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(Decapoda, Epialtidae) in the Río de la
Plata (Argentina–Uruguay)*

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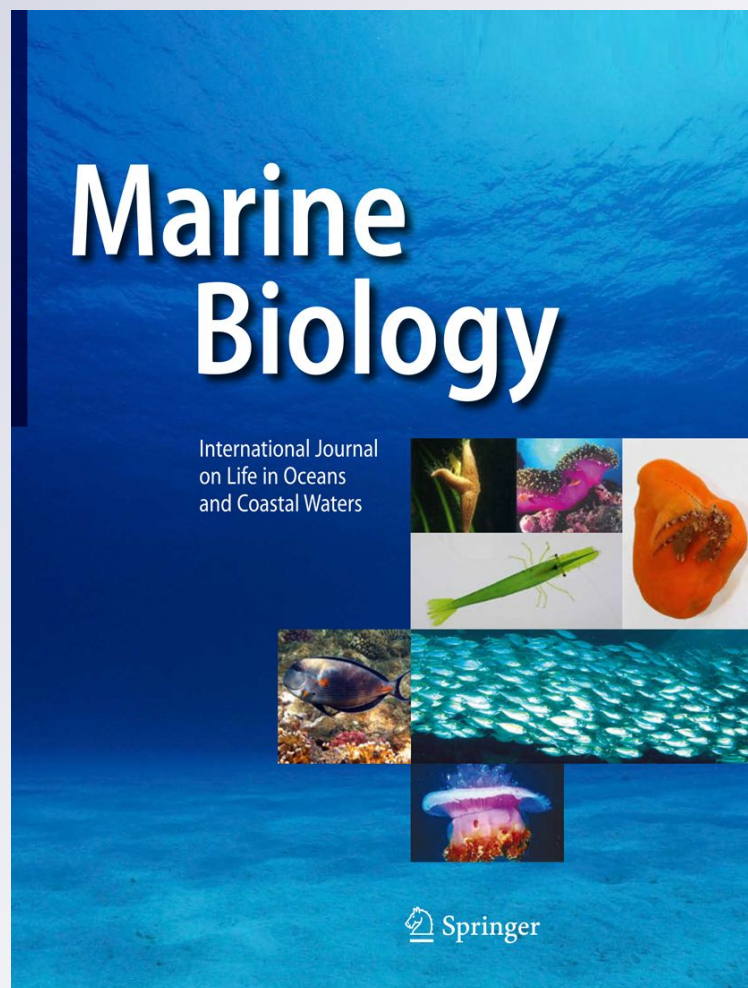
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The symbiotic relationship between *Lychnorhiza lucerna* (Scyphozoa, Rhizostomeae) and *Libinia spinosa* (Decapoda, Epialtidae) in the Río de la Plata (Argentina–Uruguay)

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Abstract Herein, we characterize a symbiotic relationship between the scyphomedusa *Lychnorhiza lucerna* and the decapod crustacean *Libinia spinosa* in Río de la Plata, South America. Of 843 specimens of *L. lucerna* examined during the study, 69 (8.2 %) hosted *L. spinosa* within sub-genital spaces. The broad spatial and temporal scale of the study, together with the large number of observations made, confirm an association between the two species. Medusae having crab associates were mature and larger than those lacking such symbionts. Adult crabs of both sexes, as well as juveniles and soft-shell individuals, were found as associates of medusae. Analysis of crab stomach contents revealed the presence of nematocysts and copepod remains. Our results suggest that medusae provide protection and possibly access to food for crabs. Benefits related to transportation were not clear and need further evaluation. Crabs of *L. spinosa* may acquire their scyphozoan symbionts either as larvae planktonic stages or as adult crabs attaching to jellyfish when aggregating close to bottom.

Introduction

Many species of crustaceans have adapted to symbiotic relationships with other invertebrates (Rohde 2005).

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Associations between brachyurans and scyphomedusae have been widely documented in coastal and estuarine environments (see Table 1). In general, crabs are thought to benefit from enhanced mobility and shelter as a result of such associations (Corrington 1927; Vaz Ferreira 1972; Nogueira and Haddad 2005; Towanda and Thuesen 2006). Moreover, some authors have suggested that crabs may also find ready access to food (Vaz Ferreira 1972; Towanda and Thuesen 2006), in some cases preying on medusae (Jachowski 1963; Phillips et al. 1969). In such associations, larval, juvenile, and adult crabs usually occur with medusae, suggesting varied benefits to each of the life stages. As for medusae, potential advantages seem unlikely (Corrington 1927), although a majority of reports indicate that medusae are not damaged by crabs. Only one study (Towanda and Thuesen 2006) suggests that the presence of crabs may increase predation on medusae. However, these interactions have been characterized with different levels of detail, and speculation about such associations in many cases is not based on empirical evidence. Additionally, different criteria have been adopted to characterize the association in relation to costs and benefits experienced by both partners, for example, commensalism (Corrington 1927; Graham 1994), exploitation (Suzuki 1965), kleptoparasitism (Towanda and Thuesen 2006), and phoresy (Ohtsuka et al. 2009).

In the Southwest Atlantic, associations between medusae and crabs, and in particular between crabs of the genus *Libinia* and medusae of the genus *Phyllorhiza* and *Lychnorhiza* (Moreira 1961; Nogueira and Haddad 2005), have been reported with different levels of detail. The association between *Lychnorhiza lucerna* Haeckel, 1880 and *Libinia spinosa* Milne-Edwards, 1834 constitutes the only example known from Argentina (Mianzan et al. 1988; Zamponi 2002) and Uruguay (Vaz Ferreira

Table 1 Associations between scyphomedusae and brachyuran crabs reported in the literature (updated from Nogueira and Haddad 2005, Towanda and Thuesen 2006)

Scyphomedusae species	Crab species	Location/period	Characteristics of the relationship	References
	Epiplatidae crabs			
<i>L. lucerna</i>	<i>L. ferreirae</i>	Paraná State, Brazil/ throughout the year	Transport of larvae	Nogueira and Haddad (2005)
<i>Phyllorhiza punctata</i>	<i>L. ferreirae</i>	São Paulo, Brazil/ February–July	Crabs under the subumbrella	Moreira (1961)
<i>L. lucerna</i>	<i>L. spinosa</i>	Punta del Este, Uruguay/January– February	Dispersion of larvae and adults, crabs eat food particles collected by medusae	Vaz Ferreira (1972)
<i>L. lucerna</i>	<i>L. spinosa</i>	Mar Chiquita Estuary, Argentina/?	Crabs ingest food particles collected by medusae	Zamponi (2002)
<i>L. lucerna</i>	<i>L. spinosa</i>	Río de la Plata estuary, Argentina/January– May	Crabs gain protection and a source of food	This study
<i>Catostylus mosaicus</i>	<i>Libinia dubia</i>	??	Crabs in association with medusae	Coleman (1977) (cit after Browne and Kingsford 2005)
<i>Chrysaora quinquecirrha</i>	<i>L. dubia</i>	Mississippi, USA/ throughout the year	Crabs feed on medusae	Phillips et al. (1969)
<i>Stomolophus meleagris</i>	<i>L. dubia</i>		Crabs associated with medusae	Phillips et al. (1969)
<i>S. meleagris</i>	<i>L. dubia</i>	North Carolina, USA/ May–December	Crabs between medusae scapulets	Rountree (1983)
<i>Chiropsalmus quadrumanus</i>	<i>L. dubia</i>	Mississippi, USA/ throughout the year	Crabs on bell medusae	Phillips et al. (1969)
<i>S. meleagris</i>	<i>L. dubia</i>	North Carolina, USA/ early summer	Crabs feed on medusae tissue	Shanks and Graham (1988)
<i>S. meleagris</i>	<i>L. dubia</i>	South Carolina, USA/ May	Crabs gain shelter and transport	Corrington (1927)
<i>S. meleagris</i>	<i>L. dubia</i>	North Carolina/?	Common association, late larvae is believed to enter bell cavity medusae	Gutsell (1928) (cit after Towanda and Thuesen 2006)
<i>S. meleagris</i>	<i>L. dubia</i>	Florida, USA/March	In laboratory, crabs eat medusae, laboratory artifact?*	Tunberg and Reed (2004)
<i>Stomolophus</i> sp.	<i>L. dubia</i>	??	Adult on oral arms	Hyman (1940) (cit after Towanda and Thuesen 2006)
<i>Aurelia aurita</i>	<i>L. dubia</i>	Chesapeake Bay, USA/ August	Crabs feed on medusae tissue	Jachowski (1963)
	Portunidae crabs			
<i>C. quinquecirrha</i>	<i>Callinectes sapidus</i>	Chesapeake Bay, USA/ August	Juvenile crabs frequently cling the medusae subumbrella	Jachowski (1963)
<i>C. quinquecirrha</i>	<i>C. sapidus</i>	Mississippi, USA/ August	Crabs perch on exumbrella medusae	Phillips et al. (1969)
<i>Lobonema</i> sp.	<i>Callinectes</i> sp.	Gulf of Tehuantepec, Mexico/?	Larvae on medusae	Bieri (unpubl data) (cit after Towanda and Thuesen 2006)
<i>Rhopilema esculentum</i>	<i>Charybdis (Charybdis) feriata</i>	Sagami Bay, Japan/ October	Transport of juveniles crabs	Suzuki (1965)
<i>Rhopilema hispidum</i>	<i>Charybdis (Charybdis) annulata</i>	Palk Bay/June–July	Under the bell	Panikkar and Prasad (1952)
<i>R. hispidum</i>	<i>C. (Charybdis) feriata</i>	Thanh Hoa, Viet Nam/ April	Transport of juveniles crabs	Nishikawa et al. (2008)
<i>Mastigias</i> sp.	<i>C. (Charybdis) feriata</i>	Cirebon, Indonesia/ September	Transport of juveniles crabs	Nishikawa (pers obs) (cit after Ohtsuka et al. 2009)

Table 1 continued

Scyphomedusae species	Crab species	Location/period	Characteristics of the relationship	References
<i>S. meleagris</i>	<i>C. (Charybdis) feriata</i>	Hong Kong, China/?	Juveniles and adults cling to medusae oral arms	Morton (1989) (cit after Towanda and Thuesen 2006)
<i>Nemopilema nomurai</i> (as <i>Stomolophus nomurai</i>)	<i>C. (Charybdis) feriata</i>	Mirs Bay, Hong Kong, China/?	Juveniles and adults on subumbrella	Trott (1972) (cit after Towanda and Thuesen 2006)
<i>Versuriga anadyomene</i>	<i>C. feriata</i>	Pari Island, Indonesia/November	Crabs between medusa oral arms	Ohtsuka et al. (2010)
<i>Phacellophora camtschatica</i>	<i>Cancer gracilis</i>	Puget Sound, Washington, USA/May–October	Magalopa feed on medusa tentacles and organisms captured by the medusae. Juvenile and adults gain protection, transport and source of food	Towanda and Thuesen (2006)
<i>Aurelia labiata</i>	<i>C. gracilis</i>	Puget Sound, Washington, USA/May–October	In laboratory, crabs consume medusae	Towanda and Thuesen (2006)
<i>Chrysaora achlyos</i>	<i>Cancer</i> sp.	San Quentin, Baja California, Mexico, to Santa Monica Beach, California/July–September	Crabs gain dispersion and nourishment*	Martin and Kuck (1991)
<i>Chrysaora fuscescens</i> (as <i>C. melanaster</i>)	<i>Cancer</i> sp.	California/Monterey Bay, USA/?	Crabs gain dispersion	Graham (1989)
<i>C. fuscescens</i>	<i>C. gracilis</i>	California, USA/summer	Juvenile crabs attach to medusae	Cooper (pers obs) (cit after Larson 1990)
<i>C. fuscescens</i>	<i>C. gracilis</i>	Monterey Bay, California, USA/May–June	Megalopa and crabs gain dispersion, protection and feeding*	Graham (1994)
<i>Chrysaora colorata</i>	<i>C. gracilis</i>	NE Pacific, California, USA/?	Megalopa larvae and juveniles on medusae bell	Garth and Abbott (1980)
<i>Pelagia colorata</i>	<i>C. gracilis</i>	California, USA/?	Early stages of crabs on medusae	Wrobel and Mills (1998)

* Laboratory experiments and observations

? Not specified

1972). Occurrence of *L. lucerna*, one of the most frequent scyphomedusae in Argentina (Mianzan and Cornelius 1999) and its vicinity, is highly seasonal and restricted to the warmer months (late December–early May) (Schariti et al. 2008). The spider crab *L. spinosa* is common in the southwestern Atlantic from Espirito Santo State, Brazil, to Chubut Province, Argentina (Melo 1996; Boschi 2000). In Argentina, it is abundant, constituting one of the most frequent crab species in catches of bottom trawlers in the northern Argentine shelf (Boschi 1964) where it plays an important role in local marine food webs (Scelzo et al. 2002). Although the association between *L. lucerna* and *L. spinosa* has previously been described (Vaz Ferreira 1972; Mianzan et al. 1988; Zamponi 2002), those earlier studies provide only brief comments based on limited samples, and no information is given to distinguish symbionts from accidental occurrences.

The goals of this study were to confirm whether an association exists between the scyphozoan *L. lucerna* and the spider crab *L. spinosa* in the Río de la Plata estuary (Argentina–Uruguay) and to characterize the relationship across broad spatial and temporal scales. We sought to provide empirical evidence on potential costs and benefits for both species, thereby improving our understanding of medusa–crab associations.

Materials and methods

Medusae of *L. lucerna* were collected in the Río de la Plata estuary (35–36°S; 54–57°W) (Fig. 1) from January to May 2006 and from January to March 2007 using several different methods: demersal trawls, pair demersal trawling, gill nets, hand nets, and manual collection of specimens stranded on the beach. All medusae were measured across

Fig. 1 Spatial distribution of the medusa *L. lucerna* and the crab *L. spinosa* in the Río de la Plata estuary (35–36°S; 54–57°W) and nearby marine waters. Locations of trawls where medusae associated with crabs (gray dots) and without crabs (white dots) are shown, together with locations of free-living *L. spinosa* (crosses, from Giberto et al. 2004; Giberto 2008). Scale bar 50 km

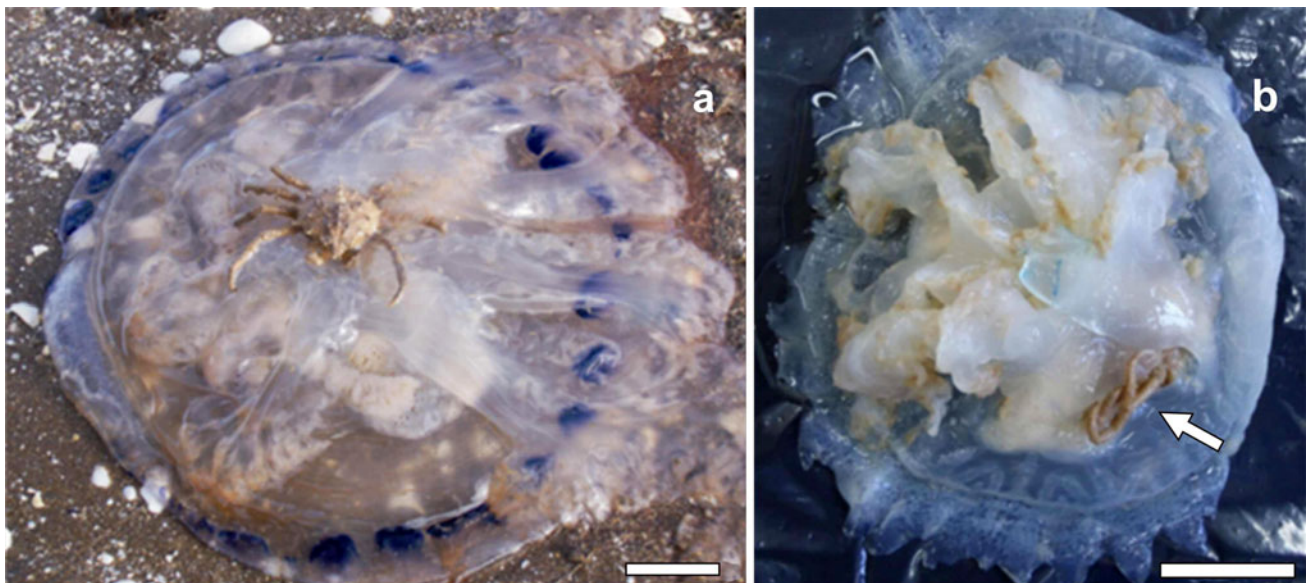
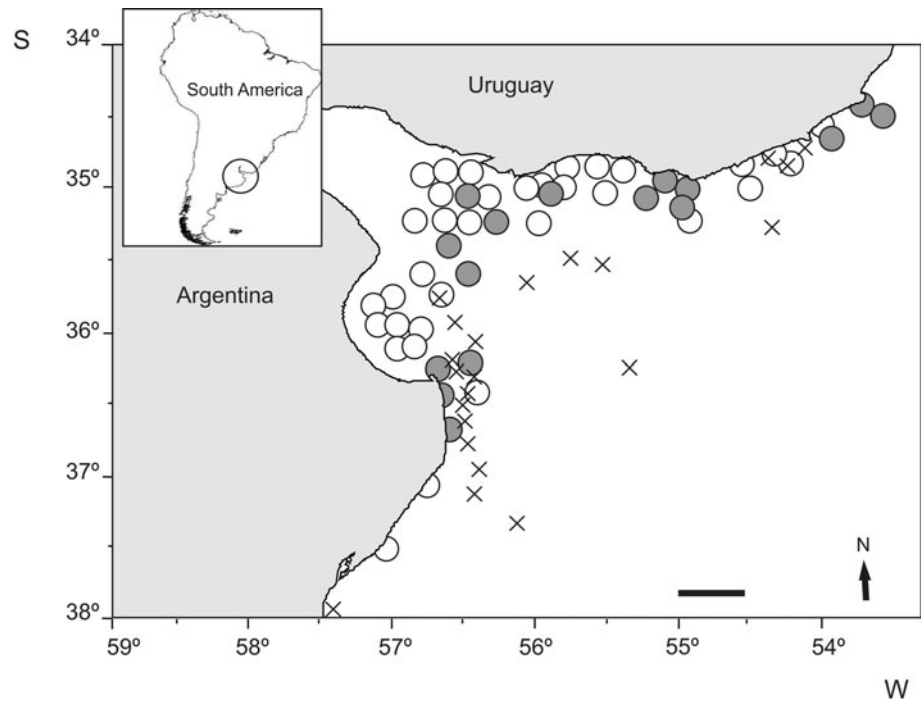


Fig. 2 A spider crab, *L. spinosa*, riding on a medusa of *L. lucerna*. **a** Stranded on San Clemente del Tuyú beach, Argentina. The specimen shown in the figure is the same as the one shown in Fig. 5d in Ohtsuka et al. (2009), which was misidentified as *L. ferreirae*.

Scale bar 2 cm. Photo by A. Schiariti. **b** Ventral view of *L. lucerna* and an adult *L. spinosa* crab within the subgenital space of the medusa, with their legs clinging through the subgenital ostia (arrow). Scale bar 5 cm

the bell diameter (BD, cm \pm 0.1). Meanwhile, various anatomical parts of medusae (exumbrella, oral arms, oral pillars, gastric cavity, subgenital space, and gonads) were examined macroscopically for presence of associated crab species. Sex of medusae was histologically determined as described in Schiariti et al. (2012).

To characterize the maturity of crab stages associated with medusae, the carapace width (CW; cm \pm 0.1) of *L. spinosa* was measured. Individuals were classified as juveniles or adults following Sal Moyano et al. (2011). Physiological maturity was defined by the presence of spermatophores in the male vas deferens and the

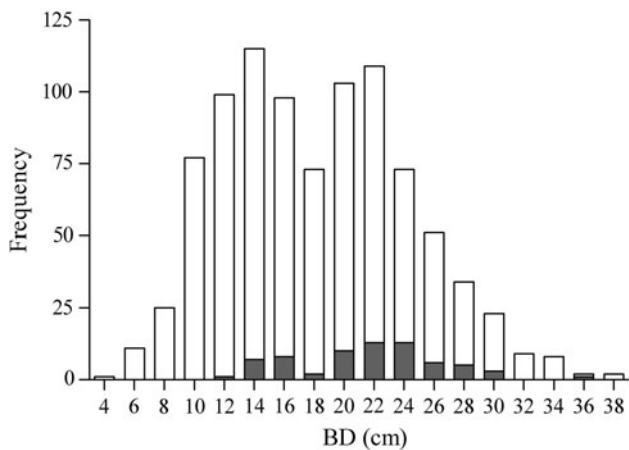


Fig. 3 Size–frequency distribution of *L. lucerna* medusae: pooled data of medusae not associated with crabs (white bars, $N = 843$) and specimens associated with *L. spinosa* crabs (black bars, $N = 69$), captured from January to May 2006 and from January to March 2007 in the Río de la Plata estuary. BD bell diameter

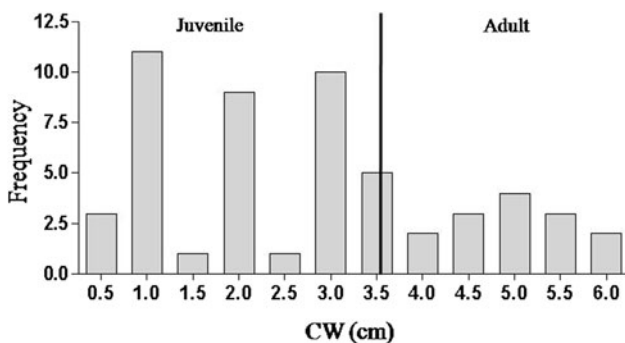


Fig. 4 Size–frequency distribution of *L. spinosa* crabs associated with medusae of *L. lucerna* captured from January to May 2006 and from January to March 2007 in the Río de la Plata estuary ($N = 73$). CW carapace width. The black vertical line separates juvenile from adult crabs

development of mature ovaries in females. Accordingly, males larger than 3.3 cm CW and females larger than 4 cm CW were considered physiologically mature. Stomach contents of a subsample of crabs ($N = 16$) were examined under a dissecting microscope. A size–frequency distribution of CW of crabs found inside medusae was conducted.

Possible differences in BD of medusae were studied, comparing the size–frequency distributions of medusae with and without crabs. The statistical significance of these patterns was analyzed using a G-test for goodness of fit (Sokal and Rohlf 1999). Two chi-square tests were conducted to test for differences in sexual proportions of (1) the pooled data corresponding to medusae with and without crabs and (2) the data corresponding only to medusae with crabs.

Results

A total of 843 medusae of *L. lucerna* were captured and studied. Of that number, 69 (8.2 %) hosted specimens of the spider crab *L. spinosa*. Most crabs remained within their host after recovery of the fishing nets. Moreover, mesh sizes were large enough to allow “free-living crabs” to escape during trawling or on recovery of the nets, and all crabs were found inside medusae when captured. Crabs were located within the subgenital spaces of medusae, with the legs of the largest ones extending through the subgenital ostia (Fig. 2a, b). Size–frequency distributions of *L. lucerna* showed that medusae having crab associates ranged from 8 to 38 cm BD, while medusae without any crabs ranged from 2 to 34 cm BD (Fig. 3). Medusae hosting crabs were thus larger than those without (Gh = 93.01, $P < 0.05$). All medusae bore mature gonads. No conspicuous damage to gonads, bell, or oral arms of medusae was detected in medusae hosting crabs. The sex ratio of pooled data was not different from 1:1 ($\chi^2 = 0.6$, $P > 0.05$). Notably, however, a ratio of $\sim 2:1$ in favor of females was observed ($\chi^2 = 5.2$, $P < 0.05$) among medusae hosting crabs.

In all, 73 individuals of *L. spinosa* were found associated with *L. lucerna*. CW of crabs of both sexes ranged from 0.4 to 6.0 cm, and included both juveniles (0.4–2.9 cm CW, 64.8 %) and adults (3.5–6.0 cm CW, 35.2 %) (Fig. 4). In 96 % ($N = 66$) of the associations, one crab was found within the subgenital space of a medusa. In the remaining 4 % ($N = 3$), two medusae hosted four crabs and one had two symbionts. Crabs in these three medusae were juvenile and occupied an individual subgenital pocket. In addition, two of the specimens of *L. spinosa* associated with *L. lucerna* had one specimen of the anemone *Antholoba* sp. attached to their carapaces. Examination of a subsample of *L. spinosa* crabs associated with *L. lucerna* ($N = 19$) showed that that six individuals (three juveniles and three adults) had recently molted, while three mature hard-shelled females were ovigerous. Examination of stomach contents of juvenile and adult crabs of both sexes revealed the presence of nematocysts (Fig. 5a–c) and remains of an unidentified but planktonic species of copepod.

In 34 % of the trawls ($N = 17$), we found at least one *L. lucerna* specimen having crab associates. The association between *L. lucerna* and *L. spinosa* was observed over the entire study area, matching the spatial distribution of the medusa population (Fig. 1). Although *L. lucerna* occurs in the study area from January to May, the association between this species and *L. spinosa* was observed only during February and March, coinciding with the times of highest biomasses of *L. lucerna* (Table 2).

Fig. 5 Stomach contents of *L. spinosa* containing nematocysts of *L. lucerna*. Structures needed to identify the type of nematocyst (shaft and spines on the thread) are not properly visible on the figure. Therefore, we prefer to omit any attempt of classification avoiding possible misinterpretations. **a** Two different types of nematocysts were differentiated and identified with white arrows. Scale bar 25 μm . **b** Detailed view of a discharged nematocyst. Scale bar 25 μm . **c** Cluster of nematocysts. Scale bar 100 μm

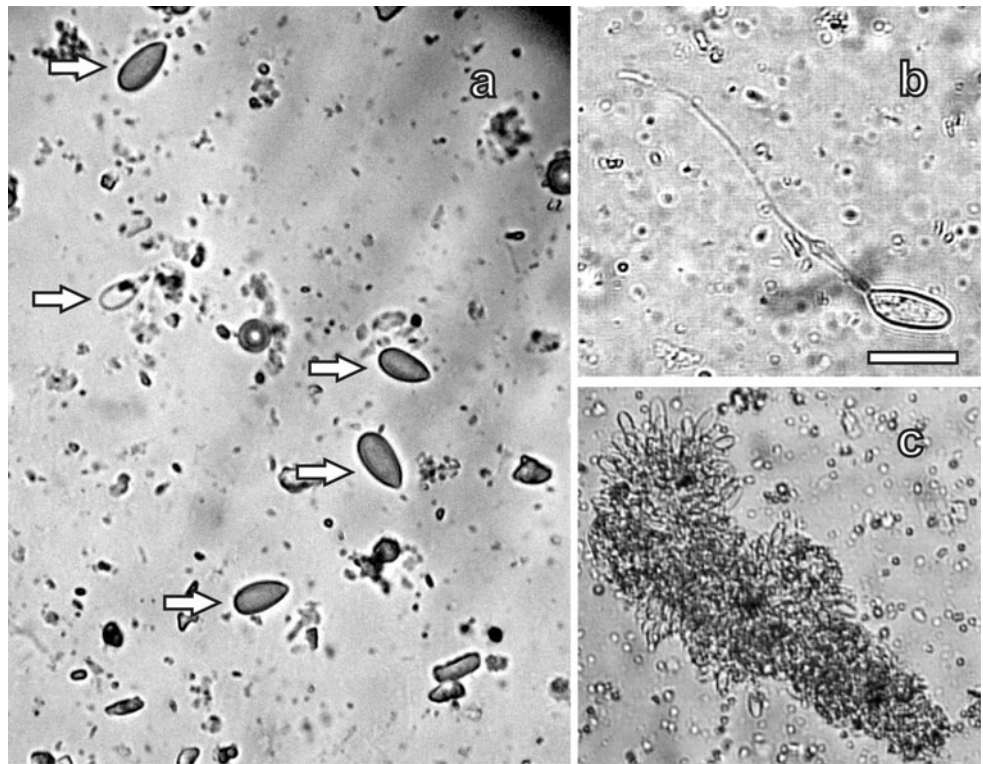


Table 2 Temporal patterns of the total number of *L. lucerna* medusae (nM) and total number and percentage of medusae associated with *L. spinosa* crabs (nMWC, %MWC; respectively); captured in the Río de la Plata estuary, Argentina–Uruguay

Month/year	n M	n MWC	% MWC
Jan-06	87	0	0
Feb-06	308	30	9.7
Mar-06	47	3	6.4
Apr-06	25	0	0.0
May-06	6	0	0.0
Jan-07	2	0	0.0
Feb-07	57	15	26.3
Mar-07	40	10	25.0
Total	843	69	8.2

Discussion

The broad spatial and temporal scale of this study, together with the large sample size, confirmed an association between *L. lucerna* and *L. spinosa* as previously suggested by Vaz Ferreira (1972), Zamponi (2002). In those studies, the authors reported the presence of one or two crabs (juveniles and adults of both sexes) per host medusa, always with each crab occupying an individual subgenital pocket. We likewise observed the presence of juvenile and adult crabs of both sexes associated with *L. lucerna*. However, in contrast to Zamponi (2002), we observed that

most medusae hosted only one crab (96 %), although we found up to four crabs within a single medusa.

Shanks and Graham (1988) proposed that some invertebrates feed directly on gonads of medusae, the more nutritious part of their hosts. In our study, specimens of *L. spinosa* were more frequent on female medusae of *L. lucerna* even though the sex ratio of the species is 1:1 (Morandini 2003; Schiariti 2008) as in most scyphozoans (Arai 1997). We did not discover evidence that *L. spinosa* feeds on gonads of *L. lucerna*, although Rountree (1983) suggested that crab predation probably does not seriously impair medusa tissue since regenerative powers are remarkable. The prevalence of *L. spinosa* on female medusae may indicate feeding on the gonads due to the higher energy content of female gonads, although this remains to be tested.

Regarding temporal patterns, the high proportions of crabs associated with medusae during late summer (February and March) coincides with and is likely tied to the peak period of abundance of *L. lucerna*. Similarly, Nogueira and Haddad (2005) found seasonal variation in the frequencies of association between *L. lucerna* and *Libinia ferreirae* in Brazil, where greatest frequencies were recorded during spring, again coinciding with the highest abundances of medusae and their largest size. Regarding spatial distribution, medusae with and without crabs was the same. Conversely, the spatial distribution of free-living *L. spinosa* crabs in the Río de la Plata estuary (Giberto

et al. 2004; Giberto 2008) overlapped that of medusae in the outer region of the estuary, but no free-living crabs were captured on muddy bottoms in upstream regions.

Whereas benefits of the association have rarely been noted for medusae, crabs are thought to benefit in several ways, including protection, feeding, and/or transportation (see Table 1). Hypotheses concerning protection against predation in crabs have been proposed for other commensal species inhabiting algae or sea urchins (Hacker and Madin 1991; Baeza and Thiel 2000). Our discovery of recently molted specimens of *L. spinosa* (juvenile and adults) associated with medusae support this hypothesis in as much as such crabs are more vulnerable to predation because of their soft-shell condition. The presence of early juveniles of *L. spinosa* within *L. lucerna* also suggests that settlement of megalopa larvae occurs within hosts. This has also been reported in other symbiotic decapods (Castro 1978; Baeza and Stotz 1998). Furthermore, Ohtsuka et al. (2009) indicated that associations between crabs and medusae are usually composed of juvenile crabs. The attachment of megalopa larvae or juvenile crabs suggests that medusae may be utilized as a floating nursery (Nogueira and Haddad 2005). The presence of the most vulnerable life stages of *Libinia* species—larvae, juveniles, and soft-shell individuals—(Nogueira and Haddad 2005; present study) suggest that medusae constitute a structure offering protection against predation in the pelagic realm.

Regarding benefits related to feeding, it has been suggested that crabs may feed on organisms adhering to the ball of mucus located on oral arms of the medusa (Martin and Kuck 1991; Zamponi 2002; Towanda and Thuesen 2006), to gonads, or to the bell of their hosts (Jachowski 1963; Phillips et al. 1969). Due to their high water content (Curl 1962; Beers 1966; Larson 1986) medusae are usually believed to be of low nutritional value. However, Shenker (1985) stated that the food value of the “nongelatinous parts of medusae” (e.g., gonads, feeding structures, stomach) can be relatively high. In fact, some predators of gelatinous zooplankton consume only those more nutritious parts (Harbison et al. 1977; Madin and Harbison 1977; Janssen and Harbison 1981). In this study, the presence of nematocysts in the stomach contents of crabs suggests that *L. spinosa* feeds upon the oral arms or gonads (lying on the gastric cirri). Crabs may also feed on organisms attached to mucus produced by the oral arms (as evidenced by the presence of copepod remains in the stomach content), ingesting parts of the oral arms and nematocysts of medusae only by accident.

Several authors have suggested that crabs may gain enhanced mobility and dispersion from their association with medusae, thereby conserving energy otherwise expended in locomotion (Corrington 1927; Suzuki 1965;

Vaz Ferreira 1972; Nogueira and Haddad 2005; Towanda and Thuesen 2006; Ohtsuka et al. 2009). However, evidence indicating that transportation constitutes a benefit for crabs is scarce. Towanda and Thuesen (2006) suggested in a metabolic study that crabs clinging to medusae may be able to develop faster through transport into warmer surface waters while also reducing energetic costs associated with locomotion. We observed that crabs are transported by *L. lucerna* to inner estuarine waters overlapping the bottom salinity front. If crabs leave their host in this “stressful” frontal area they would find a nonfavorable environment characterized by different substrata, different benthic communities, and strong salinity shifts (Mianzan et al. 2001; Giberto et al. 2004; Giberto 2008). In fact, free-living crabs are not usually found in this environment (Giberto et al. 2004; Giberto 2008). Therefore, the so-called “benefit” represented by transportation and subsequent dispersion is at least questionable in this case and requires testing in future studies.

Two alternatives have been suggested to explain how crabs gain access to their hosts (Corrington 1927): either one or more larval stages must seek shelter within the medusa, or the medusa must descend to the substratum where crabs occur at least occasionally. The presence of larval stages in association with medusae has been reported in several studies (Graham 1994; Nogueira and Haddad 2005; Towanda and Thuesen 2006). Although in the present study *L. spinosa* larvae were not observed within medusae of *L. lucerna*, this could be a methodological artifact (no microscopic examination was made). Nevertheless, we found recent juvenile instars, suggesting that larval stages can adhere to medusae and molt. The presence of adults inside medusae cannot be explained by this hypothesis because the period required for *L. spinosa* to reach such sizes is longer than the life span of medusae. Whereas *L. lucerna* occurs in the Río de la Plata estuary for 5–6 months (late December to May) (Schariti 2008), the molting period from larval stages to adult crabs takes more than 1 year (Sal Moyano unpubl data). Moreover, the presence of crabs bearing the benthic anemone *Antholoba* sp. within *L. lucerna* suggests that crabs are capable of gaining access to a medusa after their larval stages. Indeed, *L. lucerna* is usually found aggregated close to the bottom (Alvarez Colombo et al. 2003). Therefore, individuals of *L. spinosa* could hitch onto their host either during planktonic stages or as adult crabs on medusae aggregated close to the bottom.

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Conflict of interest The authors declare that they have no conflict of interest.

Ethical standards The methods and experiments comply with current laws of the country in which they were performed.

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