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ORIGINAL ARTICLE

Association between *Hyperoche martinezii* (Amphipoda: Hyperiidae) and ctenophores from the Buenos Aires coast, Argentina (South-western Atlantic Ocean)

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ABSTRACT

This survey examined the association between the hyperiid amphipod *Hyperoche martinezii* and ctenophores off the Argentinian coast (38°08'17"S, 57°31'18"W) through the evaluation of seasonality, prevalence and intensity of infection during an annual cycle. Medusae were also examined but only the ctenophores *Mnemiopsis leidyi*, *Pleurobrachia pileus* and *Beroe ovata* showed this association during the austral mid-spring to mid-summer. A total of 502 hyperiids were obtained; most (422 individuals) were larval stages, 53 juveniles and 27 adults. *Mnemiopsis leidyi* had the highest number of hyperiids with 98.6%, followed by *P. pileus* (0.80%), and *B. ovata* (0.60%). Total prevalence was 2.0 and intensity of infection ranged between 1 and 17 hyperiids per ctenophore. The host with highest prevalence was *B. ovata* (4.54), followed by *M. leidyi* (3.76) and *P. pileus* (0.1). Prevalence values had some correlations with the increase in the total length of *B. ovata* ($r = 0.480$, $P = 0.006$) and *M. leidyi* ($r = 0.501$, $P < 0.001$), and between total length and intensity in *B. ovata* ($r = 0.425$, $P = 0.017$). The hyperiid was found in different parts of the host body: larval stages were found in the canal close to the subtentacular comb row and the stomodeum, whereas juvenile/adult stages were observed with a resting posture on the external surface of the ctenophores. The known geographic distribution of *H. martinezii* was extended; this finding represents the addition of three new hosts for this hyperiid.

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Introduction

Ctenophores and medusae (here referred to as gelatinous zooplankton) have a great variety of biological interactions with different groups, including bacteria, cnidarians, trematodes, copepods, amphipods, decapods, and fish, among others (Rountree 1983; Ohtsuka et al. 2009; Daniels & Breitbart 2012). Several works have shown symbiotic associations between hyperiid amphipods and medusae, siphonophores, ctenophores, salps and radiolarians (Harbison et al. 1977; Madin & Harbison 1977; Laval 1980; Gasca & Haddock 2004). These interactions have been characterized with different levels of detail and reported under different terms including parasitoidism, ectocommensalism, endocommensalism, micropredation, epizoism, protection, buoyancy and transportation (Madin & Harbison 1977; Laval 1980; Vader 1984; Ohtsuka et al. 2009). In most cases this classification is based on assumptions

instead of direct observations that analyse the association in terms of costs and benefits experienced by both partners (Sal Moyano et al. 2012).

Hyperiid amphipods are associated with gelatinous zooplankton at the onset of their existence, when they are assumed to be strict parasites. This association is, depending on the hyperiid species, more or less intimate, and its duration varies according to biological and ecological factors. The relationship is nearly always detrimental to the host, which is usually devoured only when the hyperiid reaches the adult condition (Laval 1980). In the case of *Hyperoche martinezii* (Müller, 1864), this hyperiid could be categorized as a protelean parasite because its larval stages are endoparasitic, inasmuch as, according to Laval (1980) its pantochelis larvae dig their way into the host mesoglea as soon as they are demarsupiated; these larvae would then be able to access the inner channels of

the host and feed on the items consumed by it (Laval 1965). However, some hyperiids appear to feed directly on the host's tissues after reaching the first juvenile stage; thus, when hyperiids attain a size large enough to devour their hosts, they probably adopt a predatory behaviour (Laval 1980).

A great number of studies have detailed the role of the gelatinous zooplankton as hosts in the life cycle of hyperiids. The ways in which hyperiids are associated with the gelatinous zooplankton are quite variable (Vader 1984), and their degree of dependence varies according to species (Laval 1980). Harbison et al. (1977) and Barz & Hirche (2005) studied the role of gelatinous zooplankton as the primary habitat for hyperiids, especially in open/deep waters; Dittrich (1988) showed that the amphipod *Hyperia galba* (Montagu, 1815) uses scyphozoan medusae during the reproductive period, demarsupiating and inserting their brood into the host's mesoglea; Riascos et al. (2012) showed that the large number of *Hyperia curticephala* M. Vinogradov & Semenova, 1985 parasitizing the medusa *Chrysaora plocamia* (Lesson, 1830) may channel energy back to fishes, which feed on the parasites, i.e. the biomass of hyperiids consumed by the fish was a function of the biomass of hyperiids parasitizing the medusae; Fleming et al. (2014) found that three different species of scyphozoan jellyfish provide a short-term reproductive habitat for *H. galba*; and Riascos et al. (2015) showed the trophic relationship between the scyphomedusa *C. plocamia* and the hyperiid *H. curticephala*.

There is a variable degree of selectivity between hyperiid amphipods and gelatinous zooplankton groups; some genera and even families appear to be restricted to associations with certain host groups (Harbison et al. 1977; Laval 1980), but we are far from fully understanding the mechanisms or specificity for host selection (Dittrich 1992). These associations have been widely documented worldwide (e.g. Harbison et al. 1977; Laval 1980; Gasca et al. 2015), but the only documented record for the South-western Atlantic Ocean corresponds to *Hyperoche medusarum* (Kröyer, 1838) on the ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865 (as *Mnemiopsis maccradyi* Mayer, 1900; Sorarrain et al. 2001).

As part of a project to study the abundance and the seasonality of gelatinous zooplankton off the Argentinean coast, numerous specimens of ctenophores associated with the hyperiid amphipod *H. martinezii* were collected. The purpose of this study was to examine the nature of the association of this hyperiid with ctenophores in the temperate waters of Mar del Plata Harbour, including its seasonality, mean hyperiid abundance, prevalence, intensity of infection, and

mean intensity in different hosts. We also report for the first time the occurrence of *H. martinezii* in the region and expand its known host range.

Materials and methods

Zooplankton sampling was carried out over one year (March 2014 to March 2015) at Mar del Plata Harbour, Argentina (Figure 1). The frequency of zooplankton sampling was weekly or biweekly during the warm-period (austral spring-summer), and monthly in the cold-period (austral autumn-winter). Samples were obtained by oblique tows using a standard zooplankton net (75 cm mouth diameter, 500 µm mesh size) at four sampling stations (see Figure 1). A flowmeter attached to the net mouth allowed the calculation of the volume of water filtered at each sampling station and the numerical abundance was standardized as individuals per 100 m³. The mean monthly abundance value of gelatinous zooplankton was calculated. Depending on the bathymetry of the sampling station, water depth ranged between 5 m (stations 1 and 3) and 10 m (stations 2 and 4). Medusae and ctenophores were examined for parasites, but only ctenophores showed this association. The ctenophores were identified and measured *in vivo* to avoid the frequent damage caused by standard preservation techniques (see Mianzan 1999). Samples were then preserved in a 4% formaldehyde seawater solution buffered with sodium borate. Taxonomic identifications followed Mianzan (1999) for ctenophores and Bowman & Gruner (1973), Vinogradov et al. (1996) and Zeidler (2015) for hyperiids. Hyperiid specimens are deposited in the collection of the Universidad Nacional de Mar del Plata – Estación Costera JJ Nágera (UNMdP-NÁGERA Hy-001); catalogue numbers are indicated between brackets.

Total body length (mm) of both ctenophores and hyperiids was measured. For the ctenophores *Pleurobrachia pileus* (O. F. Müller, 1776) and *Beroe ovata* Bruguère, 1789, body length was measured from the polar plate to the mouth opening, in *Mnemiopsis leidyi* from the top of the meridional canals (aboral zone) to the oral lobes (oral zone) (see Barnett & Mianzan 2010). Hyperiid total length was taken following Álvarez Colombo & Viñas (1994), i.e. from the front of the head (excluding the antennae) to the posterior margin of the last uropods. Size-frequency histograms based on total host body length were constructed to analyse the occurrence of the different sizes of host species with and without hyperiids. Length classes were arbitrarily defined by applying the Sturges Rule (Zar 1999).

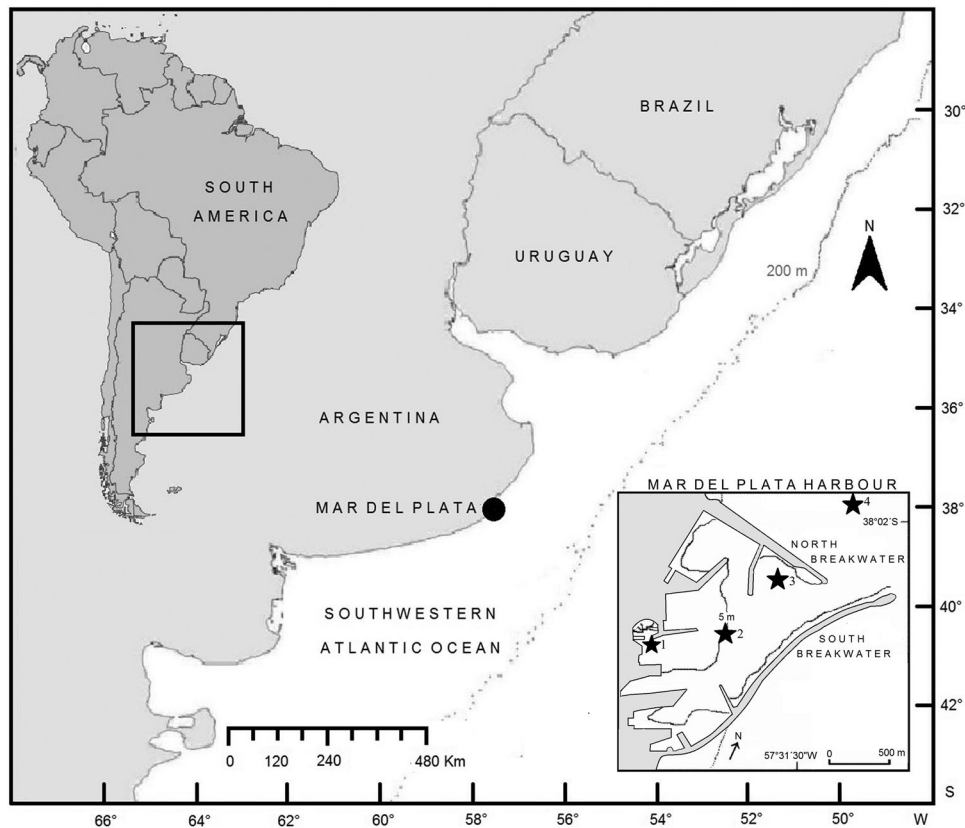


Figure 1. Map of the Buenos Aires coast (Argentina). Study area (Mar del Plata Harbour: 38°08'17" S, 57°31'18" W). Black stars indicate the sampling stations.

The temporal distribution of the mean monthly abundances of the ctenophore hosts (*M. leidyi* and *P. pileus*) was analysed but abundance values of *B. ovata* were omitted from the graphic because of the low values recorded. In addition, the total number of infested individuals per sample and the number of parasitic hyperiids present on each host were also recorded; parasitic prevalence, intensity of infection and intensity interval were estimated in the first instance for the total values (i.e. considering the three host species with the occurrence of the hyperiid) and monthly (for each host species) following Bush et al. (1997): (1) prevalence is the number of hosts infected with one or more individuals of *Hyperoche martinezii* in a sample, divided by the number of examined hosts, and expressed as a percentage; (2) intensity of infection is the number of individuals of *H. martinezii* in a single infected host; (3) intensity interval is the minimum and maximum number of *H. martinezii* by infected host.

To evaluate the possible differences between the sizes of males and females of hyperiid amphipods and the possible differences between the sizes of parasitized and non-parasitized ctenophores, Student *t*-tests were conducted (Sokal & Rohlf 1999). In order to evaluate the relationship between sizes in the

ctenophore hosts and prevalence values and intensity of infection, a Pearson's correlation coefficient (*r*) was applied after checking for the normality of the distribution of the data and the variance of homogeneity. After the calculation of this coefficient (*r*) and to evaluate its significance, a Student distribution *t*-test was applied. To estimate the distribution of *H. martinezii* in the host, the Aggregation Coefficient (*k*) of the negative binomial distribution was performed. This analysis determined whether the host species has a contagious, uniform or random distribution (Morales & Pino 1987). According to Esch et al. (1990), this analysis should be performed in species with prevalence values over 5%.

For all statistical analyses, the level of statistical significance was $\alpha = 0.05$, and the assumption of the normality of the distribution of the data (Kolmogorov–Smirnov test) and the variance homogeneity (Levene test) were met through the previous transformation of the data with $\log(x + 1)$ (Zar 1999).

Results

A total of 96 zooplankton samples were analysed during the annual cycle, of which 26 (27.1%) were positive for *Hyperoche martinezii*. Medusae were also

examined, but *H. martinezii* was found only on the three species of ctenophores present in the samples: *Mnemiopsis leidyi* (class Tentaculata), *Pleurobrachia pileus* (class Tentaculata) and *Beroe ovata* (class Nuda). All known stages of development of

H. martinezii were found in the ctenophore hosts: pantocheles, protopleon, juvenile and adults of both sexes (Figure 2a–c); in some specimens of *M. leidyi* both larval and juvenile/adult stages were observed (Figure 2d). Of the 502 amphipods examined, 422 (84.06%)

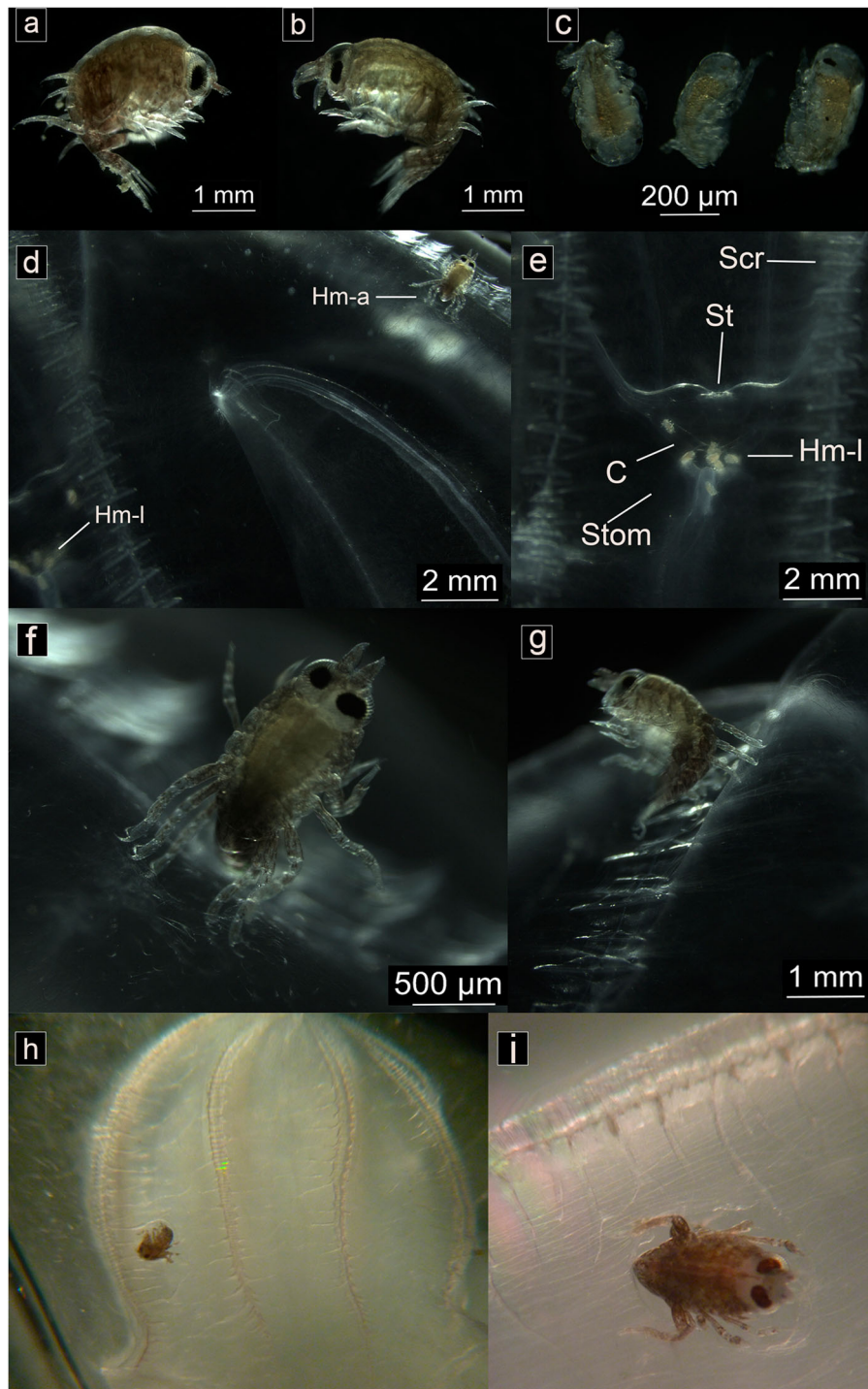


Figure 2. *Hyperoche martinezii* parasitizing ctenophores from the Buenos Aires coast, Argentina. (a) Female specimen; (b) male specimen; (c) larval stages (pantochelis/protopleon); (d) different developmental stages of *H. martinezii* in a single host (*Mnemiopsis leidyi*); (e) distribution of larval stages in the host (*M. leidyi*); (f, g) adult stage distribution on the host; (h, i) *Hyperoche martinezii* parasitizing the ctenophore *B. ovata*: observe the damage caused by the hyperiid to the host. St, statocyst; C, canal; Scr, subtentacular comb row; Stom, stomodeum; Hm-l, *H. martinezii* larvae; Hm-a, *H. martinezii* adult.

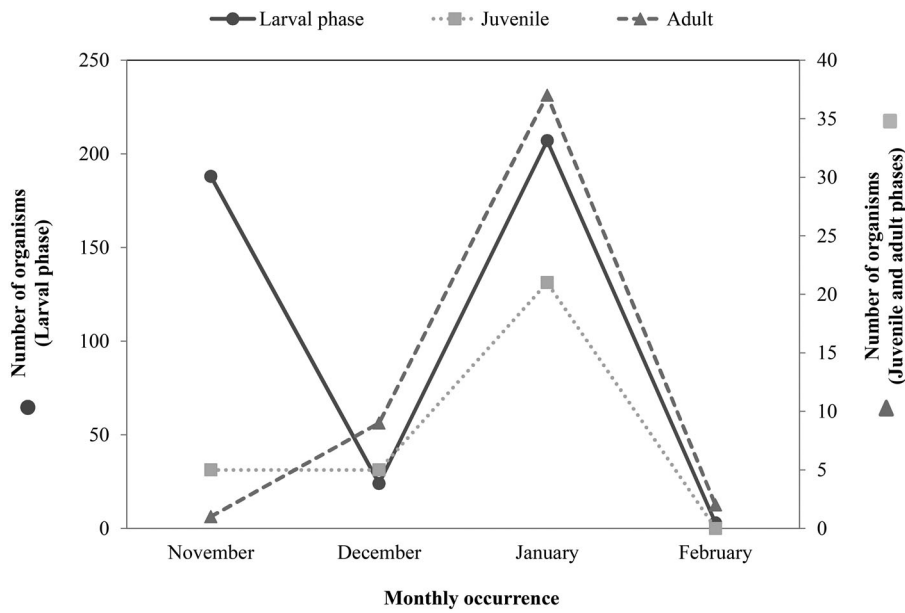


Figure 3. Seasonal distribution of the different developmental stages of *Hyperoche martinezii* in the Mar del Plata Harbour, Argentina during the surveyed period. Number of organisms by month.

corresponded to pantochelis and protopleon larval stages, and the rest were juvenile (53; 10.56%) and adult (27; 5.38%). The monthly distribution of the number of organisms of the different developmental stages of hyperiid parasites are presented in Figure 3. Pantochelis and protopleon larvae ranged from 0.33 to 0.98 ± 0.13 (mm \pm SD), juveniles from 1.12 to 2.65 ± 0.44 , and adults from 2.28 to 4.93 ± 0.66 . A total of 58 females and 22 males were identified (sex ratio = 2.6:1), and two gravid females were observed. Females (1.13 to 4.93 ± 0.91 mm) were consistently larger than males (1.53 to 4.83 ± 0.97 mm) ($t = -1.12$; $df = 43$; $P = 0.255$). Among the males, seven were

juveniles and 15 adults, while 24 and 34 females were juveniles and adults, respectively.

The ctenophore abundance monthly distribution is shown in Figure 4. Ctenophores occurred year-round, but they were highly abundant during the warm period (austral spring-summer). Hyperiids were only found during this period, with water temperatures ranging between 15.5 and 22°C. For the rest of the annual cycle hyperiids were absent from our samples, both as symbionts and free-swimming members of the zooplankton.

The ctenophore *M. leidy* had the highest number of hyperiids with 98.6% (495 individuals) of the total,

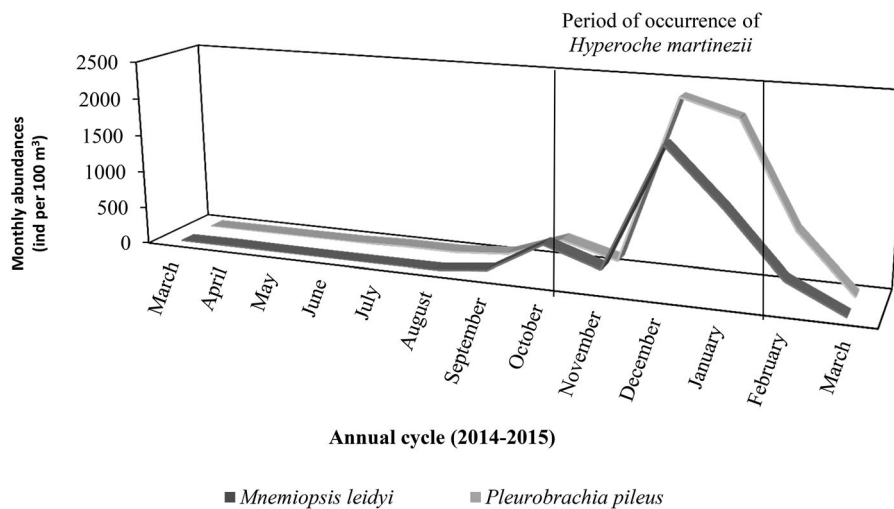


Figure 4. Seasonal distribution of the monthly abundances of the ctenophore hosts during an annual cycle in Mar del Plata Harbour, Argentina.

Table I. Monthly values of host abundances, prevalence and intensity interval for each ctenophore host from Mar del Plata Harbour, Argentina.

Ctenophore species	Parameter	November 2014	December 2014	January 2015	February 2015
<i>Mnemiopsis leidyi</i> A. Agassiz, 1865	Host abundance (\bar{x})	259.75	2283.6	1179.05	265.28
	Prevalence	6.92	1.25	14.55	8.7
	Intensity interval	1–17	1–5	1–14	1–4
<i>Pleurobrachia pileus</i> (O.F. Müller, 1776)	Host abundance (\bar{x})	146.74	2329.67	2119.54	1208.31
	Prevalence	0.23	0.08	0.08	0
	Intensity interval	1	1	2	–
<i>Beroe ovata</i> Bruguère, 1789	Host abundance (\bar{x})	2.81	4.37	33.87	11.95
	Prevalence	9.52	–	–	–
	Intensity interval	1–2	–	–	–

while *P. pileus* and *B. ovata* had 0.80% (four specimens) and 0.60% (three organisms), respectively.

Of a total of 7914 ctenophores analysed during the period of co-occurrence of the parasitic hyperiid, 158 were found to be infected (total prevalence = 2.0%) and intensity interval ranged between 1 and 17 hyperiids per ctenophore. The ctenophore species with the

highest prevalence in the period of occurrence of *H. martinezii* was *B. ovata* (4.54), followed by *M. leidyi* (3.76), and *P. pileus* (0.1). *Mnemiopsis leidyi* were found to host up to 17 hyperiids, whereas *P. pileus* and *B. ovata* had a maximum of two parasites each. These parameters varied depending on both the host species and month (Table I). The ctenophore *P. pileus* was excluded from k calculation because of low prevalence values (<5%), while *H. martinezii* distribution had an overdispersed distribution in reference to *M. leidyi* ($k = 0.64$) and *B. ovata* populations ($k = 0.22$), i.e. most of the ctenophores examined harboured few or no hyperiids, and few host individuals contained a large number of this amphipod.

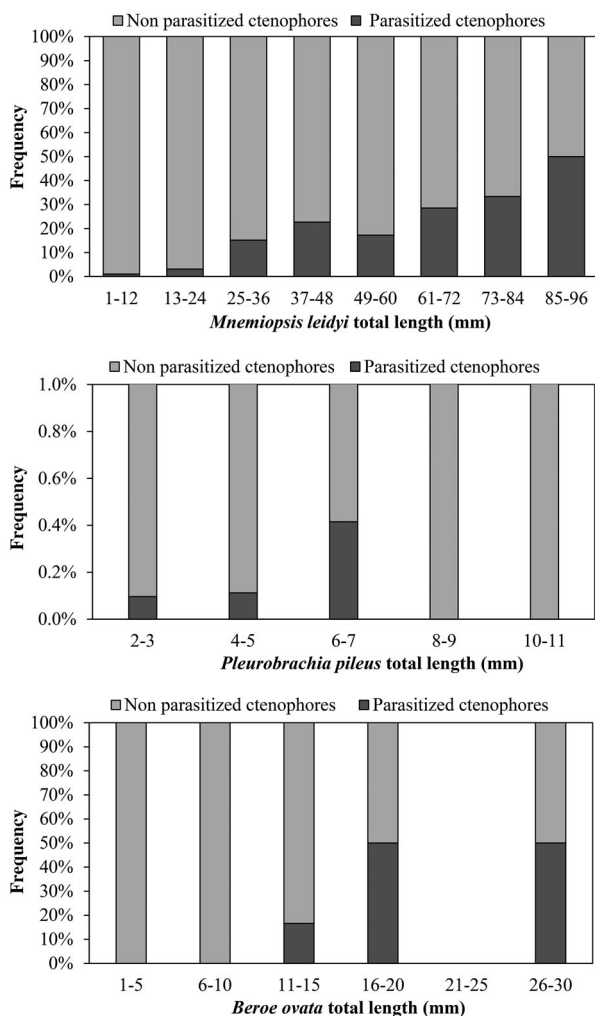
The percentage of parasitized and non-parasitized ctenophores of the different size classes is presented in Figure 5. No significant differences were found between the total length of parasitized and non-parasitized ctenophores in both *M. leidyi* and *B. ovata* ($t = 19.10$, $df = 2257$, $P < 0.001$, and $t = 3.82$, $df = 36$, $P = 0.001$, respectively), but in *P. pileus* the non-parasitized specimens were larger than the parasitized ones ($t = 0.38$, $df = 2209$, $P = 0.702$).

A positive correlation was observed between the total length of *M. leidyi* ($r = 0.501$, $n = 185$, $P < 0.001$; $t = 0.10$, $df = 183$, $P = 0.05$) and *B. ovata* ($r = 0.480$, $n = 31$, $P = 0.006$; $t = 0.28$, $df = 29$, $P = 0.05$) and the prevalence, and only for *B. ovata* ($r = 0.425$, $n = 31$, $P = 0.017$; $t = 0.29$, $df = 29$, $P = 0.05$) with the intensity of infection (Table II), i.e. the prevalence and intensity of infection increases with increasing length of these ctenophores.

Table II. Pearson correlation values (r) between total host length and prevalence (r^a) and intensity of infection (r^b).

Host species	r^a	n	P	r^b	n	P
<i>Mnemiopsis leidyi</i> A. Agassiz, 1865	0.501*	185	<0.001	0.077	54	0.579
<i>Pleurobrachia pileus</i> (O.F. Müller, 1776)	0.096	102	0.336	0.076	102	0.447
<i>Beroe ovata</i> Bruguère, 1789	0.480*	31	0.006	0.425*	31	0.017

P : significance level. * indicates a significant correlation.

**Figure 5.** Percentage of parasitized and non-parasitized ctenophores for the different host sizes classes. Grey bars: pooled data of non-parasitized ctenophores; and black bars: specimens parasitized with *Hyperoche martinezii*.

Observations *in vivo* showed that the early stages (pantochelis and/or protopleon larvae) were distributed all throughout the ctenophore body. However, they were lodged mainly in the canals adjacent to the area formed by the subtentacular comb row and the stomodeum (Figure 2e). Juvenile and adult stages seemed to prefer the substomodeal comb row zone, but some of them were observed also in the stomodeum. Other individuals showed a resting posture on the external surface of the ctenophores, using the terminal claws of the dactyls of pereopods 5–7 as anchors (Figure 2f, g).

Larval stages were observed embedded in the ctenophore tissue apparently separated from the outside; contrastingly, juveniles and adults were observed to have some communication with the surrounding seawater: one individual of *B. ovata* had a hole with an adult hyperiid inside it (Figure 2h, i).

Discussion

Hyperoche martinezii is a relatively uncommon species; there are only a few records from near-surface waters in tropical regions (Zeidler 2015). It seems to occur more frequently in the Pacific Ocean including the California region (Gasca 2009), the central Mexican Pacific (Gasca et al. 2010), off Ecuador (Guillén-Pozo 2007), the Chinese coast (Shih & Chen 1995), and between New Caledonia and New Zealand (see Zeidler 2015). From the Indian Ocean it is known from off South Africa (Dick 1970), and near Bali and India (see Zeidler 2015). Off the Atlantic coasts it has been reported in the North-western Atlantic (Gulf of Mexico) (Escobar-Briones et al. 2002) and the South-western Atlantic (Venezuela and Brazil); its southernmost record is off Rio de Janeiro, Brazil (21°11.2' S, 40°30' W) (Galan 1984; Martín & Díaz 2003; Zeidler 2015). Its occurrence in the surveyed area represents a southward expansion of its known geographic range into Mar del Plata (38° 08'17" S, 57°31'18" W), Argentina.

With reference to the associations of hyperiids and gelatinous zooplankton in the temperate waters of the South-western Atlantic Ocean, the only previous report is of *Hyperoche medusarum* with *Mnemiopsis leidyi* (as *Mnemiopsis mccradyi*) (Sorarrain et al. 2001). This hyperiid was also cited as part of the zooplankton assemblage in Argentine shelf waters (Ramírez & Viñas 1985; Fernández Aráoz et al. 1991; Padovani 2013), but according to Zeidler (2015), some of these records may be misidentifications of its congener *Hyperoche luetkenides* Walker, 1906.

The association between *H. martinezii* and the three ctenophores occurred over a relatively long time frame (i.e. almost four months), compared with other hyperiid

species like *Hyperia galba*, which was found with its jellyfish host only during a few weeks off Northern Ireland (Fleming et al. 2014). Ctenophores were not infested during the austral autumn-winter and the early spring season, thus suggesting that this association is not permanent in such habitats. The duration of this association in Mar del Plata Harbour may be determined by the decreasing abundances of the ctenophore hosts and/or by the life cycle of *H. martinezii*. The life cycles of hyperiid amphipods are both complex and poorly known; obligate parasitism for all its stages has been suggested for some species, but many species are only known from the water column (Von Westernhagen 1976; Hoogenbaum & Hennen 1985; Sorarrain et al. 2001). Conversely, for other hyperiid species the distribution of the non-parasitizing phase remains practically unknown; Dittrich (1988, 1992) observed that the seasonal occurrence of *H. galba* was correlated with that of scyphomedusae in the water column, but when the host was absent from the water column, the hyperiid was absent too.

According to this author, during the period of non-occurrence of hyperiids in the water column, it is possible that they hibernate or go through a slow-development phase on benthic polyps during the winter, followed by a fast-growth and an active reproductive pelagic phase when scyphozoan jellyfish were present in the water column, but this suggestion still needs to be verified and this is one case only.

The fact that *H. martinezii* was observed only in association with ctenophores in Mar del Plata Harbour, despite the occurrence of 14 species of jellyfish as potential hosts (including highly abundant hydromedusae such as *Liriope tetraphylla* (Chamisso & Eysenhardt, 1821) and *Eucheilota ventricularis* McCrady, 1859), suggests that this microcrustacean prefers ctenophores, as proposed by Zeidler (2015). Specifically, the high number of these hyperiids in *M. leidyi*, compared with the other two ctenophore hosts, could signal a preference for this species. This behaviour may be related to the ctenophore feeding strategy; it is basically an active predator, but unlike the other two ctenophore hosts (*Pleurobrachia pileus* and *Beroe ovata*), which are exclusively predating forms (Mianzan et al. 2009), *M. leidyi* can also filter particles by creating a steady flow of water carrying food items inside its body (Waggett & Costello 1999; Colin et al. 2010). Hence, it is likely that *H. martinezii* uses this mechanism to access the inner structures of the ctenophores and have their larvae feed either on the ctenophore tissues or on its food.

The assumed selectivity of some families of hyperiid amphipods to associate with cnidarians or ctenophores

has been documented (Harbison et al. 1977; Laval 1980). The families Lanceolidae and Lycaeidae are usually associated with scyphomedusae and hydromedusae, while other families exclusively prefer siphonophores (Laval 1980). The Oxycephalidae is frequently hosted by ctenophores (Harbison et al. 1977), and the Hyperiididae and Dairellidae are symbionts of various medusae and/or ctenophore species (Ohtsuka et al. 2009). For example, some selectivity of *H. medusarum* (Hyperiidae) for ctenophores hosts has been proposed based on observations of this hyperiid rejecting the medusae (*Cyanea capillata* (Linnaeus, 1758) and *Aurelia aurita* (Linnaeus, 1758)) as hosts when the ctenophore *Pleurobrachia* sp. is present (Evans & Sheader 1972).

The distribution of *H. martinezii* in the host body differed in relation to their developmental stages. Our observations were consistent with those reported by Laval (1965) and Madin & Harbison (1977), indicating that pantochelis larvae tend to occur inside the gastric channels and in the lumen formed by the connection of the radial canals, while most juveniles and adult phases adopt a resting posture on the host, with only the dorsal surface of the pleon in contact with the host.

All developmental stages of *H. martinezii* in the ctenophores of Mar del Plata Harbour were observed. According to Sorarrain et al. (2001) the presence of all the developmental stages of the hyperiids in the same host suggests a close dependence of these crustaceans on the ctenophores. In some species, adults remain in the host together with their offspring (Gasca et al. 2015), so the same host could be occupied by different generations of the hyperiid (Laval 1980). In order to keep the benefits of this association, there must be a balance between the hyperiid predation and the growth or regeneration ability of the host to avoid its death. Parameters such as the relative sizes of both partners, the developmental stages of the hyperiid, the number of hyperiids per host, the host's capacities for regeneration and growth, the nutritive value of the host's tissues and the amount of food captured by the host are relevant to how the interactions are conducted (Laval 1980).

The distribution of *H. martinezii* in the *M. leidy* and *B. ovata* populations agrees with the aggregate distribution pattern that is typical among parasite species (Bush et al. 2001) (most of the ctenophores examined harboured few or no parasites, and a few hosts contained a large number of parasites). These authors mentioned that the parasite aggregated distribution and/or overdispersion in the host population has the consequence that parasite-induced host mortality is

also restricted to a few hosts, i.e. only some hosts may die (Bush et al. 2001). It is the overdispersion of parasites and host deaths which produces the dynamic equilibrium of host and parasite populations (Riascos et al. 2013).

This study extends the known geographic distribution of *H. martinezii* to Mar del Plata Harbour, and extends the known host range to include the ctenophores *M. leidy*, *P. pileus* and *B. ovata*. Our results suggest some preference for ctenophores as a host, but specifically for *M. leidy*, due to the high number of hyperiids present in this species.

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Disclosure statement

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