosa*, and its morphology is congruent with the subspecies *S. spinosa uncipes* as described by Zeidler (1992). *Scina spinosa* is a common inhabitant of mid- and deep waters of the Atlantic and Pacific oceans and it does not reach the surface layers (Vinogradov et al., 1996; Vinogradov, 1999). Out of the about 110 nominal species of the Physosomata, only a few are known as symbionts of gelatinous zooplankters; this is also true for the speciose genus *Scina*. Only six out of the 50 species of this genus are known as symbionts of gelatinous zooplankters. In the Monterey Bay area, *S. spinosa* was recently recorded in association with the medusa *Haliscera bigelowi* (Gasca et al., 2007). This association was confirmed with the finding of two more records during this survey, thus suggesting that the host range of this hyperiid is limited to this medusa.

Infraorder PHYSOCEPHALATA
Family VIBILIIDAE

Remarks: Most of the previous records of associations involving species of *Vibilia* have been from different species of salps (Madin & Harbison, 1977; Laval, 1980). There is a single report of a species of this genus as a symbiont of a siphonophore (Lavaniegos & Ohman, 1999), but this was based on statistic correlation data and not on direct observation of the specimens associated. During this survey, and also in previous works in the area (Gasca & Haddock, 2004; Gasca, 2005; Gasca et al., 2007), all records of *Vibilia* associations are with salp species.

Vibilia armata Bovallius, 1887

Remarks: It has been found as a symbiont of different salp species (Laval, 1980; Hoogenboom & Hennen, 1985; Lavaniegos & Ohman, 1999), but it has not been previously recorded from *Cyclosalpa fusiformis* Cuvier, 1804; hence,

Table 1. Hyperiid amphipods associated with gelatinous zooplankton off California. ROV, remotely operated submersible; BWD, blue-water diving; juv, juvenile specimens.

Amphipod	Data of symbiont	Host	Date	Depth	Latitude N	Longitude W	Sampler
Infraorder Physosomata							
Fam. Lanceolidae							
Lanceola clausi clausi	♀juv	larvacean house*	29 September 2006	914	35°25′48.0″	122°55′26.4″	ROV
Fam. Mimonectidae							
Mimonectes gaussi? (Woltereck, 1904)	♀ juv	*Bathocyroe fosteri**	23 January 2007	1490	35°49′58.8″	122°40′01.2″	ROV
	♀ juv	*Deiopea kaloktenota**	2 October 2006	973	35°37′58.8″	122°43′58.8″	ROV
	♀ juv	*Kiyohimea usagi**	2 October 2006	628	35°37′58.8″	122°43′58.8″	ROV
Mimonectes sphaericus	♂ juv	*Nectadamas diomedeae*	14 May 2006	1344	35°37′58.8″	122°43′58.8″	ROV
		Bythotiara sp.	13 May 2006	690	35°37′58.8″	122°43′58.8″	ROV
Family Scinidae							
Scina spinosa	♀ juv	*Haliscera* sp.	4 October 2006	1263	36°42′00.0″	122°34′30.0″	ROV
Scina uncipes	♀ adult	*Haliscera* sp.*	17 May 2006	449	36°42′43.2″	122°11′13.2″	ROV
Scina sp.		*Bythotiara depressa* Naumov, 1960*	1 December 2007	494	36°42′00.0″	122°34′30.0″	ROV
Infraorder Physocephalata							
Family Vibiliidae							
Vibilia armata Bovallius, 1887	♀w/eggs	*Salpa fusiformis*	2 October 2006	<30	35°37′58.8″	122°43′58.8″	BWD
Vibilia caeca		*Vitreosalpa gemini**	17 May 2006	469	36°42′43.2″	122°11′13.2″	ROV
Vibilia caeca		*Vitreosalpa gemini*	17 May 2006	422	36°42′43.2″	122°11′13.2″	ROV
Vibilia caeca	juv ♀	*Vitreosalpa gemini*	29 September 2006	604	35°25′48.0″	122°55′26.4″	ROV
Vibilia chuni	♀ juv	*Cyclosalpa affinis**	28 September 2006	<30	35°49′58.8″	122°40′01.2″	BWD
Vibilia viatrix?		*Pegea confoederata*	2 October 2006	<30	35°37′58.8″	122°43′58.8″	BWD
Vibilia sp.		*Cyclosalpa affinis*	28 September 2006	<30	35°49′58.8″	122°40′01.2″	BWD
Vibilia sp.		*Vitreosalpa gemini*	22 January 2007	1763	36°34′01.2″	122°31′19.2″	ROV
Family Paraphronimidae							
Paraphronima gracilis	juv	*Rosacea cymbiformis**	17 May 2006	430	36°42′43.2″	122°11′13.2″	ROV
Family Phronimidae							
Phronima sp.		Barrel	2 October 2006	<30	35°37′58.8″	122°43′58.8″	BWD
Phronima atlantica		Barrel	2 October 2006	<30	35°37′58.8″	122°43′58.8″	BWD
Phronima atlantica	adult♂	*Salpa fusiformis*	2 October 2006	<30	35°37′58.8″	122°43′58.8″	BWD
Family Hyperiidae							
Hyperia medusarum	♀ juv	*Solmissus* sp.*	27 September 2006	498	36°42′43.2″	122°11′13.2″	ROV
	2♂ juv	*Leuckartiara octona* (3 ind)*	29 September 2006	<30	35°25′48.0″	122°55′26.4″	BWD
Hyperia sp.		*Haliscera bigelowi**	29 September 2006	<30	35°25′48.0″	122°55′26.4″	BWD
Hyperia sp.		*Hormiphora californensis**	12 September 2006	210	36°41′45.6″	122°04′58.8″	ROV
Hyperia sp.	25 juv	*Hormiphora californensis*	12 September 2006	197	36°41′45.6″	122°04′58.8″	ROV
Hyperia sp.	15 juv	*Hormiphora californensis* (2 ind)	27 September 2006	150	36°42′43.2″	122°11′13.2″	Trawl
Hyperia sp.		*Solmissus* sp.	12 September 2006	435	36°41′45.6″	122°04′58.8″	ROV
Hyperia sp.		*Solmissus* sp.	29 September 2006	396	35°25′48.0″	122°55′26.4″	ROV
Hyperia sp.	♀ juv	Radiolarian*	1 October 2006	<30	34°17′09.6″	124°03′07.2″	BWD
Hyperia sp.	3	Undescribed Mertensiid*	2 October 2006	<30	35°37′58.8″	122°43′58.8″	BWD
Hyperoche mediterranea	1♀juv	*Pleurobrachia bachei*	29 September 2006	<30	35°25′48.0″	122°55′26.4″	BWD
	♀w/eggs	*Pleurobrachia bachei* 2 ind	2 October 2006	<30	35°37′58.8″	122°43′58.8″	BWD
		*Hormiphora californensis**	2 October 2006	<30	35°37′58.8″	122°43′58.8″	BWD

Continued

Table 1. Continued

Amphipod	Data of symbiont	Host	Date	Depth	Latitude N	Longitude W	Sampler
	♀w/hatch	*Hormiphora californensis*	2 October 2006	<30	35°37′58.8″	122°43′58.8″	BWD
	2 ♀ w/hatch 1 male	*Lampea pancerina* 4 ind)	28 September 2006	<30	35°49′58.8″	122°40′01.2″	BWD
	juv?	*Lampea* sp.*	28 September 2006	<30	35°49′58.8″	122°40′01.2″	BWD
	juv	*Leucothea pulchra**	3 October 2006	<30	35°37′58.8″	122°43′58.8″	BWD
	(1 ad, 2 juv)	Pandeidae* (unknown)	21 August 2007	374	36°41′45.6″	122°04′58.8″	ROV
Hyperoche shihi		*Aegina citrea**	21 August 2007	554	36°41′45.6″	122°04′58.8″	ROV
Family Iulopididae							
Iulopis loveni	Adult ♀	*Aegina citrea**	22 January 2007	83	36°34′01.2″	122°31′19.2″	ROV
Iulopis mirabilis		*Aegina citrea**	1 October 2006	1478	34°17′09.6″	124°03′07.2″	ROV
		Aegina citrea	1 October 2006	1286	34°17′09.6″	124°03′07.2″	ROV
	adult + juvs	*Tima* spp.*	30 September 2006	<30	34°17′09.6″	124°03′07.2″	BWD
Family Pronoidae							
Eupronoe minuta	♀ juv	*Rosacea cymbiformis**	6 August 2006	161	36°41′45.6″	122°04′58.8″	ROV
Family Anapronoidae							
Anapronoe reinhardti	1♀, 1♂ juv	*Resomia ornicephala**	10 May 2006	254	36°36′10.8″	122°22′33.6″	ROV
Family Lycaeidae							
Simorhynchotus antennarius	♀w/eggs	*Liriope tetraphylla**	9 June 2006	<30			BWD
Family Tryphanidae							
Tryphana malmi		*Eutonina indicans**	13 May 2006	202	35°37′58.8″	122°43′58.8″	ROV
	♀w/hatch	*Solmisus incisa*	17 May 2006	295	36°42′43.2″	122°11′13.2″	ROV
	♀w/eggs	*Resomia ornicephala**	17 May 2006	204	36°42′43.2″	122°11′13.2″	ROV
		*Physophora hydrostatica**	11 January 2006	116	36°41′45.6″	122°04′58.8″	ROV
	1 adult +1 juv	*Resomia ornicephala*	10 May 2006	254	36°36′10.8″	122°22′33.6″	ROV
Family Brachyscelidae							
Brachyscelus sp.	juv	*Solmisus incisa**	13 May 2006	497	35°37′58.8″	122°43′58.8″	ROV
Family Oxycephalidae							
Oxycephalus clausi	♀w/eggs	*Cestum veneris*	12 June 2006	<30			BWD
Oxycephalidae	juv	*Cestum veneris*	12 June 2006	<30			BWD
Oxycephalidae	juv, very small	*Thalassocalyce inconstans**	24 January 2007	601	36°41′45.6″	122°04′58.8″	ROV
Streetsia sp.		*Thalassocalyce inconstans**	15 January 2008	205	36°41′45.6″	122°04′58.8″	ROV
Glossocephalus sp.		*Bathocyroe fosteri**	21 February 2007	728	36°41′45.6″	122°04′58.8″	ROV
Glossocephalus sp.	(2 ad, 17 juv)	*Bathocyroe fosteri*	21 August 2007	830	36°41′45.6″	122°04′58.8″	ROV
Glossocephalus sp.		*Bathocyroe fosteri*	6 September 2005	568	36°42′00.0″	122°04′01.2″	ROV
		Bathocyroe fosteri	11 April 2005	557	36°41′55.2″	122°03′25″	ROV
Family Platyscelidae							
Tetrathyrus forcipatus	Andult ♀ plus juvs	*Corolla spectabilis**	12 June 2006	<30			BWD

Table 2. The maximum depth at which hosts were found to be associated with amphipods, based on the ROV video record. (Specimens not necessarily collected or identified to species.) Taxa are sorted by maximum depth from shallowest to deepest.

Host	Depth
Praya	99
Physophora hydrostatica	116
Octogonade	194
Octogonade mediterranea	204
Lensia conoidea	241
Resomia ornicephala	256
Nanomia bijuga	270
Rhopalonematidae	275
Trachymedusae	318
Neoturris	337
Calycopsis	360
Calycopsidae	379
Cydippida	379
Anthomedusae	401
Aeginura	422
Desmophyes haematogaster	438
Frillagalma	441
Haliscera	452
Mitrocoma cellularia	464
Beroe gracilis	469
Narcomedusae	473
Frillagalma vityazi	502
Beroe cucumis	513
Prayinae	551
Periphylla periphylla	598
Phialidium	600
Tima	619
Kiyohimea usagi	632
Leuckartiara	646
Ptychogena lactea	663
Solmaris	691
Haliscera conica	696
Vogtia	754
Lampocteis cruentiventer	758
Ctenophora	770
Hormiphora californensis	781
Chuniphyes	804
Pandea rubra	914
Deiopea	973
Thalassocalyce inconstans	1012
Deepstaria	1036
Erenna cornuta	1058
Modeeria rotunda	1066
Lobata	1069
Pegantha	1082
Chromatonema	1099
Beroe abyssicola	1114
Earleria purpurea	1144
Bolinopsis	1184
Leptomedusae	1234
Cunina	1242
Arctapodema	1299
Heterotiara	1304
Solmissus	1339
Aegina citrea	1479
Periphyllopsis	1533
Nausithoe	2030
Eutonina indicans	2185
Pantachogon	2198
Eutima	2331
Hydromedusae	2362
Haliscera bigelowi	2836
Bathocyroe fosteri	2986
Undescribed ctenophore	3165
Poralia rufescens	3492

this is the first report of this association and an expansion of its host range among salps.

Vibilia caeca Bulycheva, 1955

Remarks: Two and one specimens of *V. caeca* were recorded from two specimens of the salpid *Vitreosalpa gemini* Madin & Madin, 2004 in the surveyed area. This is the first information about the symbiotic relationship of *V. caeca*. This species is known from the north-western sector of the Pacific Ocean (Vinogradov *et al.*, 1996). There was no previous information about the symbiotic associations of this species.

Vibilia chuni Behning & Woltereck, 1912

Remarks: As *V. armata*, this species has been reported as a symbiont of different salps species (Madin & Harbison, 1977), but it has not been previously found as a symbiont of *Cyclosalpa affinis* Chamisso, 1819, thus expanding its known host range.

Vibilia viatrix Bovallius, 1887

Remarks: In this survey it was found as a symbiont of the salp *P. confoederata* (Forskål, 1775). As some of its congeners, this

Fig. 1. The hyperiid *Mimonectes sphaericus* as a symbiont of the medusa *Bythotiara* sp., from off California, photo *in situ* obtained during the survey.

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hyperiid has been previously reported from different salps, as summarized by Lavaniegos & Ohman (1999). Reported hosts include *P. confoederata* (Gasca *et al.*, 2007) so this association is confirmed herein with new observations.

Vibilia sp.

A few unidentifiable juvenile specimens of this genus were recorded from the salps *Cyclosalpa affinis* and *Pegea confoederata*.

Family PARAPHRONIMIDAE
Paraphronima gracilis Claus, 1879

Remarks: A single specimen of *P. gracilis* was observed in association with the siphonophore *Rosacea cymbiformis* (delle Chiaje, 1830), thus expanding the known host range of this amphipod. This hyperiid has been recorded in the California area as a symbiont of the siphonophore *Sphaeronectes gracilis* (now accepted as *S. koellikeri* Huxley, 1859) and the salp *Ritteriella picteti* (Lavaniegos & Ohman, 1999). The other species of the genus, *P. crassipes* is known only as a symbiont of siphonophores including *Rosacea cymbiformis* (Laval, 1980).

Family PHRONIMIDAE
Phronima atlantica Guérin-Méneville, 1836

Remarks: In this survey this species was found as a symbiont of *Salpa fusiformis*, as previously reported by Laval (1980). A single specimen was found in a salp barrel (Laval, 1980), the usual host of members of this genus.

Family HYPERIIDAE
Hyperia medusarum (Müller, 1776)

Remarks: During this survey this species was found as a symbiont of two medusae, *Solmissus* sp. and *Leuckartiara octona* (Fleming, 1823). The only previous record of this hyperiid species in Monterey Bay was as a symbiont of another medusa: *Mitrocoma cellularia* (Gasca *et al.*, 2007). This species has been known as a host of several other species of medusae worldwide (von Westernhagen, 1976; Thurston, 1977; Brusca, 1981; Buecher *et al.*, 2001). *Solmissus* sp. (Fewkes, 1886) is among the most common hydromedusae in Monterey Bay.

Hyperia sp.

Remarks: Several unidentifiable juvenile specimens of *Hyperia* were found on several hosts in associations not previously known among species of the genus, including records on the ctenophore *Hormiphora californensis* (Torrey, 1904), an undescribed mertensiid ctenophore, the hydromedusa *Haliscera bigelowi* (Kramp, 1947) and also on an unidentified radiolarian. The finding of adult specimens will allow an accurate record of these associations.

Hyperoche mediterranea Senna, 1908

Remarks: An ovigerous female was found on the ctenophore *Hormiphora californensis*, and a juvenile on the ctenophore *Leucothea pulchra* Matsumoto, 1988; adults and juveniles were obtained from an undescribed pandeid medusa. This is the first record of this association with these ctenophores and Pandeidae. Hitherto, it was also recorded from the ctenophore *Lampea pancerina* (Chun, 1879) (Laval, 1980; Hoogenboom & Hennen, 1985) and from *Pleurobrachia bachei* A. Agassiz, 1860, as previously recorded by Hirota (1974), Flores & Brusca (1975). This species has been previously recorded as a symbiont mainly of ctenophores but it has also been recorded from medusae and siphonophores (Steuer, 1911; Hirota, 1974; Laval, 1980).

Hyperoche shihi Gasca, 2005

Remarks: This is the second record of this species after its original description. It was first found in a symbiotic association with the mesopelagic medusa *Chromatonema erythrogonon* (Bigelow, 1919) (Gasca, 2005). During this survey it was found on *Aegina citrea*, thus expanding the known host range of this hyperiid. The hyperiid was crawling outside the umbrella.

Family IULOPIDIDAE
Iulopis lovenii Bovallius, 1887

Remarks: In this survey *I. lovenii* was recorded as a symbiont of the medusa *Aegina citrea*, representing an expansion of its known host range; hitherto, it was found in association with the medusa *Pandea conica* (Quoy & Gaimard, 1827) (Harbison *et al.*, 1977).

Iulopis mirabilis Bovallius, 1887

Remarks: As reported here in reference to its congener *I. lovenii*, this species was found on the medusan host *Aegina citrea* and also on another two medusae of the genus *Tima.* There are no previous data about the symbiotic associations of *I. mirabilis*.

Family PRONOIDAE
Eupronoe minuta Claus, 1879

Remarks: This is the first report of *E. minuta* as a symbiont of the siphonophore *Rosacea cymbiformis*. This species has been recorded with the siphonophores *Agalma elegans* (Harbison *et al.*, 1977), *Apolemia uvaria* and *Sulculeolaria quadrivalvis* (Laval, 1980) and also from a salp (Spandl, 1927).

Family ANAPRONOIDAE
Anapronoe reinhardti Stephensen, 1925

This is the second record of this species in the Monterey Bay as a symbiont. It was first reported by Gasca *et al.* (2007) from the same undescribed physonectid siphonophore.

Family LYCAEIDAE
Simorhynchotus antennarius (Claus, 1871)

During this survey it was found as a symbiont of the abundant medusa *Liriope tetraphylla* (Chamisso and Eysenhardt, 1821), which is closely related to *Geryonia*, thus expanding the known host range of this amphipod. This species has been reported only in association with the medusa *Geryonia proboscidalis* (Laval, 1980) and with the siphonophore *Sulculeolaria quadrivalvis* (Lima & Valentin, 2001).

Family TRYPHANIDAE
Tryphana malmi Boeck, 1870

Remarks: During this survey, an adult female of *T. malmi* was found from the medusa *Solmisus incisa* (Fewkes, 1886); its marsupium contained several larval individuals. In addition, an egg-bearing female was found as a symbiont of an

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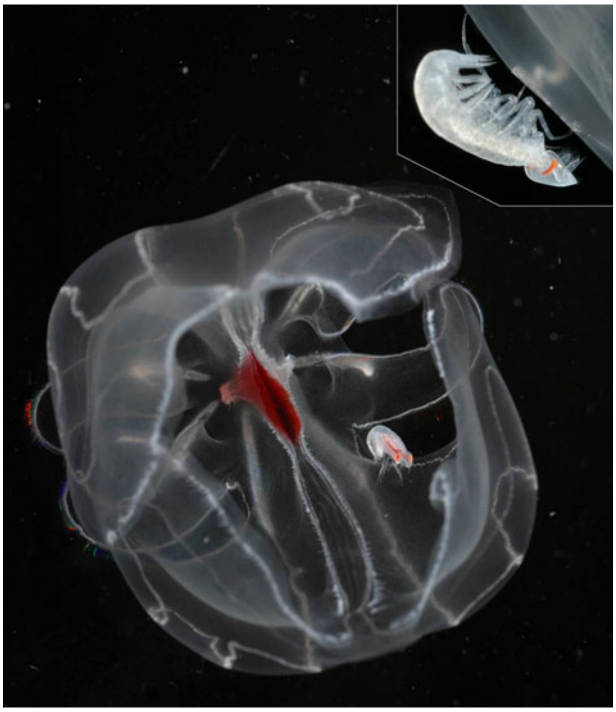

Fig. 2. Juvenile of the hyperiid *Glossocephalus* sp. found on the ctenophore *Bathocyroe fosteri* from off California, *in vivo* photo obtained during the survey.

undescribed physonectid siphonophore and of *Physophora hydrostatica* Forskål, 1775. This amphipod has been found previously in Monterey Bay as a symbiont of the lepto-medusa *Mitrocoma cellularia* and the narcomedusa *S. incisa* (Gasca *et al.*, 2007). This is the third finding of the species in association with gelatinous zooplankton and the second time it has been found in association with a siphonophore, after a record by Laval (1980) from the abylid *Ceratocymba sagittata* in the north-east Atlantic. Apparently, this species tends to associate with both medusae and siphonophores. *Tryphana malmi* is considered an anti-equatorial species, distributed in the epipelagic layer (Vinogradov *et al.*, 1996).

Family BRACHYSCELIDAE
Brachyscelus sp.

Remarks: An unidentifiable juvenile individual of this genus was observed in the narcomedusa *Solmisus incisa*. Members of *Brachyscelus* are frequently found as symbionts of medusae and salps (Laval, 1980).

Family OXYCEPHALIDAE
Oxycephalus clausi Bovallius, 1887

Remarks: During this survey a female with eggs and a few juvenile individuals of *O. clausi* were observed as symbionts of the ctenophore *Cestum veneris* Lesueur, 1813. This species has been known from other ctenophore species and also with thaliaceans (Madin & Harbison, 1977; Harbison *et al.*, 1978). In addition, several immature specimens of members of this family (*Oxycephalus* sp. and *Streetsia* sp.) were found in association with the ctenophore *Thalassocalyce inconstans* Madin & Harbison, 1978.

Glossocephalus sp.

Remarks: These specimens were found to represent an undescribed species of *Glossocephalus* that is currently in the process of description. During this survey it was recorded always as a symbiont of the ctenophore *Bathocyroe fosteri* Madin & Harbison, 1978 (Figure 2). The genus has been found associated with ctenophores only (Steuer, 1911; Krumbach, 1911; Harbison *et al.*, 1977, 1978; Laval, 1980).

Family PLATYSCELIDAE
Tetrathyrus forcipatus Claus, 1879

Remarks: Its finding in association with the gelatinous pteropod mollusc *Corolla spectabilis* Dall, 1871 in the present study represents the first record of a non-siphonophore host for this hyperiid. The pteropod is known to host at least two other species of hyperiids: *Lycaea bovalloides* (Harbison *et al.*, 1977) and *Streetsia steenstrupi* (Lavaniegos & Ohman, 1999). *Tetrathyrus forcipatus* has been recorded as a symbiont of two species of siphonophores: *Agalma clausi* and *Nanomia bijuga* (Harbison *et al.*, 1977).

DISCUSSION

Most of the symbiotic associations reported in the literature involve hyperiid species of the Infraorder Physocephalata (Laval, 1980). The same tendency was observed in this and previous works in the California area (Gasca & Haddock, 2004; Gasca *et al.*, 2007) as most hyperiids recorded herein belong to this group. It is also remarkable that more records of physocephalatous hyperiids are consistently being discovered as our sampling capabilities improve. Overall, associations in this Infraorder might be much more common than believed in the past. It is clear that these kinds of deep-water samples represent a unique opportunity to reveal details of these associations that are not available from traditional net plankton samplings.

Members of the family Phronimidae (Thiel, 1976, 2000) and Oxycephalidae (Gasca & Haddock, 2004) have been recognized among the few pelagic crustaceans for which maternal care has been reported. The mothers feed and keep the larvae within barrel-shaped salp tests after demarsupiation. *Oxycephalus clausi* takes care of its juveniles after they are demarsupiated in a ctenophore (see Gasca & Haddock, 2004). In this survey juveniles of this hyperiid were found as symbionts of the ctenophore *Cestum veneris*, thus supporting the notion that ctenophores are used for protection of immature individuals.

As noted by Gasca (2005), most symbiotic amphipods have been recorded as juveniles (males and females). It is less frequent to find gravid or larvae-bearing females, and adult males are rare. The same pattern was observed in this survey and suggests the relevance of the gelatinous zooplankters as an adequate substratum to complete the life cycle of the hyperiid symbionts; it is probable that most of the vulnerable growth phases of many species occur during this symbiotic association. In some species adults remain in the host together with their offspring. Laval (1980) stated that males are probably free-living and aggregate under certain circumstances (moon phases); the non-ovigerous adult females are deemed more independent than juvenile or egg-carrying females. In some species, such as *Hyperoche medusarum*, there is evidence

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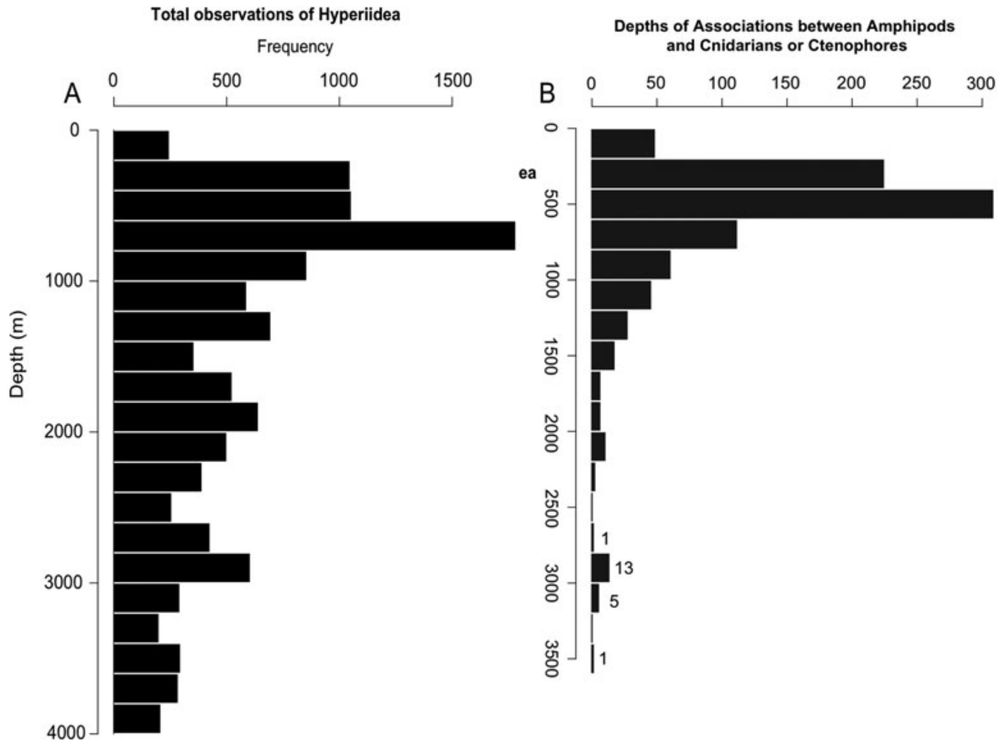

Fig. 3. Histograms of depth of observations from the MBARI video database, 1989–2014. (A) Total number of observations of Hyperiidea with depth. (B) Number of *in situ* observations of amphipods seen in direct association with planktonic cnidarians and ctenophores.

suggesting that the same host could be 'used' by different generations. Juveniles at different developmental stages were found coexisting in the same host individual with gravid females (Laval, 1980; personal communication).

The findings of this survey increase the previous knowledge about these symbiotic associations both in the Monterey Bay area and worldwide. In this survey we provide data of 51 certain records of hyperiid/gelatinous zooplankton associations, of which 34 are new and 16 have already been observed in the area. The depth distributions we obtained (Figure 3A, B, Table 2) show that amphipod associations with gelatinous zooplankton continue down below 2000 m, and in fact, amphipods are known to be some of the deepest-living organisms (e.g. Kobayashi *et al.*, 2012). We expect that additional surveys in the bathypelagic zone will produce many more examples of new species and new symbiotic associations.

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