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CLEANER SHRIMP (CARIDEA: PALAEMONIDAE) ASSOCIATED WITH SCYPHOZOAN JELLYFISH

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PERICLIMENES PAIVAI
CARIDEA
SHRIMP
JELLYFISH
COMMENSALISM

ABSTRACT. – Shrimp are found in association with many hosts (sponges, anthozoans, mollusks, echinoids, ascidians and fish). Shrimp are rarely observed in association with jellyfish. The interaction between the cleaner shrimp *Periclimenes paivai* and jellyfish is poorly known, with only one published report for Brazilian waters. We add new information about this association, based on field and laboratory observations. Shrimp were collected from three locations on the coast of São Paulo State (Cananéia, Santos and São Sebastião) and from two species of scyphozoan medusae: *Chrysaora lactea* and *Lychnorhiza lucerna*. We classify the association as facultative commensalism, since the shrimp gain protection and probably feed on mucus produced by the jellyfish. The maximum carapace length of the shrimp collected was 9.2 mm. Medusa bell diameter ranged between about 10 and 19 cm for *C. lactea* and between 4.5 and 25 cm for *L. lucerna*. We also provide a list of records of *Periclimenes* in association with different scyphomedusae, and additional information on the size and coloration of *P. paivai*.

INTRODUCTION

Among aquatic crustaceans, a wide variety of taxa including amphipods, copepods, crabs, isopods and shrimps have been described as symbionts of macroinvertebrates around the world. Many crustacean species show different kinds of association with their benthic hosts, ranging from parasitism to mutualism (e.g., Thiel & Baeza 2001). For instance, the first reported eusocial marine invertebrate, *Synalpheus regalis* Duffy, 1996, is a small shrimp that lives in close association with large tropical sponges (Duffy 1996), while other shrimps such as *Palaemonella rotumana* (Borradaile, 1898) or *Periclimenes elegans* (Paulson, 1875) can be found in many anthozoan species, as well as free-living (Bruce 1970, Chace & Bruce 1993, Marin *et al*. 2004), showing a weak linkage or independence from their facultative hosts.

Most cases of crustacean symbiosis have been reported in the benthic environment, with the exception of parasitic copepods, a diverse group containing many species with pelagic hosts (Boxshall & Halsey 2004). Various crustaceans also occur in association with pelagic cnidarians, such as copepods (Humes 1953, Browne & Kingsford 2005), cirripeds (Pagès 2000), hyperiid amphipods (Laval 1980, Condon & Norman 1999), isopods (Moreira 1972, Nogueira Jr. & Silva 2005), mysids (Martin & Kuck 1991), caridean shrimps (Marliave & Mills 1993, Moore *et al*. 1993) and brachyuran crabs (Corrington 1927).

Pontoniinid shrimps are commonly found associated with a wide range of benthic hosts: ascidians, bivalves, crinoids, echinoids, gorgonians, nudibranchs, scleractinian corals, sea anemones and sponges (Chace 1969, Omori *et al*. 1994, Spotte *et al*. 1994, Udekem D'Acoz & Wirtz 2002). More rarely, these shrimps have been observed in association with pelagic organisms such as jellyfish (Chace 1969, Bruce 1972, 1988, Berggren 1994).

The most extensive work on parasitism, symbiosis and commensalism with medusae was presented by Thiel (1976). The author listed different forms of associations between medusae and other organisms (e.g., Actiniaria, Cestoda, Nematoda, Trematoda, Turbellaria and a wide range of crustacean groups). However, nothing was mentioned about the shrimp genus *Periclimenes* Costa 1844.

At present, few published records exist concerning crustacean associations with medusae for the southwestern Atlantic coast. Zamponi (2002) recorded an association between *Libinia spinosa* (H. Milne-Edwards, 1834) (Brachyura, Majidae) and the scyphomedusa *Lychnorhiza lucerna* Haeckel, 1880 from an estuary in Argentina. Nogueira Jr. & Haddad (2005) provided the incidence of the association and insights into the life cycle of another majiid species, *Libinia ferreirae* Brito Capello, 1871, and its relationship with *L. lucerna*. Nogueira Jr. & Silva (2005) reported the occurrence of four parasitic isopods

on jellyfishes from the southern coast of Brazil.

The genus *Periclimenes* contains more than 175 species of small carideans, commonly known as "cleaner shrimps". The species *P. paivai* Chace, 1969 was described based on specimens collected at Cananéia and Ubatuba (on the southern and northern coasts of São Paulo state, respectively), found in association with a medusa identified as *Mastigias* sp., collected in Ubatuba (Chace 1969). Actually, the medusa referred to by Chace is *Phyllorhiza punctata* von Lendenfeld, 1884, at that time known from the area as *Mastigias scintillae* Moreira, 1961 (see Silveira & Cornelius 2000, Morandini *et al*. 2005). However, the distribution and ecological associations of the shrimp species are not clear: some authors reported the shrimp from the sea bottom at about a meter depth or less (Ramos-Porto & Coelho 1990) or associated with macroalgae in trawls (G. Bond-Buckup 2006, personal communication). This is the second record of *P. paivai* accompanying jellyfish.

Some species of *Periclimenes* were already reported from the Brazilian coast: *P. anthophilus* Holthuis & Eibl-Eibesfeldt, 1964 from Fernando de Noronha archipelago and the states of Ceará and Rio Grande do Norte; *P. longicaudatus* (Stimpson, 1860) from the states of Pará to Bahia; *P. magnus* Holthuis, 1951 from the Fernando de Noronha archipelago and Rio Grande do Norte; *P. paivai* from the states of São Paulo and Santa Catarina; and *P. yucatanicus* (Ives, 1891) from Bahia (Ramos-Porto & Coelho 1990, Young 1998, Coelho Filho 2006, G. Bond-Buckup, personal communication). The species *P. iridescens* Lebour, 1949 is also known from the northeast coast of Brazil (G.A.S. de Melo, personal communication), and *Kemponia americana* (Bruce 2004), once known as *P. americanus*, from the states of Amapá to Pernambuco and Espírito Santo. Nevertheless, *P. paivai* was, up to now, the only one of these species found on scyphozoan hosts.

The original description of *P. paivai* by Chace (1969) lacks information on the animal coloration, because it was based on preserved specimens. Variable characters such as the number of teeth on the dorsal and ventral margins of the rostrum were overlooked because only one male and eight ovigerous females were available for analysis. Herein we present information on these characters, based on 48 specimens, and discuss the interactions of *P. paivai* and its scyphozoan hosts.

METHODS

We studied the shrimps associated with two scyphomedusae species from three different localities on the coast of São Paulo state (Fig. 1). Cleaner shrimp associated with the discomedusae species *Lychnorhiza lucerna* (Fig. 2A) and *Chrysaora lactea* Eschscholtz, 1829 (Fig. 2B) were collected near the surface at Cananéia (from 1999-2002, and on July 2006) (Fig. 1A).

Shrimp were also captured in association with *L. lucerna* in the São Sebastião Channel on July 2004 (Fig. 1C), and in Santos Bay on August 2005 (Fig. 1B). The shrimp were removed from the medusae with the aid of a forceps or by gently shaking the jellyfish, and were preserved in 4% formaldehyde solution in seawater or 70 % ethanol.

The medusae were collected in the Cananéia estuary, with a large plastic bucket and hand nets. They were transferred to an aquarium for further observation. Some of them were kept alive in an aquarium, and some were preserved in 4 % formaldehyde in seawater for identification. The shrimp were observed alive by stereomicroscope. The diameter of the umbrella of the medusae was measured with a plastic ruler (in cm).

We determined the sex of the shrimp by the presence of the *appendix masculina*, and measured total body (from the end of the telson to the tip of the rostrum) and carapace length (from the tip of the rostrum to the posterior border of the carapace)

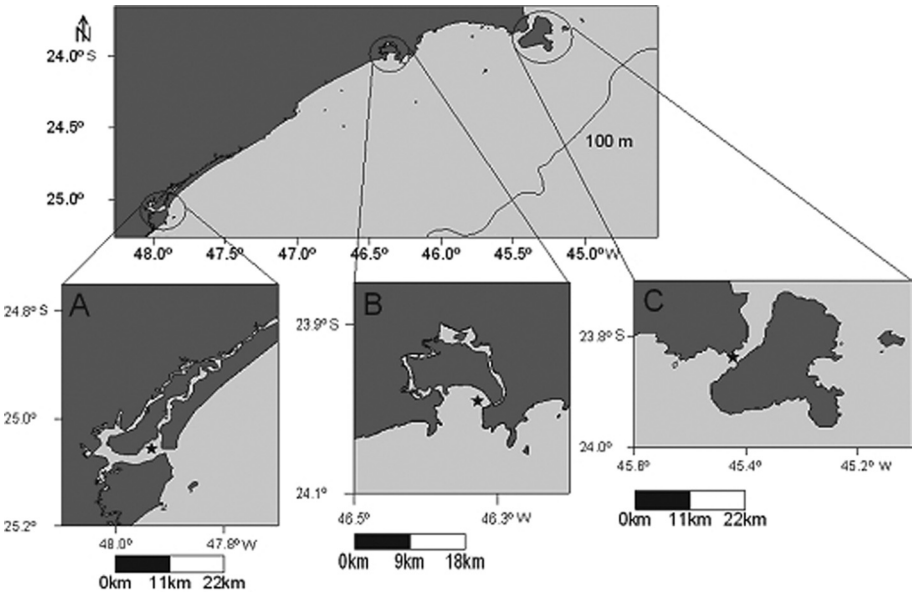

Fig. 1. - Map of the coast of São Paulo state, showing the three sites where the animals were collected. A: Cananéia, B: Santos Bay, C: São Sebastião Channel.

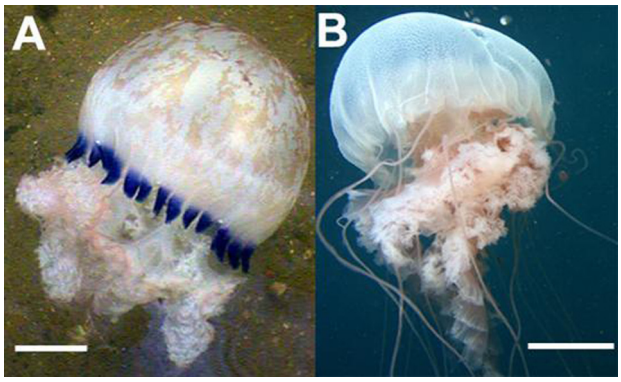

Fig. 2. - Host scyphozoan medusae of the cleaner shrimp *Periclimenes paivai*. **A**: *Lychnorhiza lucerna* (photograph by F. L. da Silveira). **B**: *Chrysaora lactea* (photograph by O. M. P. Oliveira). Scale = 5 cm.

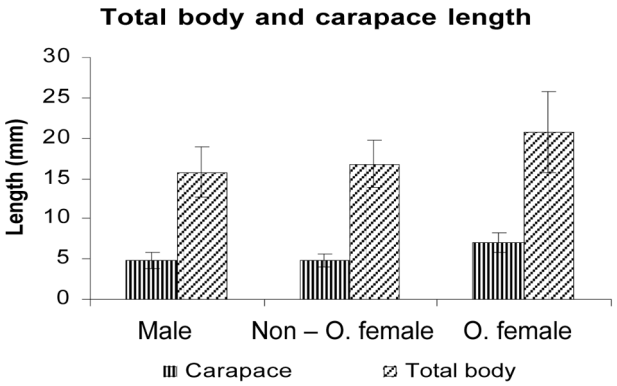

Fig. 3. - Variation of total body and carapace length for *Periclimenes paivai*. The values represent the means. O. = ovigerous.

using a digitizing tablet (Summa Sketch). The scyphozoans were identified based on Morandini *et al*. (2005), and Chace (1969) and Corrêa (1977) for the shrimp.

Voucher specimens of the medusae were deposited in the cnidarian collection of the Museu de Zoologia of the Universidade de São Paulo (MZUSP) (*C. lactea* MZUSP 342 and 824; *L. lucerna* MZUSP 350, 813 and 821). Selected specimens of *Periclimenes paivai* were deposited in the MZUSP crustacean collection under number MZUSP 17360.

The estuarine complex of Cananéia-Iguape (Fig. 1A) is a well-preserved region of the coast of the state of São Paulo. Mangrove areas and large freshwater influents contribute to high concentrations of nutrients and organic matter (Schaefer-Novelli *et al*. 1990). Santos Bay (Fig. 1B) is a densely occupied coastal region, and harbours the largest shipping port in Brazil. High concentrations of nutrients, organic matter, heavy metals, detergents and petroleum derivatives are found in the bay (Abessa *et al*. 2005). São Sebastião Channel (Fig. 1C) is a coastal region with relatively low freshwater inflow and organic matter (compared to Cananéia-Iguape) from the continent and São Sebastião Island. During the summer, larger amounts of organic matter are released into the channel.

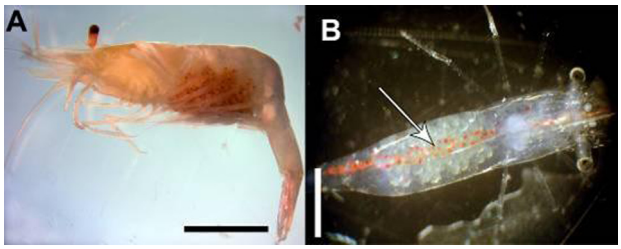

Fig. 4. - Photographs of *Periclimenes paivai* under a stereomicroscope. **A**: Preserved specimen in lateral view. **B**: Living specimen in dorsal view, showing the chromatophores. Scale = 5 mm.

RESULTS

A total of 48 cleaner shrimp individuals in association with jellyfish were collected, from three localities: 33 from Cananéia, 9 from Santos Bay and 6 from São Sebastião. Of 48 shrimp, 14 were male, 6 were non-ovigerous females, 24 were ovigerous females and 4 were not sexed (juveniles).

The carapace length of 42 animals was determined, and ranged from 3.4 to 9.2 mm. Ovigerous females were the largest animals (4.3 to 9.2 mm; mean 7.1 ± 1.2 mm). Males and non-ovigerous females were similar in size (3.4 to 6.1 mm; mean 4.8 ± 1 mm for males and 3.7 to 5.7 mm; mean 4.8 ± 0.8 mm for non-ovigerous females). Total body length was 20.8 ± 5 mm for ovigerous females ($n = 23$), 16.8 ± 2.9 mm for non-ovigerous females ($n = 5$) and 15.8 ± 3.2 mm for males ($n = 14$) (Fig. 3).

The information necessary for a better understanding of the interaction (such as location and date of sampling, medusae species and bell diameter and number, sex and size of associated shrimp) is provided in Table I. Data are missing for the number of cleaner shrimp in association with *Chrysaora lactea* and in some cases with *Lychnorhiza lucerna* at Cananéia during 1999-2000. One to nine shrimp in association with the jellyfish were found on the six cases described. Ovigerous females were generally more common than non-ovigerous females or males.

Laboratory observations: In the aquarium, most cleaner shrimps (Fig. 4 A) left the medusae after about 30 to 60 minutes. Medusae carried *Periclimenes paivai* on their subumbrellar surfaces, or rarely on the exumbrella. One to four shrimp were observed per jellyfish, "walking" on the subumbrellar surface and oral arms. These cleaner shrimps are transparent and bear two dorsal rows of chromatophores, from the anterior border of the antennal scale to the telson and uropods, and on the eyestalk (Fig. 4 B). The *P. paivai* specimens manipulated, with their oral appendages, the mucous material that collects around the oral arms of the medusa, and were probably feeding on it.

A wider variation in the number of teeth on the dorsal and ventral margins of the rostrum was found in this study. The number of dorsal teeth ranged from 7 to 10, and on the ventral margin from 0 to 2 in the 42 shrimps analysed. According to Chace (1969), these structures

Table I: Location, date of sampling and bell diameter of *Lychnorhiza lucerna* hosting individuals of *Periclimenes paivai*. The number, sex and carapace length of the commensal shrimp are provided. M. D. = missing datum; *: Ovigerous female.

Location	Date	Host size (bell diameter, cm)	No. of shrimp	Male (mm)	Female (mm)
Cananéia	19/072006	11.9	4	5.15	5.33
				-	5.73
				-	7.03*
Cananéia	19/072006	8	3	M. D.	M. D.
Cananéia	02/14/2000	M. D.	1	-	6.99*
Cananéia	12/15/1999	M. D.	7	6.124	5.59*
				-	6.42*
				-	6.77*
				-	7.04*
				-	7.52*
				-	9.15*
São Sebastião	11/25/2004	25	6	3.36	6.37*
				3.76	-
				4.18	-
				4.24	-
				4.64	-
Santos	08/15/2005	11	9	5.13	4.26
				M. D.	6.56*
				-	7.16*
				-	7.48*
				-	8.99*
				-	9.12*
				-	9.19*

ranged from 8 to 10, and 1 or rarely 2, respectively. Only two individuals lacked teeth on the ventral margin of the rostrum in this study, one male (4.2 mm carapace length) and one ovigerous female (6.3 mm carapace length).

DISCUSSION

Only a few species of the genus *Periclimenes* have previously been observed in association with scyphozoan jellyfishes. Half of the observations were made for species of the genus *Cassiopea* Péron & Lesueur, 1810, which are medusae with benthic habits (see Table II).

There are several reasons why this association is documented. Sampling gear, such as plankton nets, tends to damage the scyphozoans, and the shrimp may abandon their host during the trawl. Plankton nets may also create artefacts, since many organisms are compressed on the sieve, or cause avoidance (Sameoto *et al*. 2000). Moreover, the shrimp rapidly abandons the host, as we observed in the laboratory. Sampling must be done with care, using large containers to prevent the shrimp from leaving the medusae.

Specimens of *P. paivai* are transparent, which makes them difficult to observe on the jellyfish. The original species description (Chace 1969) gave no information about the colour of live animals, or about the rows of chromatophores; this is the first observation of these pigments for this species (see Fig. 4B) as well as the transparency of the living organisms. Most species of *Periclimenes* are coloured or semi-transparent; a few species are almost transparent, such as *P. inornatus* Kemp, 1922, *P. ornatellus* Bruce, 1979 (Bruce 1979 a, b) and *P. paivai*. Rows of white and red chromatophores were also described by Bruce (1979 b) for some species, e.g., *P. brevicarpalis* Schenkel, 1902.

The carapace length in the original description was based on only nine specimens. In the present study, this length was considerably larger and showed a wider amplitude. Ovigerous females were larger than the holotype specimen (Chace 1969). The carapace length of females was greater than that of males, as found for *P. anthophilus* (1.9 ± 0.15 mm for males and 2.16 ± 0.38 mm for females) and *P. ornatus* (Nizinski 1989, Omori *et al*.1994).

A wider variation in the number of teeth on both dorsal and ventral margins of the rostrum is given, because of

Table II. List of *Periclimenes* species found in association with scyphozoan hosts worldwide. * Host observed in the present study.

Species	Host	Reference	Locality
P. holthuisi	*Cassiopea andromeda*? Forskål, 1775	Bruce (1972)	Hong Kong, Zanzibar harbor, Tanzania
P. nomadophila	*Rhopilema nomadica* Galil, 1990	Berggren (1994)	Portuguese Island and Delagoa Bight, Mozambique
P. tonga	*Cassiopea* sp.	Bruce (1988)	Nuapapu Island, Tonga
P. paivai	*Chrysaora lactea**, *Lychnorhiza lucerna**, *Phyllorhiza punctata*	Chace (1969)	Cananéia estuary, Santos Bay, Guarujá, Ubatuba, São Sebastião Channel, Brazil
P. pedersoni	*C. xamachana* Bigelow, 1892	Criales (1984)	Santa Marta region, Colombia
P. yucatanicus	*C. xamachana*	Criales & Corredor (1976), Criales (1984)	Santa Marta Bay, Colombia

the larger number of specimens analysed here. This variation is not related to sex, but to the size of animals. For instance, the only specimens that had 10 teeth on the dorsal margin of the rostrum were the two largest ovigerous females, which also had two teeth on the ventral side. The number of teeth on the ventral margin of the rostrum is an important species diagnostic character within this genus in identification keys (Chace 1972, Corrêa 1977). This character should be used with care in identifying this species, because it is subjected to variation.

The closeness of the association between these cleaner shrimps and their different hosts is poorly known, although it is understood for some other species. *Periclimenes brevicarpalis* is an obligate symbiont in sea anemones (Fautin *et al*. 1995). *Periclimenes ornatus* is also an obligate symbiont of the sea anemone *Parasicyonis maxima* Wassilieff, 1908, as observed by Omori *et al*. (1994). Other authors found this animal associated with different actinian species (Suzuki & Hayashi 1977, Marin *et al*. 2004). *Periclimenes anthophilus* exhibited the same behaviour as *P. ornatus*: both species are restricted to the surrounding substrate that is within the reach of host's tentacles (Nizinski 1989).

The association described here between *P. paivai* and scyphozoan jellyfish seems to be common, because the shrimps were found on most medusae collected from different locations. The observations in the laboratory, where the shrimps left the medusae, can be explained by a facultative commensalism (Odum & Barrett 2004). When the mutual aspects become unfavourable, commensalism is not more consolidated and one of the organisms leaves the association. This is very common in other kinds of associations (e.g. sea anemones and fish) (Elliot 1992). This phenomenon probably occurs for certain shrimp species where several hosts were identified, or for species found in association with its hosts, but also observed in diverse habitats on the sea bottom (Bruce 1970, Chace & Bruce 1993, D'Acoz & Wirtz 2002, Marin *et al*. 2004). The reports from other authors of *P. paivai* caught on the bottom (Ramos-Porto & Coelho 1990) support our hypothesis.

About one to nine shrimps were observed on the same jellyfish, probably forming unstructured aggregations within the jellyfish. This behaviour was noticed by Nizinski (1989) and Sargent & Wagenbach (1975) for *P. anthophilus*, which colonizes the surface of the anthozoan *Condylactis gigantea* (Weinland, 1860) in small groups. The same was observed for other species that colonize other anthozoan hosts, such as *P. pedersoni* Chace, 1958 (Limbaugh *et al*. 1961), *P. antipathophilus* Spotte, Heard & Bubucis, 1994 (Spotte *et al*. 1994) and *P. patae* Heard & Spotte, 1991 (Heard & Spotte 1991).

Our suggestion is based on the information provided in Table I, where only one of the six cases showed fewer than 3 shrimps per host. Female shrimps are probably more abundant than males in these aggregations, but a better sampling effort is needed to validate this hypothesis. Unfortunately, there are missing data for the number of shrimps per host, host size, and shrimp sex and size in material collected in Cananéia between 1999 and 2002. It is not possible to correlate the size of the medusae with the number of shrimps (only four cases contained all the necessary information). However, our data suggest that the number of *P. paivai* may not be related to the size of *Lychnorhiza lucerna*. Data were gathered from different collectors and sample series, which may explain some of the variations in the results.

Dispersion, feeding and predator avoidance may be advantages for these cleaner shrimps while they are associated with the medusae. The distribution of *Lychnorhiza lucerna* is known (Morandini *et al*. 2005), and the species is often found in estuaries during high tide. This could be a form of transport for the shrimp from different environments on the inner continental shelf. Dispersion of the hatched larvae may also be an advantage, since 24 out of 44 shrimps for which sex was determined were ovigerous

females. Mating may also occur inside the host, since both sexes and ovigerous females were found in several occasions. The reproductive season of *P. paivai* is not known, but probably occurs year-round, as for *P. ornatus* (Omori *et al*. 1994) and *P. americanus* (Williams 1984), since ovigerous females were found in every month for which samples were available (February, August, September, November and December). In this case, commensalism would be a reproductive advantage, a secure spot for mating and maintaining the aggregations.

Juvenile shrimps may be excluded or expelled by adults from the jellyfish, since only 4 out of 48 shrimps were not adults. This behaviour is common for *Periclimenes ornatus* in association with sea anemones (Omori *et al*. 1994), and would explain the low incidence of younger individuals within the aggregations. It was not possible to observe the existence of territoriality or aggressive behaviours of the shrimps in this study, as observed for a few species such as *P. pedersoni* (Mahken 1972).

Our observations also suggest that *P. paivai* may feed on mucous aggregates produced and attached to the medusae oral arms, since the animals were seen manipulating the material with their pereiopods and cephalic appendages. Feeding on the host tissue (tentacles) was previously documented for *P. holthuisi* and *P. brevicarpalis* associated with sea anemones (Khan *et al*. 2004).

Predation pressure may be lower during the association, since this rhizostome species is a large-sized jellyfish (umbrella diameter is almost 30 cm), providing a habitat "free" of predators. All the medusae collected at Cananéia during 2006 were healthy, and were returned to the sea after two days in the aquarium. The association probably would not harm *L. lucerna*, although it is not clear if the medusae would derive any benefit from this interaction. Jellyfish do not seem to be stressed by carrying the shrimp, and the hitchhikers, being small, may not cause the medusa to spend more energy while swimming.

The mystery of how the association begins remains unsolved. The interspecific and intraspecific encounter rates, switching among different host individuals, time of contact and duration of the "ride" are unknown.The first contact probably occurs when the medusae reach the sea bottom or when the planktonic juveniles of *P. paivai* encounter the medusae. All the medusae were collected near the surface, in less than a meter deep; sampling at different depths may add information about the initial interaction between the species.

Sampling younger medusae may also be useful to determine the duration of the interaction. *In situ* observations using scuba diving devices would also be useful for gathering information about the interaction between these species in the environment.

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