Zoological Studies

Spatial Distribution of Medusa *Cunina octonaria* and Frequency of Parasitic Association with *Liriope tetraphylla* (Cnidaria: Hydrozoa: Trachylina) in Temperate Southwestern Atlantic Waters

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This study examined the spatial distribution of the medusae phase of *Cunina octonaria* (Narcomedusae) in temperate Southwestern Atlantic waters using a total of 3,288 zooplankton lots collected along the Uruguayan and Argentine waters (34–56°S), which were placed in the Medusae collection of the Universidad Nacional de Mar del Plata, Argentina. In addition, we reported the peculiar parasitic association between two hydrozoan species: the polypoid phase (stolon and medusoid buds) of *C. octonaria* (parasite) and the free-swimming medusa of *Liriope tetraphylla* (Limnomedusae) (host) over a one-year sampling period (February 2014 to March 2015) in the coasts of Mar del Plata, Argentina. We examined the seasonality, prevalence, and intensity of parasitic infection. Metadata associated with the medusa collection was also used to map areas of seasonality where such association was observed. *Cunina octonaria* was found from southern Uruguay to the coast of Mar del Plata (34.8–38.2°S, 57.2–54.0°W), with the highest abundances and frequency of occurrence in the Río de la Plata estuary. The parasitic association was identified from the austral warm period (spring-summer season) until mid-autumn. Out of the 21,734 *L. tetraphylla* specimens that were examined, 316 were parasitized (prevalence = 1.5%) exclusively in the manubrium and gastric peduncle, with an infection intensity of 1 to 2 stolons per host. Furthermore, the medusoid buds per stolon ranged from 11 and 29 at different stages of development. No significant differences were observed between the umbrella diameter of parasitized and non-parasitized *L. tetraphylla* specimens, nor was any significant correlation identified between umbrella diameter and prevalence, and intensity of infection. According to the aggregation coefficient, *C. octonaria* had an overdispersed distribution in the host population. All parasitized hosts showed stomach vacuity due to the location of the stolon, which blocked the mouth of the host. We identified the parasitic association in the coasts of Mar del Plata, as well as in both coasts of the Río de la Plata Estuary (Uruguayan-Argentinean coasts). In the Southwestern Atlantic, several biological interactions between medusae and other groups have been identified; however, the specific host selectivity of *C. octonaria* for *L. tetraphylla* was not previously identified. Here we discuss the ecological importance of this association during the

holoplanktonic life history of the narcomedusae. Additionally, we report the southern limit of the spatial distribution of this particular parasitic association in the Southwestern Atlantic, thus increasing the knowledge of biological associations of gelatinous zooplankton (Cnidaria and Ctenophora) on Uruguayan and Argentinean coasts.

Key words: Argentine Sea, Stolon phase, Medusoid buds, Limnomedusae, Narcomedusae.

BACKGROUND

Medusae (*i.e.*, Medusozoa, which includes Hydro-, Scypho-, Cubo-, and Stauromedusae) (see Marques and Collins 2004; Lewis Ames 2018) are an abundant group distributed in a wide spectrum of aquatic ecosystems, including marine-coastal environments (Larson 1986; Suchman and Sullivan 2000) and some continental freshwaters systems (Arbačiauskas and Lesutienė 2005) occurring in all latitudes (Mills 1995), from polar to tropical waters, whereas in the water column they can be found from the surface to abyssal depths (Vinogradov 1968), including benthic and planktonic environments (Miranda et al. 2016). One of the ecological roles of this group includes a great variety of biological interactions with several groups such as protists, cnidarians, trematodes, mollusks, crustaceans, echinoderms, fish, among others (Ohtsuka et al. 2009 and references therein).

The study of the medusae community from temperate Southwestern Atlantic waters (SWAw) (southern Brazil, Uruguay, and Argentina) has allowed us to identify the hydromedusae faunal composition, the spatial distribution (mainly of the most abundant species) (Genzano et al. 2008; Oliveira et al. 2016; Dutto et al. 2019), and some of the above mentioned interactions (*e.g.*, Sal Moyano et al. 2012; Díaz Briz et al. 2012 2017). However, knowledge of the spatial distribution of some species, such as *Cunina octonaria* McCrady, 1959 (Trachylina: Narcomedusae: Cuninidae), is scarce. The present study represents the first attempt to describe *C. octonaria*'s spatial distribution along this vast area of the SWAw, as well as the association between this species and *Liriope tetraphylla* (Chamisso and Eysenhardt, 1821) (Trachylina: Limnomedusae: Geryoniidae), which has not been previously reported in SWAw. We highlight this particular parasitic relationship because the two species of hydromedusae are involved, each one in a specific stage of its life cycle: *L. tetraphylla* acts as host during its free-swimming medusa phase and *C. octonaria* acts as a parasite during its polypoid phase (stolon and medusa buds). In addition, although the polypoid phase and the free-swimming medusa of *C. octonaria* are the same species, each one has different reproductive strategies and energy requirements.

Hydrozoans are a group of cnidarians with complex and diverse life cycles, as well as reproductive strategies that result in a wide range of diversity of polyps, colonies, and medusa morphologies, as well as complete loss or reduction of the polyp or medusa stage in some species (Cartwright and Nawrocki 2010). Morphological and molecular data have allowed us to classify to Hydrozoa into two sister groups: Hydroidolina and Trachylina (Bouillon et al. 2006). Trachylina includes the most enigmatic cnidarians, as they differ from other hydrozoans in their morphology, development, and life cycles (Collins et al. 2008). This group includes four orders: Limnomedusae, Narcomedusae, Trachymedusae, and Actinulida. Order Limnomedusae is a small group with a dimorphic benthic-pelagic cycle, characterized by a small or even nonexistent polyp in some species (Bouillon et al. 2004). When there is no polyp, its embryo directly transforms into the medusa (*e.g.*, *L. tetraphylla*) (Osadchenko and Kraus 2018). For Narcomedusae species, development is indirect and does not include a real intermediate sessile polyp stage (Mayer 1910); their connection to organic, benthic substrates is lost and their entire life cycle occurs in the pelagic realm (Bouillon 1987; Bentlage et al. 2018). However, there is another way to establish an association with substrates: by using another living organism during a larval stage (Bouillon 1987), which may develop in a sessile stage that lives in parasitic association with other cnidarians (*e.g.*, *C. octonaria*) (Bouillon 1987; Osborn 2000).

This type of association may be necessary for some species at a certain phase of their life-cycles and may, or may not, present host specificity. The larval stages of several Narcomedusae (such as *C. octonaria*) parasitize the gastrovascular system and manubrium of other medusae, using their host's food and tissues (Boero and Bouillon 2005; Raskoff and Robison 2005). Once grown, they leave their hosts and live freely (Boero and Bouillon 2005).

Although medusae have a wide range of morphologies and complex life history patterns (Bouillon and Boero 2000), few published studies

describe the association between hydromedusae and other cnidarians. The study of biological associations has implications for marine biodiversity (Purcell and Arai 2001). Forming an association with medusae can enhance the population or diversity of the commensals, since medusae provide shelter, act as food (Masuda et al. 2008), and protect the larval stages from predators (Ohtsuka et al. 2009). Analyzing this intragroup association (*i.e.*, intrahydrozoan) revealed aspects of its population dynamic, life history, life cycle variation (Benovic et al. 1987; Giagrande et al. 1994; Lucas and Reed 2009), and ecological role (*e.g.*, trophic and ecological niches) (Marcogliese 2005). These aspects are essential to understanding how populations develop and persist through the year (Graham et al. 2001; Lucas and Reed 2009). Parasites may be useful indicators of food-web structure and function because they depend on the presence of other hosts in their life cycles for transmission (Marcogliese 2005). There are numerous advantages of using parasites as indicators of trophic processes and food structure; for example, identifying direct trophic links between the host and other organisms, host trophic level, and predators (Marcogliese 2005).

MATERIALS AND METHODS

Spatial distribution of *Cunina octonaria*

To analyze the historical distribution of *C. octonaria* in temperate SWAw, we examined 3,288 zooplankton samples of the Medusae collection (MedCol) of the J.J. Nágera Coastal Station, Universidad Nacional de Mar del Plata (UNMdP), Argentina were revised. The collection includes zooplankton samples taken over 36 years (from 1980 to 2016) along the Uruguayan and Argentine continental shelves (34–56°S, 52–70°W), comprising an area ~7 million km^2 (Fig. 1). The sampling was done using fishery research vessels operated by the Instituto Nacional de Investigaciones y Desarrollo Pesquero (INIDEP, Argentina), as well as local research programs designed by the Instituto de Investigaciones Marinas y Costeras (IIMyC-CONICET, Mar del Plata, Argentina) and the Instituto Argentino de Oceanografía (IADO-CONICET/UNS, Bahía Blanca, Argentina). A variety of plankton nets (Bongo, Nackthai, Motoda, Pairovet, Calvet, and Multinet) were used in oblique trawls from the proximity of the bottom to the surface. The medusae were sorted, counted, and identified, and the abundances were calculated and expressed as ind.m^3 of filtered waters. *Cunina octonaria* occurrence was plotted based on its presence/absence in the set of samples. The

spatial distribution of *L. tetraphylla* has been previously described in Dutto et al. (2019).

To analyze and compare the possible differences between austral warm (spring-summer) and cold periods (autumn-winter) regarding the frequency of occurrence and abundances of *C. octonaria* along with the geographical distribution, the dataset was divided into two periods: October to March (spring-summer) and April to September (autumn-winter). Then, we plotted the presence/absence data and abundances of both periods; we performed Pearson's chi-square test to test the possible differences between both periods and Student t-test for the abundances differences (Sokal and Rohl 1999).

Parasitic association

While analyzing the temporal variation in the gelatinous zooplankton species (GZ) species in the Mar del Plata Harbor (Argentina) (38°08'17"S–57°31'18"W) (Fig. 1), we identified the parasitic association between the polypoid phase of *C. octonaria* and the free-swimming medusa of *L. tetraphylla*; therefore, we used these samplings to described the seasonality of this association. The zooplankton sampling was performed over a one-year sampling period (February 2014 to March 2015). The samples were collected with weekly or biweekly frequency during the warm period and monthly frequency during the cold period with oblique tows using a standard zooplankton net (mouth diameter: 75 cm; mesh size: 500-μm) and a flowmeter attached to the net mouth, which allowed us to calculate the volume of filtered water to estimate the numerical abundance (ind.m^3) of the GZ. We first analyzed this parasitic association by describing the temporal variation in the abundances of the involved species. For *L. tetraphylla*, we reviewed the previous reports of Puente-Tapia and Genzano (2019), and for *C. octonaria* we carried out several analyses: a one-way ANOVA to test if abundances of the medusa phase were significantly different between seasons. If significant differences were present, then a *post hoc* Tukey's HDS test was performed to examine which seasons showed differences (Zar 1999). Data were previously normalized by logarithmic transformation to fulfill the assumption of homogeneity of variances (Levene test). The analyzed specimens were stored at the MedCol with the tag *Cunina-Liriope*-001).

The total number of parasitized organisms per sample was recorded, as were the number of stolons on each host specimens. With these data, the A) parasitic prevalence and B) intensity of infection were described. We determined these infection levels first in terms of the total values (*i.e.*, considering the period of occurrence

of the association) and later for each month. According to Bush et al. (1997): A) prevalence is the number of hosts infected with one or more *C. octonaria* polypoid structures per sample divided by the number of hosts and expressed as a percentage; B) intensity of infection is the number of stolons of *C. octonaria* in a single infected host. In addition, we recorded the number of medusoid buds of *C. octonaria* in each stolon.

The total umbrellar diameter (UD, in mm) of the hosts was measured under a stereomicroscope to determine the relationship between host size and parasite load (considering only the number of stolons). Thus, the specimens were immersed in water to adopt a similar position that is observed in the marine
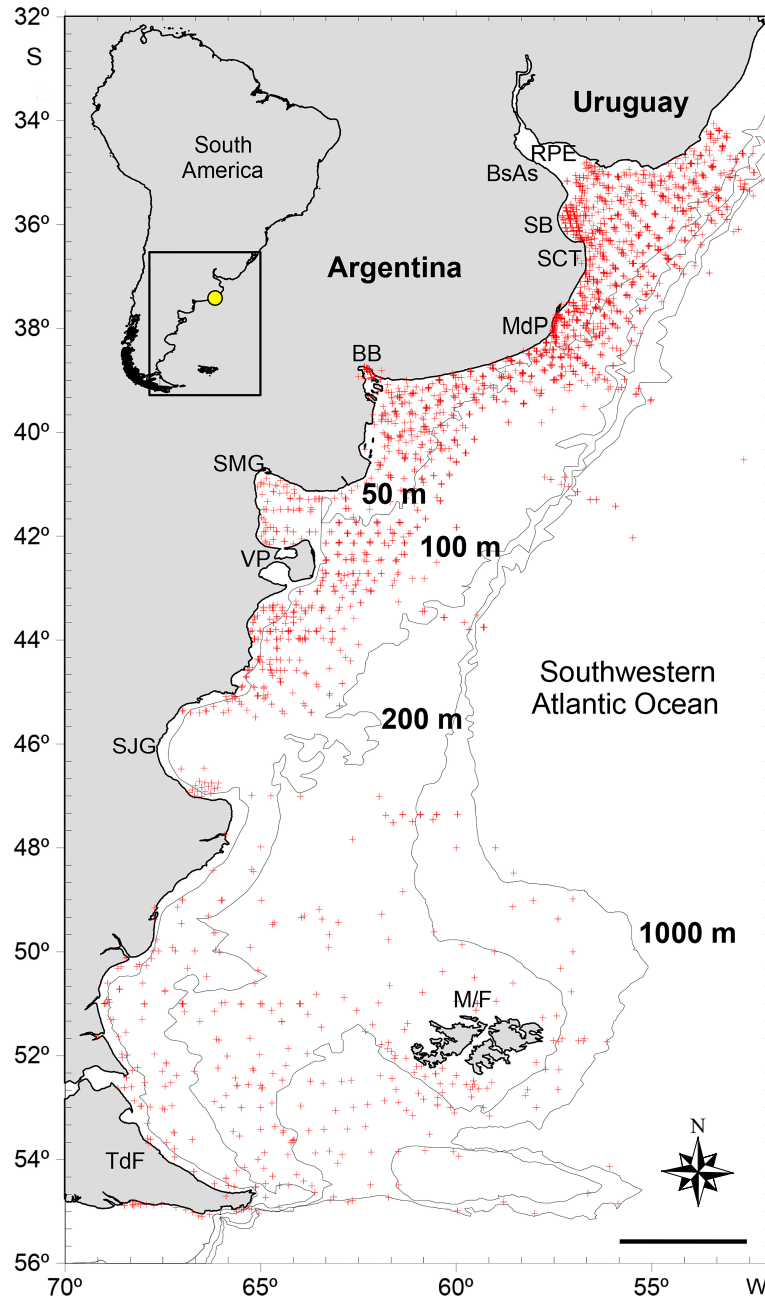

Fig. 1. Map of the study area: temperate Southwestern Atlantic waters. Yellow circle indicates the area studied for seasonality variation (Mar del Plata Harbor, Argentina, 38°08'17"S-57°31'18"W); red crosses represent the zooplankton samples of the dataset from the Medusae collection. RPE (Rio de la Plata estuary); BsAs (Buenos Aires); SB (Samborombón Bay); SCT (San Clemente del Tuyú); MdP (Mar del Plata); BB (Bahía Blanca); SMG (San Matías Gulf); VP (Valdés Peninsula); SJG (San Jorge Gulf); TdF (Tierra del Fuego); M/F (Malvinas/Falkland Islands). The fine lines represent the 50, 100, 200, and 1000 m isobaths in the region. Scale bar = 250 km.

environment. A general size-frequency histogram per host was constructed to analyze the occurrence of the different host sizes with the presence/absence of polypoid phase of *C. octonaria*. The length classes were arbitrarily defined by applying the Sturges' rule (Zar 1999). Possible differences between the sizes of parasitized and non-parasitized hosts were analyzed by a Student's t-test (Sokal and Rohlf 1999).

After checking for the normality of the data distribution and homogeneity of variance, we used Pearson's correlation coefficient (r) (Zar 1999) to analyze the relationship between the host size and prevalence and intensity of infection for each size group. After calculating the coefficient (r) and evaluating its significance, a Student's t-distribution test was applied. Considering the number of medusoid buds per host and using the r-coefficient, we examined the correlation of each size group. The level of statistical significance was $P \leq 0.05$ for all analyses. The assumption of normality of data (Kolmogorov-Smirnov test) and homogeneity of variance (Levene test) were verified using the previous normalization with logarithmic transformation of the data (Zar 1999). To estimate the distribution of *C. octonaria* in the host population, we calculated the aggregation coefficient (k) of the negative binomial distribution. This analysis determined whether the host species had a normal, random or overdispersed distribution (Morales and Pino 1987).

The concept of host range (Rohde 2005) was used to classify parasitic species as specialists or generalists. According to this concept, a specialist parasite species has a marked affinity for a specific host family, genus or species, while a generalist parasitizes hosts from a number of different taxa. For this analysis, we reviewed the available literature on the associations between genus *Cunina* and other hosts species. We examined the gut content of the all *L. tetraphylla* organisms (including parasitized and non-parasitized) in terms of vacuity (*i.e.*, presence or absence of stomach content), which could be an indicator of the negative effects *C. octonaria* caused *L. tetraphylla*. Subsequently, the metadata associated with the MedCol served to determine A) the areas of spatial co-occurrence of *L. tetraphylla* and *C. octonaria* and B) geographical areas and the seasonality where this parasitic association was observed.

RESULTS

Spatial distribution of *Cunina octonaria* in temperate Southwestern Atlantic waters

According to the data from the MedCol, this narcomedusa was found in 28 of 3,288 zooplankton samples (0.85%). It had a spatial distribution from 34.8–38.2°S and 57.5–54.0°W (*i.e.*, from southern Uruguayan coasts to waters of central-northern Buenos Aires Province, Argentina) (Fig. 2A). The main occurrence was observed in the estuarine area of the Río de la Plata. All samples showing *C. octonaria* specimens were collected at a depth lower than 50 m. Although, 92.85% of these samples ($n = 26$) were collected during the warm period and only 7.14% ($n = 2$) during the cold period, no significant differences were observed ($x^2 = 2.0$, *d.f.* = 1, $P = 0.16$) regarding the frequency of occurrence between both periods. During the cold period, the specimens were collected only in San Clemente del Tuyú (~36°S–56.8°W) and Mar del Plata coasts (~38°S–57.5°W), with abundances of 0.04 to 1.08 ind.m^3 (Fig. 3A). During the warm period, the abundances ranged between 0.003 and 28.05 ind. m^3, showing the highest abundances ~130 km south of the Samborombón Bay, followed by the Río de la Plata estuarine area (close to Uruguay) (Fig. 3B). No significant differences were found in abundances between the warm and cold periods ($t = 0.89$, *d.f.* = 24, $P = 0.38$). *Liriope tetraphylla* showed a southern limit up to ~38°50'–40°S, ~60–61°W (~Bahía Blanca estuary, the adjacent shelf of El Rincón and Monte Hermoso, Buenos Aires Province, Argentina) (Fig. 2B) (see Dutto et al. 2019).

Analysis of parasitic association

In samples collected over the year (February 2014 to March 2015) in Mar del Plata Harbor, the free-swimming medusa of *C. octonaria* was only observed during the spring and summer seasons, with abundances ranging from 0.003 (October) to 3.82 ind. m^3 (February) (Table 1). In terms of seasonality, no significant differences were observed in the abundance values (ANOVA: $F = 1.62$; $P = 0.34$). *Cunina octonaria* was found in salinities ranging from 33.7 to 36, while the water temperature oscillated between 14 and 22.3°C. *Liriope tetraphylla* occurred year-round, with the highest abundances occurring during the warm period and the lowest in the cold seasons. Their monthly abundances ranged from 0.01 ind.m^3 (May) to 80.98 ind.m^3 (March) (Table 1). Significant differences were observed between climate seasons (ANOVA: $F = 14.30$, $P = 0.01$), particularly between autumn-spring (Tukey's HSD test = -1.70, $P = 0.01$), autumn-summer (Tukey = -2.28, $P < 0.01$), and winter-summer (Tukey's HSD test = -1.50, $P = 0.01$), *i.e.*, between the cold and warm periods.

A total of 18 gelatinous species were identified (14 hydromedusae, 1 scyphomedusae, and 3 ctenophores), of which the polypoid phase of *C. octonaria* was

only observed in association with *L. tetraphylla*. The parasites were observed during the spring and summer seasons, with water temperatures ranging from 14.0 to 22.0°C, and salinity from 34.0 to 36.0. Of the 21,734 *L. tetraphylla* individuals analyzed during the period of co-occurrence, 316 were infected (total prevalence = 1.45%). All hosts had a single stolon structure (intensity of infection) with medusoid buds, except for one that had two stolons. The number of medusoid buds per host ranged from 11 (December) to 29 (January). These values varied monthly (Table 2).

However, the umbrellar diameter (UD) of *L. tetraphylla* ranged from 0.5 to 14.3 mm, parasitized specimens oscillated from 1.7 to 7.0 mm. Medusae between 5 and 6 mm of the size-frequency histogram showed the highest number of parasitized specimens, with prevalence values of 2.5 and 3.5%, respectively (Fig. 4). No significant differences were observed between the UD of parasitized and non-parasitized specimens ($t = 1.0$, $d.f. = 281$, $P = 0.30$). No significant correlations between the UD and prevalence were observed ($r = 0.02$, $n = 244$, $P = 0.72$), nor between UD
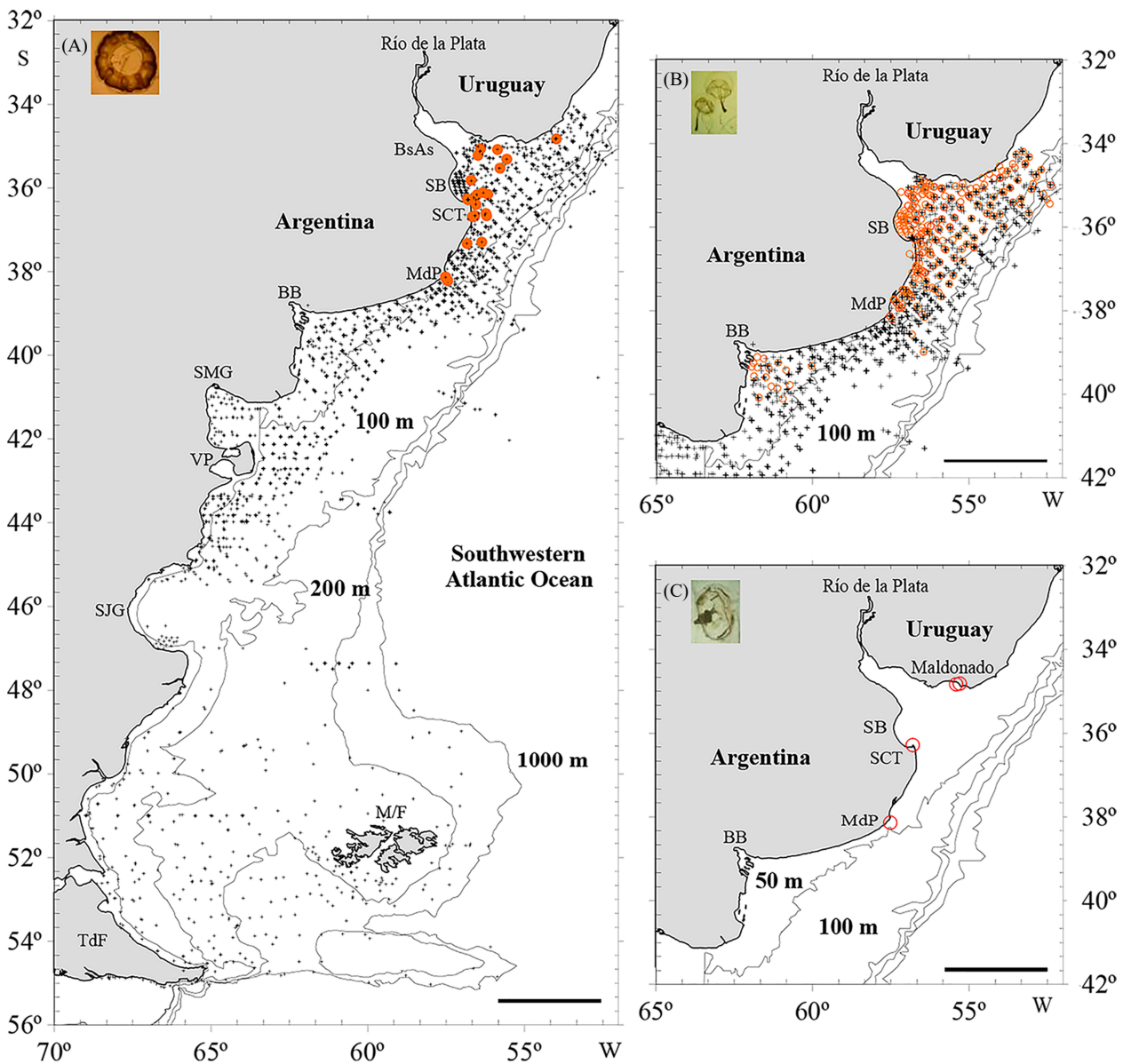

Fig. 2. Spatial distribution in temperate Southwestern Atlantic of the free-swimming medusa phase of *Cunina octonaria* (A) and *Liriope tetraphylla* (B) (including parasitized and non-parasitized specimens). Orange cycles represent the samples of zooplankton with species of medusa; black crosses represent the lack of individuals. (C) Areas of the association between the polypoid phase of *C. octonaria* and *L. tetraphylla* (red cycles). Acronyms in figure 1. Scale bars = 250 km.

and intensity of infection (number of stolons). However, a significantly positive correlation between the number of medusoid buds per host and the UD was observed ($r = 0.61$, $n = 73$, $P < 0.01$, $t = 0.16$, $d.f. = 71$, $P < 0.05$): *i.e.*, the number of medusoid buds increased as the UD of the *L. tetraphylla* increased.

The host species showed a parasite overdispersed distribution according to the aggregation coefficient ($k =$ 0.32). That is, most of the examined organisms harbored few or no parasites. In contrast, several host individuals contained a large number of this narcomedusa.

Observations *in vivo* showed that the stolon of *C. octonaria* had several medusoid buds in different growth stages; they protruded from the characteristic manubrium and gastric peduncle of *L. tetraphylla*. A section of the stolon was inside the manubrium and
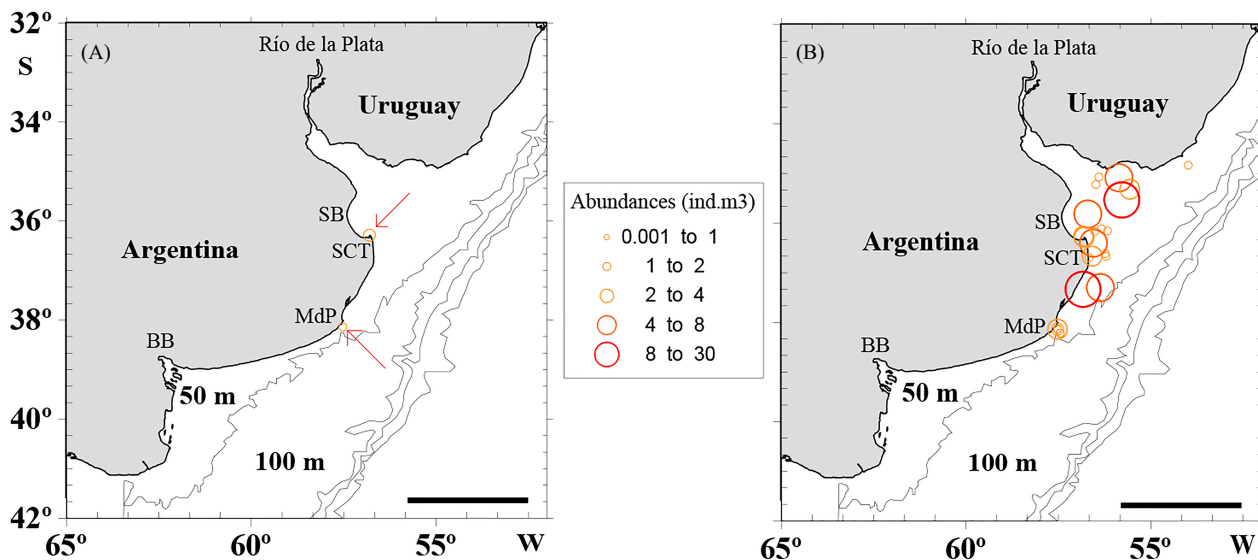

Fig. 3. Comparison of the spatial distribution of the abundances (ind.m3) of the free-swimming medusa phase of *Cunina octonaria* between the (A) austral cold (autumn-winter) and (B) warm periods (spring-summer) in temperate Southwestern Atlantic waters. Red arrows (2A) indicate the regions where in which abundances were recorded during the cold period. Acronyms in figure 1. Scale bars = 250 km.

Table 1. Abundance values (ind.m^3) of the free-swimming medusa phase of *Cunina octonaria* and *Liriope tetraphylla* during the study year (February 2014 to March 2015) in Mar del Plata Harbor, Argentina

	Cunina octonaria	*Liriope tetraphylla*	Water temperature (°C)	Salinity
2014				
February	0.29	10.90	22.0	35.0
March	0.08	80.98	19.1	35.0
April	0.04	0.27	15.3	35.0
May	0	0.01	14.2	35.0
June	0	0.08	11.7	34.0
July	0	0.41	10.4	35.0
August	0	1.45	9.8	35.0
September	0	0.26	11.8	34.0
October	0.003	4.22	14.0	33.7
November	0	0.73	16.3	36.0
December	1.16	19.53	18.8	34.0
2015				
January	0.73	20.99	19.3	35.3
February	3.82	5.22	21.2	36.0
March	0	19.95	22.3	36.0

another one on the outside (Fig. 5A–D). All stolon structures had medusoid buds. The stolon had an elongated and cylindrical shape widening in the basal region to the interior of the manubrium, while the external side had flat or oval shapes (Fig. 5C–D). Newly liberated medusae and free-swimming medusa of *C. octonaria* are shown in figure 5E–F.

In addition to the Mar del Plata, we identified the association in San Clemente del Tuyú (Argentina) (36°21'S–56°43'W), but Castiglioni and Failla Siquier (personal observations) also identified it in Maldonado, Uruguay (34°38'S–54°5'W). These findings indicate that the association is present off both coasts of the Río de la Plata estuarine area (Uruguay-Argentina) (Fig. 2C). On Mar del Plata coasts, the association was observed in the austral spring (October and December) and summer (from January to March), while in San Clemente del Tuyú, it was observed during the mid-autumn (mid-April and mid-May). Finally, on the Uruguayan coasts, it was identified from January to March (summer to early autumn).

A general analysis of the gut content of all individuals of *L. tetraphylla* when associations occurred showed that the stomachs of the parasitized individuals were completely empty, whereas some of the non-parasitized organisms had chaetognaths, crustaceans, and detritus. This vacuity might be due to the location of the polypoid phase, which prevented food intake.

DISCUSSION

Spatial distribution of *Cunina octonaria* and *Liriope tetraphylla* in temperate Southwestern Atlantic waters

Cunina octonaria is a Narcomedusae widely distributed in the Pacific, Atlantic, and Indian Oceans (Burke 1975; Segura-Puertas 1984; Galea 2007; Segura-Puertas et al. 2009; Andrade Ruíz 2010; Oliveira et al. 2016; Schuchert 2020). In the SWAw it has been identified from Colombia to Argentina (Oliveira et al. 2016). In the present study, we described the distribution in temperate waters, going from the southern Uruguayan to Mar del Plata coasts (~38°S) as the southern limit, with the higher abundances and frequency of occurrence in the Río de la Plata estuary and adjacent waters. However, according to Zamponi (1983), isolated records have shown its presence near the Malvinas/Falkland Islands (~51°46'S–59°31'W). Although we reviewed more than 3,200 zooplankton samples, ~20% ($n = 647$) of which were distributed under this latitude, *C. octonaria* was not found in the samples from the region indicated by Zamponi (1983); therefore, his finding could not be confirmed.

During the study year in Mar del Plata, *C. octonaria* was found in temperatures between 14 and 22.3°C. According to Soares Moreira (1978), in laboratory conditions, *C. octonaria* shows little
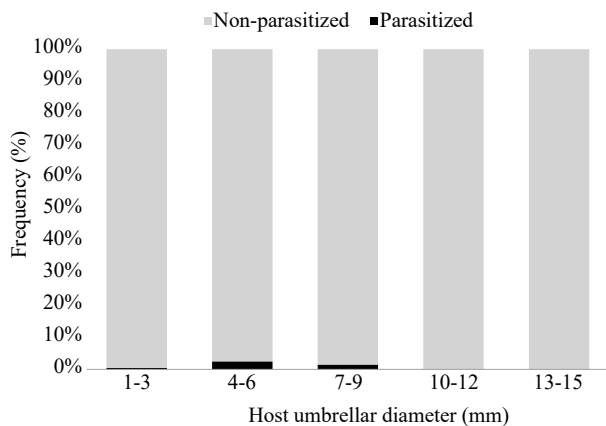

Fig. 4. Percentage of parasitized and non-parasitized *Liriope tetraphylla* for the different size classes. Grey bars: pooled data of non-parasitized hosts; black bars: specimens parasitized with polypoid phase of *Cunina octonaria*.

Table 2. Period of co-occurrence and parasitological parameters (prevalence and intensity of infection) of the association between *Liriope tetraphylla* (*Lt*) and *Cunina octonaria* (*Cu*) at Mar del Plata Harbor, including measurements of physicochemical and biological parameters

Period of co-occurrence	Total number of *Lt* analyzed	Total number of *Lt* parasitized	Prevalence (%)	Intensity of infection	Number of medusoid buds of *Cu* Min-Max	Surface water temperature (°C)	Salinity
February 2014	336	7	2.1	1	11-14	22.0	35.0
March 2014	14,757	44	0.3	1	12-21	19.1	35.0
October 2014	1,925	2	0.1	1	11-13	14.0	33.7
December 2014	549	1	0.2	1	12-18	18.8	34.0
January 2015	4,167	262	6.3	1-2	13-39	21.2	36.0
Total	21,734	316	1.5	2			

tolerance to low temperatures, and grows ideally at 15°C. At 10°C the specimens crumped, while at 5°C they became completely quiet. Therefore, it is possible that the Patagonian and Sub-Antarctic regions are unfavorable zone for *C. octonaria* due to their low temperatures, mainly during the austral cold period.

During the cold period, the shelf circulation of the temperate SWA consists of the northward flow cold waters of the Malvinas/Falkland Current, which is characterized by low-salinity and nutrient-rich waters. In contrast, during the warm period, the influence is from the southward tropical-subtropical flow warm waters of the Brazil Current, characterized by oligotrophic and salty waters (Piola and Matano 2001; Piola et al. 2010). According to Vannucci (1957) and Navas-Pereira (1973), *C. octonaria* is a typical species in the Brazil Current. Earlier records confirm this to be a widely distributed frequent species in warm waters (Kramp 1965); consequently, the fact that this narcomedusa was only found during the warm period and sporadically at the early autumn could be due to

passive transportation through the warm current. In this context, the contribution of the Río de la Plata waters are a natural barrier to the distribution of different marine organisms (Boltovskoy et al. 1999). However, this barrier is intermittent because, in periods of low flow and with the effects of northeastern winds, it is possible to find species that usually live in northern areas of Argentina (Uruguay and Brazil), in southern regions and localities such as Mar del Plata (Mianzan et al. 2001; Mianzan and Acha 2008).

On the other hand, several studies have focused on *L. tetraphylla* because it is the most frequent taxon in temperate SWAw (Dutto et al. 2019). This species was mainly found in the Río de la Plata estuary and surrounding areas (Fig. 4B). During the study year in Mar del Plata, *L. tetraphylla* was observed in temperatures between 9.8 and 22.3°C and salinity ranging from 33.7 to 36 (Puente-Tapia and Genzano 2019). According to Vannucci (1957), this species showed optimal temperatures from 20 to 25°C and 35–36 of salinity. However, it was observed in strongly
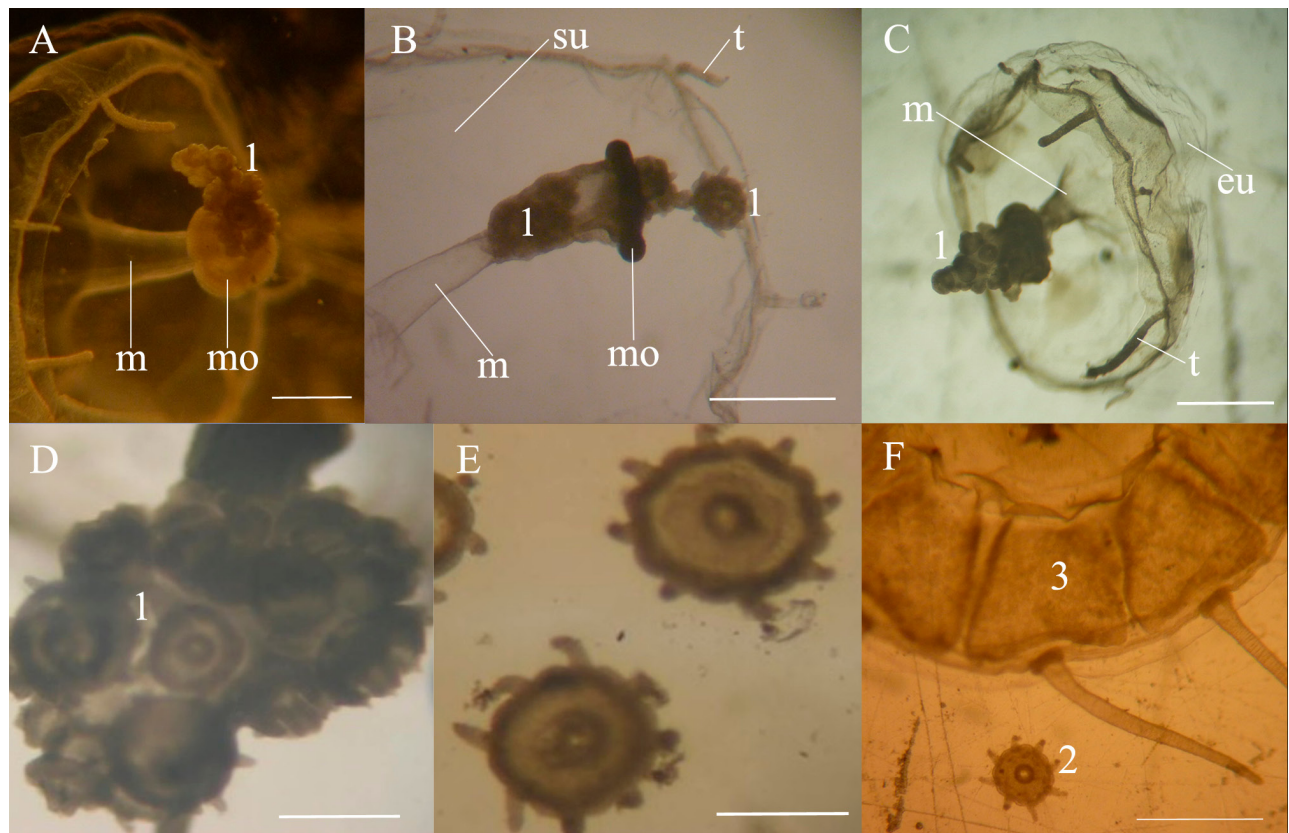

Fig. 5. Parasitic association between the polypoid phase of *Cunina octonaria* (1) (parasite) and *Liriope tetraphylla* (host) from Mar del Plata, Argentina. (A-D) Location of the stolon in the manubrium and gastric peduncle of *L. tetraphylla*; (D) detail of the stolon and the medusoid buds; (E) newly liberated medusae from the stolon; (F) comparison between newly liberated medusa (2) and adult individual (3) of *C. octonaria*. Lowercase letters indicate the structure of the host species: m (manubrium); mo (mouth); su (subumbrella); t (tentacles); eu (exumbrella). Scale bars: A–C and F = 1 mm; D–E = 500 μm.

diluted surface waters at the mouth of the Amazon river. The spatial distribution of *L. tetraphylla* was observed up to ~Bahía Blanca estuary, the adjacent shelf of El Rincón and Monte Hermoso coasts (Buenos Aires Province, Argentina). Historically, this medusa has been identified as a dominant species in the zooplankton community in some productive areas of the Argentine Sea (Zamponi and Genzano 1994; Sorarrain 1998); it reaches high abundances up to 4.7×10^6 ind.m^3 (Mianzan et al. 2000). Even though *L. tetraphylla* is one of the most abundant and common medusae in temperate SWAw (Mianzan and Guerrero 2000; Mianzan et al. 2000; Gaitán 2004; Failla Siquier 2006; Dutto et al. 2017), the parasitic association with *C. octonaria* had not previously been reported in the region.

Host selectivity

Analyzing the parasitic association over a year in Mar del Plata allowed us to observed the host specificity of *L. tetraphylla*. We took several factors into account to try to identify the reason behind this selectivity in this South Atlantic region: A) the parasite feeding, B) spatial distribution, C) abundances, and D) swimming behavior of the host, and E) the characteristic manubrium and gastric peduncle of *L. tetraphylla*. These factors are discussed below; however, these aspects arose when we compared our observations with the background information.

A) *Parasite feeding strategy*: host specificity is often the result of eco-biological factors such as parasite feeding (Rohde and Rohde 2005). We found feeding similarities between the polypoid phase of *C. octonaria* and its medusa phase; thus, analyzing both phases might explain the selectivity. Some parasites infect many hosts, but only those with similar feeding habits (Rohde and Rohde 2005). Although *L. tetraphylla* feeds on crustaceans, chaetognaths (Puente-Tapia personal observations), fish eggs, and larvae (Mianzan et al. 2012), Narcomedusae seem to feed primarily on soft-bodied prey such as pelagic individuals (Purcell and Mills 1988). However, in *Cunina*, the parasitic polypoid phase not only absorbs the reproductive tissues of the host (gelatinous individual), but also ingests food captured by the host (Raskoff and Robison 2005). Therefore, this polypoid structure shares a similar diet with the medusa phase, feeding on gelatinous organisms, with an additional food source to "steal" from the host. According to Lima and Valentin (2001), the associations may be that of a simple guest (only feed on the food taken by the host) or as a parasitism if the parasite uses the tissue of the host as a source of nutrition. The polypoid of *C. octonaria* exhibits both feeding strategies.

B) *Spatial distribution of the host*: The spatial distribution of the parasites may be determined by the host distribution (Marcogliese 2002). Both *C. octonaria* and *L. tetraphylla* share almost the same spatial distribution, with a southern limit of co-occurrence on the Mar del Plata coasts. In Argentina Sea, some of the host species previously identified for *C. octonaria* have been reported (Table 3), which shown a southernmost limit distribution (Patagonian and Sub-Antarctic regions) with respect to *L. tetraphylla* (Rodríguez 2012). Despite that, *C. octonaria* was absent off of these coasts, suggesting a close relationship with *L. tetraphylla*. There is no "universal" parasite that infects all available microhabitats on all available host species. In other words, each parasite species occupies a particular niche: it is microhabitat-and host-specific (Marcogliese 2005).

Although *C. octonaria* is considered an oceanic species (Johnson and Allen 2005), in the temperate SWAw it was located at a depth less than 50 m, that is, shallow waters. Although some *L. tetraphylla* individuals were observed between the 50 m and 100 m isobaths, a high proportion of the positive samples were located at less than 20 m deep (Fig. 2B). Certain ecological patterns emerge from the distribution of parasites in marine waters. Horizontal gradients exist in parasite diversity, with more species in shallow waters as a result of the wide range of available hosts (Marcogliese 2002). In pelagic waters, parasite species richness declines with depth and then increases in the bottom waters (Marcogliese 2005 and references therein).

C) *Host abundances*: *Cucina octonaria* and *L. tetraphylla* showed a co-occurrence during the warm period. During this period, *L. tetraphylla* had high abundances (Mianzan et al. 2000), which is a factor that could facilitate the encounter between the two species (in this instance, the medusa phase of *L. tetraphylla* and the larval stage of *C. octonaria*) and begin the parasitic association. Being extremely diffuse, the marine environment forms unique barriers that theoretically could prevent parasite infection. In some cases, parasites are typically short-lived (Marcogliese 2005) and needs to rapidly find the host individual. The highest abundances of *L. tetraphylla* occur during the warm period and coincide spatiotemporally with *C. octonaria*, which might represent an advantage for the parasite phase of this narcomedusa and help it penetrate the host and continue its life cycle. However, during the warm period of the study year, we identified other medusae with similar or even higher abundances than *L. tetraphylla*, such as the leptomedusae *Obelia* sp. and *Eucheilota ventricularis* McCrady, 1859 on the coasts of Argentina (Puente-Tapia and Genzano 2019), and *Eucheilota maculata* Hartlaud, 1894 and

Clytia hemisphaerica (Linnaeus, 1767) on the coasts of Uruguay (Failla Siquier personal observation). A question arose from observing these medusae: Why was *L. tetraphylla* the only host species? The ability to infect a wide range of hosts further helps parasites to survive in an otherwise unforgiving habitat (Marcogliese 2005).

D) *Swimming behavior of the host*: Parasitism of hydromedusae is not unusual, and the slow movement of many species allows pelagic or benthic parasites to take up residence for either locomotion or protection (Lucas and Reed 2009). According to Osborn (2000), the swimming behavior of the medusae might favor contact with parasites and increase the encounter rate. The feeding strategy of *L. tetraphylla* involves spreading its tentacles and remaining still in that position to wait for its prey (Mills 1981; Puente-Tapia personal observations). This posture could make it easier for the larvae of *C. octonaria* to be pulled or sucked into the stomach cavity or gastric system (including the manubrium), where they may remain during their development.

In general, we observed two types of feeding-swimming strategies of the most abundant species during the study year: filter-feeding (*Obelia* sp. and *E. ventricularis*) and ambush predation (*L. tetraphylla*) (Sutherland et al. 2016). During filter-feeding, the umbrella of the species continuously pulses, bringing water into the individual's mouth (Boero et al. 2007), which could prevent *C. octonaria* from entering into the umbrella cavity. In ambush predators, the individual remains in apparent quiet for at least several seconds while waiting for its prey (Puente-Tapia personal observations).

Some parasite stages may be transmitted by swimming and searching out a susceptible host and penetrating it. Those forms that are passively transmitted are usually ingested by the appropriate host during the life cycle, allowing transmission to occur (Marcogliese 2005). In the case of medusae, the ciliated planula larva has been interpreted as having a motile stage (Bouillon and Boero 2000), which lasts only from a few hours to a few days (Bouillon 1994). Therefore, it is essential to analyze the possible chemical signals of the host species to determine if the larva is attracted. Thereon, infective stages exhibit further morphological and behavioral adaptations that increase the probability of parasitism. Those that are passively transmitted may resemble typical prey of the target host. Actively transmitted stages display behaviors such as phototropism, geotropism, or the timing of hatching or

Table 3. List of species in the genus *Cunina* under parasitic association with other hydromedusae as hosts

Parasite species	Host species			Reference
	Order	Family	Species	
Cunina octonaria	Anthomedusae	Cytaeididae	*Cytaeis tetrastyla*	9,10
		Protiaridae	*Halitiara inflexa*	9,10
		Teissieridae	*Teissiera medusifera*	10
		Oceaniidae	*Turritopsis nutricula*	2,5,6,13
	Leptomedusae	Laodiceidae	*Laodicea undulata*	7,10
		Campanulariidae	*Clytia hemisphaerica*	11
	Trachymedusae	Rhopalonematidae	*Aglaura hemistoma*	13
			Aglaura sp.	2
			Rhopalonema velatum	13
	Limnomedusae	Geryoniidae	*Liriope tetraphylla*	2,9,10,12,13
			Geryonia proboscidalis	3,7,10,13
	Narcomedusae	Cuninidae	*Cunina octonaria*	1,13
Cunina peregrina	Trachymedusae	Rhopalonematidae	*Aglaura hemistoma*	7,10,13
			Rhopalonema velatum	3,7,10,13
	Narcomedusae	Cuninidae	*Cunina octonaria*	8
			Cunina peregrina	13
		Solmarisidae	*Pegantha martagon*	10
		Solmundaeginidae	*Solmundella bitentaculata*	10
Cunina proboscidea	Limnomedusae	Geryoniidae	*Geryonia proboscidalis*	4,13
Cunina becki	Narcomedusae	Cuninidae	*Cunina peregrina*	10,13

1) Mayer (1910); 2) Vannucci (1957); 3) Kramp (1959); 4) Kramp (1961); 5) Calder (1968); 6) Calder (1971); 7) Bouillon (1978); 8) Goy (1979); 9) Bouillon et al. (1986); 10) Bouillon (1987); 11) Zhenzu and Huiduan (1994); 12) present study; 13) references cited in Bouillon (1987).

emergence that serve to place them in the target host habitat (Williams and Jones 1994). These stages may be chemically attracted to the host over small spatial scales (Marcogliese 2005).

E) *Manubrium and gastric peduncle of the host*: The peculiar manubrium and the cylindrical gastric peduncle of *L. tetraphylla*, which is longer than umbrella diameters (Bouillon et al. 2004), are possibly some of the most visible morphological differences between *L. tetraphylla* and the other medusae species identified in the study area. For example, the leptomedusae *Obelia* sp. and *E. ventricularis* have a small manubrium or lack gastric peduncle (*Obelia* sp.) (Bouillon et al. 2004). But is the manubrium one of the determining factors of host selectivity in the region? The manubrium and gastric peduncle of the previously identified host species of *C. octonaria* display various forms and sizes: *Turritopsis nutricula* McCrady, 1857 has a large manubrium; *Aglaura hemistoma* Péron and Lesueur, 1810 has a small manubrium and a somewhat shorter gastric peduncle than subumbrella radius; *Rhopalonema velatum* Gegenbaur, 1857 has a manubrium narrow reaching extended almost velar opening; *Geryonia proboscidalis* (Forsskål, 1775) is almost similar to *L. tetraphylla* (Bouillon et al. 2004); while *C. octonaria* lacks a manubrium (Bouillon et al. 2004 2006). Therefore, the manubrium does not seem to be the determining factor in host selectivity.

Other remarks

The parasitic association was observed in three different areas: Maldonado (Uruguay), San Clemente del Tutú and Mar del Plata coasts (Argentina). However, in different sectors of the Brazilian coasts, the larval phase of *Cunina* sp. parasitizes *T. nutricula* and *Proboscidactyla ornata* (McCrady, 1859); two larvae of *C. octonaria* were observed on *Aglaura* sp. (Vannucci 1957); while in the São Sebastião Channel (Brazil; Tropical SWAw), the manubrium of *L. tetraphylla* was observed with larvae of *Cunina* (Migotto 2020).

After the reviewing the available literature, we found four different species in the genus *Cunina* that had parasitic associations with other medusae. Eleven hosts species have been identified for *C. octonaria*. Hence, this review allowed us classify *C. octonaria* as a generalist species according to the concept of host range (Rohde 2005) (Table 3). Three other species in the genus *Cunina* have been found to parasite medusae: *C. peregrina* Bigelow, 1909 was observed in association with six species, while *C. proboscidea* Metschnikoff and Metschnikoff, 1871 and *C. becki* Bouillon, 1985 had exhibit only one host species each, until now. Although parasites are often generalists, they are linked

to particular types of host functional groups or feeding guilds. Members of such guilds share lifestyles, diet preferences, and depth ranges. Consequently, members of these guilds often share a similar parasite fauna whose constituent species follow common transmission pathways (Marcogliese 2002).

Moreover, the present study found only one stolon of *C. octonaria* per host (only one specimen had two stolons), but Bouillon (1987) described specimens parasitized by up to three different stolons in a single host (two was the most common number). We could not analyze all the negative effects of the polypoid of *C. octonaria* on *L. tetraphylla*; however, we observed that all parasitized organisms had an empty stomach, possibly due to the location of the stolon in the mouth opening, which prevented *L. tetraphylla* from feeding.

The distribution of *C. octonaria* in *L. tetraphylla* populations agrees with the aggregate distribution pattern that is typical in parasite species (Bush et al. 2001). Most parasite species are not randomly or uniformly distributed in host populations; they show an aggregated (overdispersed) distribution, that is, some individuals of host populations are more heavily infected than expected in a random distribution, and others are less infected of not infected at all (Rohde 1984). Several factors contribute to the aggregation distribution: a single parasitic individual may multiply on or in the host, as observed in the *C. octonaria* life cycle. This distribution pattern stabilizes the host-parasite association. Some biological function of this parasitic aggregation could be considered an effect "in favor" of the host population. Since few hosts were heavily infected, only they died. The death of these hosts could ensure the completion of the life cycle of a parasite that depends on being eaten by the next host, but the host population as a whole is not greatly affected (Rohde 1984 and references therein).

CONCLUSIONS

The life cycle with indirect metagenetic and parasitic development of *Cunina octonaria* (Bouillon 1987) has some advantages; for example, the use as substrate a free swimming medusa, allows it to have access to additional food sources (Raskoff and Robison 2005), as well as greater spatial dispersion compared to a species with benthic polyps (Boero et al. 2008). The diversity and plasticity of the "traditional" life forms and life history modes across Medusozoa means that medusae can colonize a plethora of ecosystems (Lewis Ames 2018 and references therein). Based on previous observations, it has been concluded that the advantages to parasitism include brooding, protection and enhanced

survival of young by providing a safe, nutritive, and internal habitat for development (Osborn 2000).

An important factor that limits the number of hosts could be the availability of suitable host species (Rohde and Rohde 2005). The Uruguayan and Argentine waters are characterized by high species diversity, including multiple corporal forms, life cycles, seasonality, abundances, feeding strategies, and swimming behavior. However, taking into account the parasite feeding, spatial distribution, abundances, swimming behavior of *L. tetraphylla*, and its characteristic manubrium and gastric peduncle, it is difficult to explain the host selectivity toward *L. tetraphylla* in this temperate region. The combination of two or more of the above mentioned factors could explain the host selectivity of *C. octonaria*. Therefore, extensive research using molecular markers or chemical analysis is needed to prove this specificity (Ohtsuka et al. 2009).

Temperate SWAw represents a favorable region for both *C. octonaria* and *L. tetraphylla* to complete their particular life cycles. The food availability in this region meets the energy requirements of both species. The medusa phase of *C. octonaria* could benefit from the large amount of available food, to eat and reproduce, while their larva stage could use the high abundances of *L. tetraphylla* to facilitate the encounter, start the parasitic phase and the subsequent feeding and reproductive advantages. Thus, a chain of hydro-eco-biological events is observed, in which each species benefits from some of these factors to complete their life cycle.

Our dataset indicates that the Argentine Sea represents the southern limit of the distribution of this interaction in the SWAw. Finally, this study increases the knowledge about biological associations between GZ and other groups living on the Uruguayan and Argentinean coasts. However, it is necessary to conduct more zooplankton studies to identify the exact moment when the interaction begins, possible chemical-molecular signals between host and larva of *C. octonaria*, the effects on the host, and other regions where the association could exist.

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