

Biodiversity of planktonic hydrozoans from a subtropical estuary: evidence of assemblage structure change

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The present study provides a comprehensive survey of the planktonic hydrozoan fauna from the Paranaguá Estuarine System (PES; southern Brazil, 25°S 48°W), a subtropical estuary considered a Natural World Heritage site by UNESCO. Extensive collections were performed throughout the estuary in five sampling campaigns during the summer and winter periods of 2012 and 2013 and summer of 2014, totalling 185 samples. About 49,000 organisms were analysed which together with the few previous records resulted in a total of 36 hydromedusae and three siphonophore species. We highlight the presence of Cnidostoma fallax in high abundance (>19,000 individuals captured; ~40% of all planktonic hydrozoans). The high abundance of this species throughout three consecutive summers suggests a change in the local assemblage structure, since previous reports in the 1980s, 1990s and 2000s had shown Liriope tetraphylla recurrently as the dominant species which now ranks fourth. It is difficult to ascertain the causes of such changes due to the paucity of previous studies on Brazilian estuaries, but one possibility is that C. fallax has been recently introduced. In any case, the high dominance of this hydromedusa was not expected and this scenario would potentially cause changes in the local food web since C. fallax and L. tetraphylla are quite different morphologically and ecologically and thus probably play different trophic roles. Future studies are necessary to check the long-term permanency of C. fallax and to assess its biology and ecology and the impact of this assemblage change on the ecosystem.

Keywords: *Cnidostoma fallax*, NIS jellyfish, introduced species, ecosystem change, hydromedusae, siphonophores, marine conservation

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INTRODUCTION

The knowledge of species composition of a given ecosystem is one the most basic aspects of biodiversity research, being essential for natural resource management and to assure quality in biological and ecosystem sciences (Costello *et al.*, 2013). Many areas lack comprehensive systematic inventories and this is particularly true for marine ecosystems that in general are much less studied than terrestrial ones (Bouchet, 2006). Additionally, biodiversity is often considered to be under major threat mostly due to anthropogenic pressure (Carlton, 1996, 2000; Dulvy *et al.*, 2003; Costello *et al.*, 2013). However, the lack of historical data hampers an accurate detection of assemblage changes such as invasions and/or local extinctions. This may be particularly true for planktonic hydrozoans which are typically small, delicate and historically under-studied worldwide (e.g. Bouillon *et al.*, 2004), and particularly in Brazil (Haddad & Marques, 2009), underscoring

the need for comprehensive efforts to develop taxonomic inventories such as the present study.

Estuarine ecosystems are particularly vulnerable since they harbour an abundant and diversified biota (Dolan & Gallegos, 2001; Bouchereau *et al.*, 2008; Paiva *et al.*, 2013; Seguro *et al.*, 2015) and are often pressured by human occupation and activities nearby with associated impacts (e.g. Cremer *et al.*, 2006). Among the many human pressures, such as pollution and habitat fragmentation, growing attention has been given to non-indigenous species. There is an increased awareness that invasive species can change abundance of indigenous species and play an important role in species extinctions (Gallardo *et al.*, 2016), being considered a great threat to marine ecosystems.

The Paranaguá Estuarine System (PES) is one of the largest estuarine systems of South America, with ~550 km² of total water body (Noernberg *et al.*, 2006). PES harbours a large biodiversity and has been adopted a Natural World Heritage site by UNESCO (2016). Besides its ecological importance, PES is also important for harbouring two ports; the port of Paranaguá, the main South American grain-shipping port (Marone *et al.*, 2000), and the port of Antonina. No comprehensive surveys on planktonic hydrozoans from PES have been performed, despite their ecological importance (e.g. Matsakis & Conover, 1991; Mills, 1995) and high diversity. The few existing studies recorded 18 species, three of them

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regarded as probably exotic (Montú & Cordeiro, 1988; Nogueira Júnior & Oliveira, 2006; Bardi, 2011; Haddad *et al.*, 2014). In the present study we aim to provide a comprehensive overview of planktonic hydrozoan diversity from PES, along with evidence of regional assemblage change compared with the past decades.

MATERIALS AND METHODS

Planktonic hydrozoans were collected in five seasonal sampling campaigns: summer (13–16 March) and winter (23 and 24 August) 2012, summer (21 and 22 February) and winter (18 and 19 June) 2013, and summer (28 and 29 March) 2014. For each campaign, 37 stations were sampled (Figure 1), totalling 185 samples. PES can be divided in five sectors (Paranaguá, Antonina, Laranjeiras and Pinheiros Bays and a mixing zone) based on Noernberg *et al.* (2006). In the present study, with exception of Antonina Bay, all the sectors, along with two main tidal channels were sampled.

Oblique tows (speed = 2 knots for 2 min) from near the bottom to the surface were made, with a WP-2 plankton net (2 m long, 0.5 m mouth diameter, 200 μ m mesh) equipped with calibrated mechanical flowmeters Hydrobios in 2012 samplings campaigns and General Oceanics in 2013. Samples ($N = 185$) were preserved with a 4% formaldehyde (borax-buffered) solution for later analysis in the laboratory. In addition, surface temperature and salinity were measured at each station with a mercury thermometer and calibrated portable refractometer Atago, respectively.

Whole samples were analysed in the laboratory under a stereomicroscope and all the planktonic hydrozoans were sorted and identified (mostly following Bouillon, 1999 and Pugh, 1999). A list with all species found, along with the literature records was compiled and is presented (Table 1). Classification follows Schuchert (2016). The number of analysed individuals (colonies for siphonophores) and the frequency of capture of a given species are also tabulated.

Species accumulation curves and diversity estimators such as Chao 1 and 2, and Jackknife 1 and 2 were constructed for all sampling campaigns, using the program Primer v6 (Clarke & Gorley, 2006).

RESULTS AND DISCUSSION

In the present study we have sampled and analysed about 49,000 hydrozoan specimens belonging to 34 species, these being three siphonophores and 31 hydromedusae, apart from actinula larvae (Table 1). Some representative examples are shown in Figures 2–14. In many cases the quality of the material was not good, as is usual with these delicate organisms and therefore for detailed morphological analyses, examination of live organisms is recommended whenever possible. In the present collection, the diagnostic characters could be seen in most cases, allowing a reliable identification aided by the strong taxonomic background of some of the authors (LSN and MNJ). In fact, damaged unidentifiable organisms did not represent a significant proportion of the collection and accounted for less than 1% of the total organisms

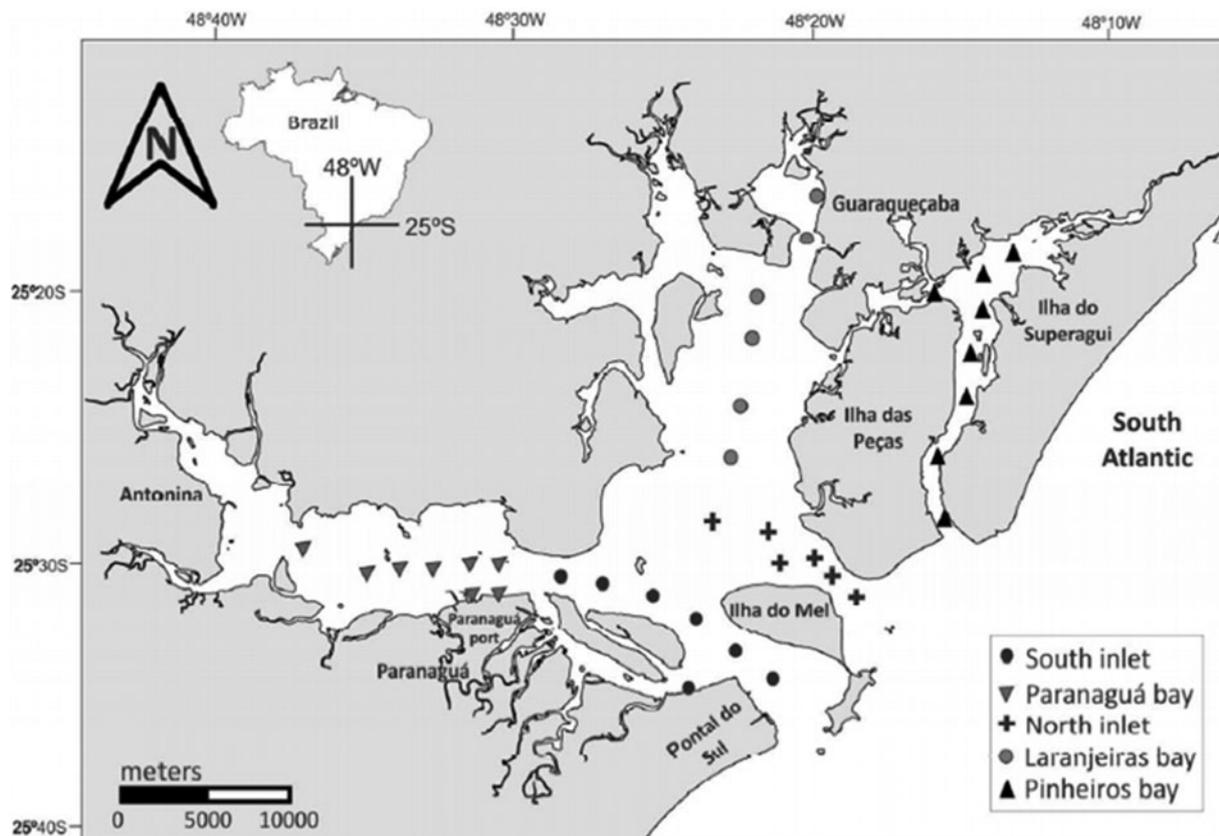


Fig. 1. Map of Paranaguá Estuarine System, southern Brazil, showing the 37 stations sampled on March and August 2012, February and June 2013, and March 2014, in each sector: inlets, mixing zone, Paranaguá, Laranjeiras and Pinheiros Bays. Map was made in the QGIS 2.18 software.

Table 1. Taxonomic classification, frequency of capture (FC) and number of individuals (colonies for siphonophores) of planktonic hydrozoans recorded in the present study, in Paranaguá Estuarine System, southern Brazil, from 185 plankton hauls.

Species	FC (%)	Number of individuals						S	T (°C)	PES sector	Data Source
		Total	Summer 2012	Winter 2012	Summer 2013	Winter 2013	Summer 2014				
Actinula larvae	23.2	945	667	121	145	0	12	33–23	30–19	In/MZ/Pguá/Lar/Pin	1
Subclass Hydroidolina Order Anthoathecata											
Suborder Filifera											
Family Bougainvillidae											
<i>Bougainvillia muscus</i> (Allman, 1863) ^a	19.4	92	34	29	4	7	18	34–16	29–20	Pguá/Pin	1,3
<i>Bougainvillia frondosa</i> Mayer, 1900	1.6	6	0	6	0	0	0	34–30	21–20	Pin	1
<i>Bougainvillia carolinensis</i> (McCrary, 1859)	2.1	8	8	0	0	0	0	29–10	30–20	Pguá/Lar	1,3
Family Hydractiniidae											
<i>Cnidostoma fallax</i> Vanhöffen, 1911	52.9	19455	16260	112	2910	1	172	34–17	31–20	In/MZ/Pguá/Lar/Pin	1
<i>Podocoryna loyola</i> Haddad et al., 2014 ^a	18.4	355	1	6	3	16	329	34–16	29–19	In/Pguá/Lar	1, 6
Family Rathkeidae											
<i>Lizzia blondina</i> Forbes, 1848	4.8	20	5	14	1	0	0	34–15	30–21	Pguá	1, 3
Family Oceaniidae											
<i>Turritopsis nutricula</i> McCrary, 1857	5.4	12	3	2	5	2	0	34–14	30–20	MZ/Pguá/Lar/Pin	1
Family Pandeidae											
<i>Amphinema dinema</i> (Péron & Lesueur, 1810)	7.0	157	0	154	1	0	2	34–16	28–19	In/MZ/Pguá/Pin	1
Family Proboscidae											
<i>Proboscidea ornata</i> (McCrary, 1857)	9.2	131	2	26	102	1	0	33–16	30–15	In/MZ/Pguá/Lar/Pin	1, 3
Family Rathkeidae											
<i>Podocorynoides minima</i> (Trinci, 1903)	–	–	–	–	–	–	–	30–10	31–19	Pguá	3
Suborder Capitata Family Corymorphidae											
<i>Corymorpha gracilis</i> (Brooks, 1883)	51.3	2739	246	1090	277	315	811	34–15	30–20	In/MZ/Pguá/Lar/Pin	1, 3
<i>Corymorpha forbesii</i> (Mayer, 1894)	2.7	27	0	0	1	26	0	30–21	29–20	Lar/Pin	1
<i>Corymorpha januarii</i> Steenstrup, 1855	1.6	5	0	0	2	1	2	30–21	28–20	Pguá/Lar	1
Family Moerisiidae											
<i>Moerisia inkermanica</i> Paltschikowa-Ostroumowa, 1925	–	–	–	–	–	–	–	20–0	30–24	MZ	2, 3
Family Corynidae											
<i>Stauridiosarsia reesi</i> (Vannucci, 1956)	7.0	19	10	3	6	0	0	33–20	31–21	In/MZ/Pguá/Pin	1
<i>Coryneeximia</i> Allman, 1859	–	–	–	–	–	–	–	15–10	–	MZ	3
Family Tubulariidae											
<i>Ectopleura dumortierii</i> van Beneden, 1844	31.9	950	150	696	88	14	2	34–16	31–21	In/MZ/Pguá/Lar/Pin	1, 3
Order Leptothecata Suborder Conica Family Blackfordiidae											
<i>Blackfordia virginica</i> Mayer, 1910	7.0	31	20	4	5	2	0	29–2	28–20	MZ/Pguá/Lar	1, 2, 3
Family Cirrholovenidae											
<i>Cirrholovenia tetranema</i> Kramp, 1959	2.2	4	1	0	2	1	0	31–20	31–21	MZ/Pin	1
Family Eirenidae											
<i>Eutima mira</i> McCrary, 1857	2.2	6	5	0	1	0	0	28–14	30–27	Pguá/Lar/Pin	1
<i>Helgicirra</i> sp.	2.7	8	0	1	0	2	5	25	20	Pguá	1

Continued

Table 1. Continued

Species	Number of individuals							S	T (°C)	PES sector	Data Source
	FC (%)	Total	Summer 2012	Winter 2012	Summer 2013	Winter 2013	Summer 2014				
Family Laodiceidae											
<i>Laodicea minuscula</i> Vannucci, 1957	2.2	7	4	2	0	0	1	31–28	30–24	MZ/Pguá/Pin	1
Family Lovenellidae											
<i>Eucheilota duodecimalis</i> A. Agassiz, 1862	51.3	1628	266	579	666	5	112	34–15	31–19	In/MZ/Pguá/Lar/Pin	1, 3
<i>Eucheilota paradoxica</i> Mayer, 1900	12.4	104	7	91	1	0	5	33–20	30–20	In/MZ/Pguá/Pin	1, 3
<i>Eucheilota maculata</i> Hartlaub, 1894	14.1	240	0	0	0	77	163	34–15	30–20	MZ/Pguá/Lar/Pin	1, 3
Family Malagazziidae											
<i>Malagazzia carolinae</i> (Mayer, 1900)	1.1	6	2	0	4	0	0	24–16	29	Pguá	1
Suborder Proboscoida											
Family Campanulariidae											
<i>Obelia</i> spp. ^a	80.5	8285	807	3011	2690	196	1581	34–15	30–19	In/MZ/Pguá/Lar/Pin	1, 3
<i>Clytia</i> spp. ^a	80.5	7609	1383	2688	3361	98	79	34–15	31–19	In/MZ/Pguá/Lar/Pin	1, 3
Order Siphonophora											
Suborder Calycophora Family Abylidae											
<i>Abylopsis tetragona</i> (Otto, 1823)	1.1	2	0	1	1	0	0	33–26	29–24	In	1
Family Diphyidae											
<i>Muggiaea kochii</i> (Will, 1844)	2.2	5	0	3	0	1	1	34–30	24–21	In/MZ	1, 5
Suborder Physonectae Family Agalmatidae											
<i>Nanomia bijuga</i> (delle Chiaje, 1844)	3.8	9	2	5	0	2	0	33–23	31–20	In/MZ/Pguá/Pin	1
Subclass Trachylina Order Limnomedusae Family Olindiasidae											
<i>Gossea brachymera</i> Bigelow, 1909	1.6	4	1	3	0	0	0	33–28	28–20	MZ/Pin	1
Family Olindiidae											
<i>Olindias sambaquiensis</i> Müller, 1861 ^b	–	–	–	–	–	–	–	–	–	Pguá	1
<i>Aglauropsis kawari</i> Moreira & Yamashita, 1972	0.5	1	0	0	0	0	1	32	27	In	1
Order Narcomedusae Family Cuninidae											
<i>Cunina octonaria</i> McCrady, 1857	10.2	67	0	58	9	0	0	34–17	28–19	In/MZ/Pguá/Lar/Pin	1
Family Solmarisidae											
<i>Solmaris</i> sp.	13.0	285	11	11	0	24	239	34–23	28–20	In/MZ/Pguá/Pin	1
Order Trachymedusae Family Geryoniidae											
<i>Liriope tetraphylla</i> (Chamisso & Eysesenhardt, 1821)	63.8	5547	707	3100	780	778	182	34–17	31–10	In/MZ/Pguá/Lar/Pin	1, 3, 4, 5
<i>Geryonia proboscoidalis</i> (Forsskål, 1775)	–	–	–	–	–	–	–	–	–	MZ/Lar	4
Family Rhopalonematidae											
<i>Aglaura hemistoma</i> Péron & Lesueur, 1810	0.5	1	0	0	0	1	0	34	21	MZ	1

Damaged and unidentifiable organisms (N = 173) were not included. Salinity (S) and temperature (T, in °C) range and PES sector occurrence of each species in the present study and in previous studies are also shown.

^aSpecies whose polyps have also been recorded in PES.

^bSpecimen only sighted. Data source: 1=present study; 2=Nogueira Júnior & Oliveira (2006); 3=Bardi (2011); 4=Montú & Cordeiro (1988); 5=Lopes *et al.* (1998); 6=Haddad *et al.* (2014); Bettim & Haddad (2017). In, inlets; MZ, mixing zone; Pguá, Paranaguá Bay; Lar, Laranjeiras Bay; Pin, Pinheiros Bay.

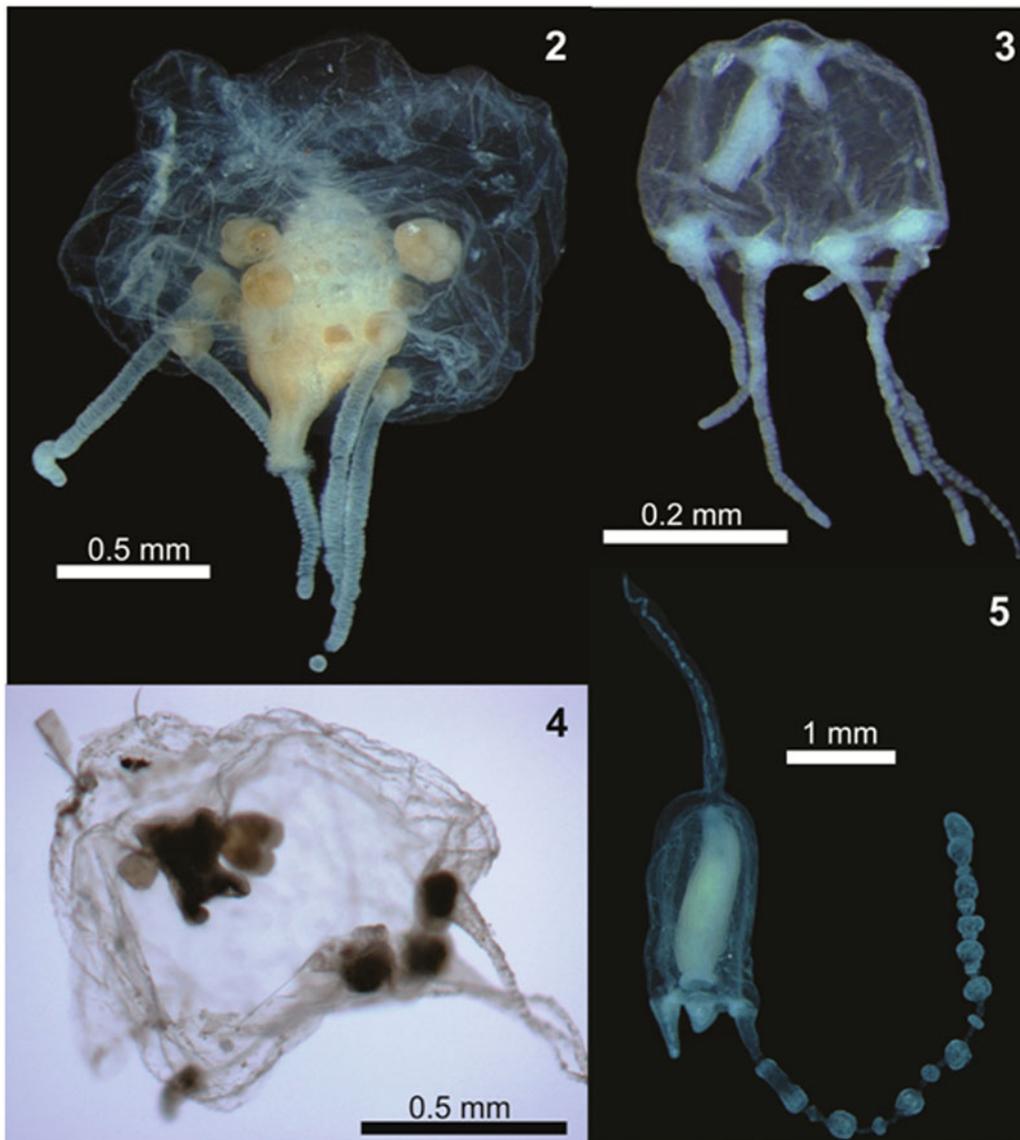


Fig. 2–5. Examples of planktonic hydrozoans from Paranaguá Estuarine System, southern Brazil. *Cnidostoma fallax*, lateral view (2); *Podocoryna loyola*, lateral view (3); *Proboscidaactyla ornata*, lateral view (4) and *Corymorpha gracilis*, lateral view (5).

recorded here. Four taxa, namely *Clytia* spp. (Figure 9), *Obelia* spp., *Solmaris* sp. and *Helgicirrha* sp. (Figure 8), could not be identified to species level since the latter is probably an undescribed species, and all the other genera have taxonomic problems (Nagata *et al.*, 2014a). All the planktonic hydrozoan species found here have already been recorded for the Brazilian coast (Oliveira *et al.*, 2016), but 19 species are new records for PES and nine for Paraná State (Table 1; Nagata *et al.*, 2014a). Although these new records fill gaps in their distribution their occurrence was expected, since polyps and/or medusae of them have been found to the south and/or north of the PES (Oliveira *et al.*, 2016).

The accumulated number of sampled species nearly stabilized (Figure 15), and the diversity recorded here (34 spp.) is quite similar to the estimators that reached up to 36 in the Jackknife 2, and is considerably greater than that estimated by the Chao 2 (Figure 15). Therefore, the diversity of planktonic hydrozoans estimated here can be considered robust, and only a few additional species are likely to be found in

future studies. Yet, the total species richness reported probably still is slightly underestimated due to the difficulty of identifying the different species of *Clytia* and *Obelia* based on medusa morphology, the notorious fragility of planktonic hydrozoans which result in damaged and unidentifiable individuals (even when relatively few) that could represent additional species. Moreover, the use of different gear types also may help to find additional species such as *Rhacostoma atlanticum* and *Olindias sambaquiensis*, not sampled here but known to commonly occur in coastal waters nearby and occasionally entering estuaries (Nogueira Júnior *et al.*, 2010; Nogueira Júnior, 2012). These species are usually large-sized (reaching up to >40 mm) and thus rarely sampled in standard zooplankton nets as used here (Nagata *et al.*, 2014a). In fact, *O. sambaquiensis* has been observed a few times in the PES tidal channels in samples with larger nets not included here (LSN, personal observations). Sampling in other seasons also could result in additional species. For instance, *Octophialucium haeckeli* was not found here at PES perhaps due to absence

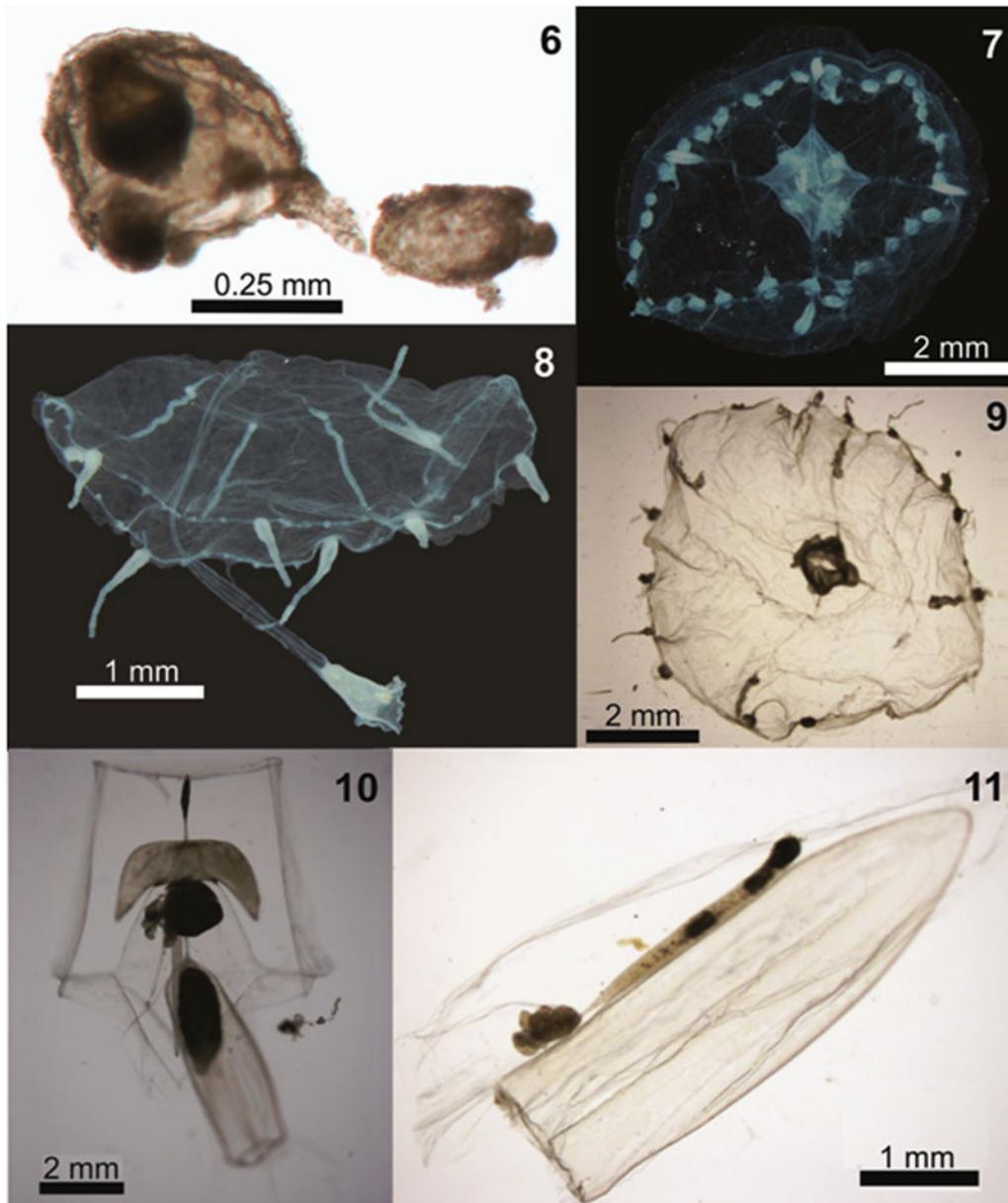


Fig. 6–11. Examples of planktonic hydrozoans from Paranaguá Estuarine System, southern Brazil. *Corymorpha forbesii*, lateral view (6); *Malagazzia carolinae*, oral view (7); *Helgicirrha* sp., lateral view (8); *Clytia* spp., oral view (9); *Abylopsis tetragona* eudoxid (10) and *Muggiaea kochii*, lateral view (11).

of sampling in autumn and/or spring seasons when this medusa was found in more southerly estuarine waters (Nogueira Júnior *et al.*, 2015). Nevertheless, the other three species exclusively found in these seasons (see Nogueira Júnior *et al.*, 2015; their supplementary online material table 1), namely *Amphinema dinema*, *Gossea brachymera* and *Abylopsis tetragona*, were sampled in the present study (Table 1).

The limited literature data available indicate that four additional species can be included in the PES planktonic hydrozoan checklist: *Moerisia inkermanica* Paltschikowa-Ostroumowa, 1925, *Coryne eximia* Allman, 1859, *Podocorynoides minima* (Trinci, 1903) and *Geryonia proboscidalis* (Forsskål, 1775) (Montú & Cordeiro, 1988; Nogueira Júnior & Oliveira, 2006; Bardi, 2011; Table 1), that along with *O. sambaquiensis* (see above) totals 39 species. The general species composition of planktonic hydrozoans from PES is a highly diverse estuarine

fauna, with many brackish-water tolerant species. Typical examples are *Cnidostoma fallax*, *Moerisia inkermanica* and *Malagazzia carolinae* which are more abundant or exclusive inside estuaries (Teixeira-Amaral *et al.*, 2017; Nogueira Júnior *et al.*, 2018; Nogueira Júnior & Silva Nascimento, 2018) rather than on the adjacent shelf (Vannucci, 1957, 1963; Nagata *et al.*, 2014a).

The PES fauna is quite similar to other tropical/subtropical estuaries from the south-western Atlantic (Nogueira Júnior *et al.*, 2018) and elsewhere (e.g. Vannucci *et al.*, 1970; Santhakumari *et al.*, 1997, 1999). This high diversity is similar to the few other comprehensively sampled nearby estuaries (Nogueira Júnior *et al.*, 2018), but contrasts with the general view that estuarine hydrozoan fauna is impoverished (Calder, 1971; Santhakumari *et al.*, 1997, 1999). In fact, tropical/subtropical estuarine systems in the south-western Atlantic seem to harbour more hydromedusae

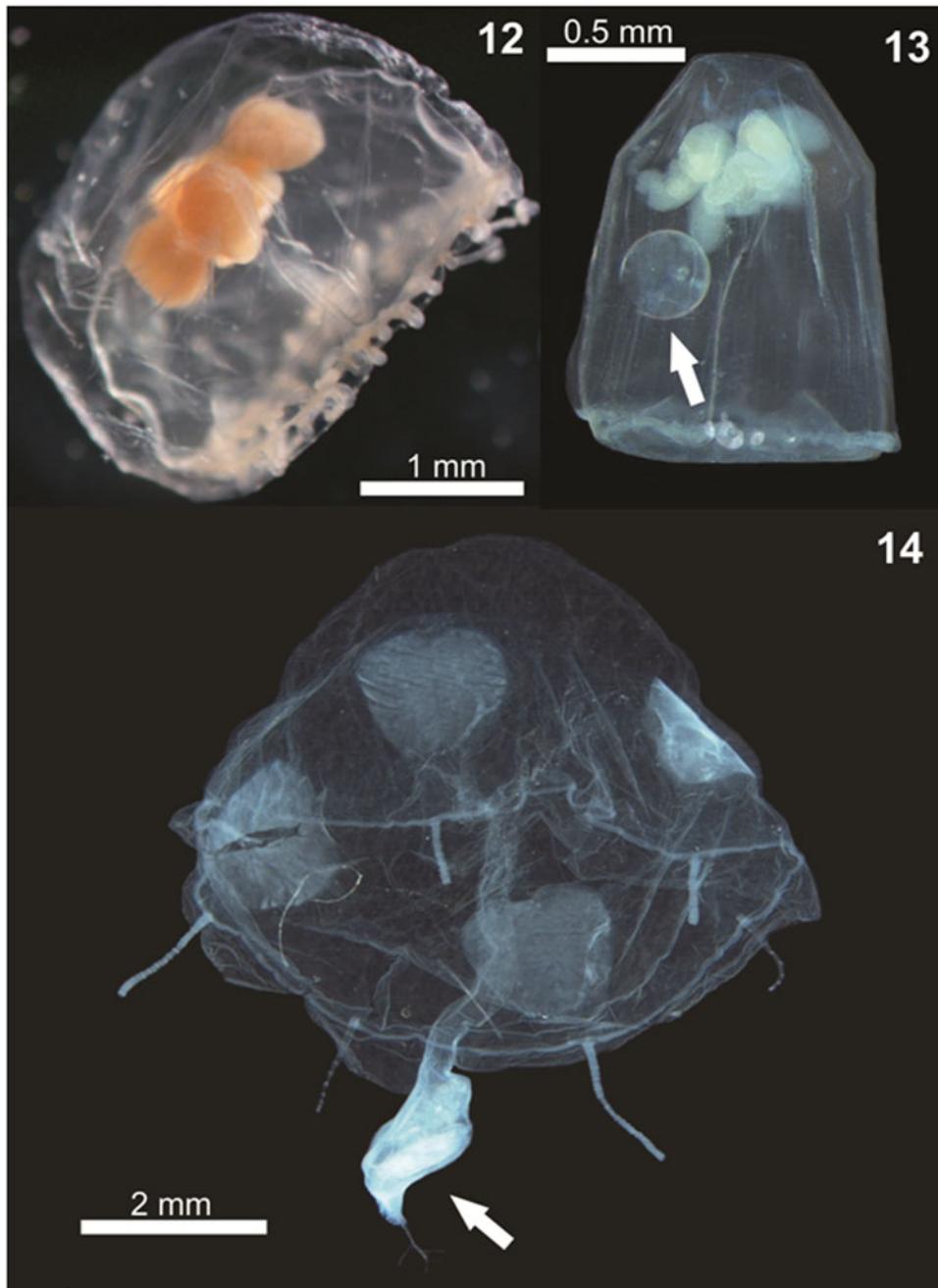


Fig. 12–14. Examples of planktonic hydrozoans from Paranaguá Estuarine System, southern Brazil. *Aglauroopsis kawari*, lateral view (12); *Aglaura hemistoma*, lateral view, white arrow indicates a diatom inside the umbrella (13) and *Liriope tetraphylla*, lateral view, white arrow indicates copepods as possible prey in digestion process (14).

species (e.g. Nogueira Júnior, 2012 – 36 spp.; present study – 36 spp.; Aguilar *et al.*, 2015 – 35 spp.) than adjacent shelf regions (e.g. Vannucci, 1957 – 27 spp.; Vannucci, 1963 – 17 spp.; Nagata *et al.*, 2014a, b – 22 spp.). These observations emphasize the necessity of comprehensive sampling of other tropical/subtropical estuaries from the south-western Atlantic and worldwide. These could potentially harbour high diversity and are commonly poorly studied, since most previous studies focus on temperate estuaries commonly with considerably lower diversity (e.g. Calder, 1971; Petrova *et al.*, 2011; Pesticó *et al.*, 2012; Vansteenbrugge *et al.*, 2015; Zuo *et al.*, 2016; Dutto *et al.*, 2017).

Meroplanktonic species represented 79% of total PES planktonic hydrozoans (30 spp.), as is typical from tropical and subtropical estuaries (Navas Pereira, 1980; Santhakumari *et al.*, 1997, 1999; Nogueira Júnior, 2012). Meroplanktonic Anthoathecata from PES represent 24.6% of those recorded from Brazil and 15.7% from the South Atlantic, while meroplanktonic Leptothecata represent 22% and 18.6%, and Limnomedusae represent 40 and 22.2%, respectively (Bouillon, 1999; Oliveira *et al.*, 2016). These proportions are quite high considering that PES (~550 km²), harbours nearly a quarter of all meroplanktonic hydrozoans so far recorded from the >8000 km of Brazilian coastline.

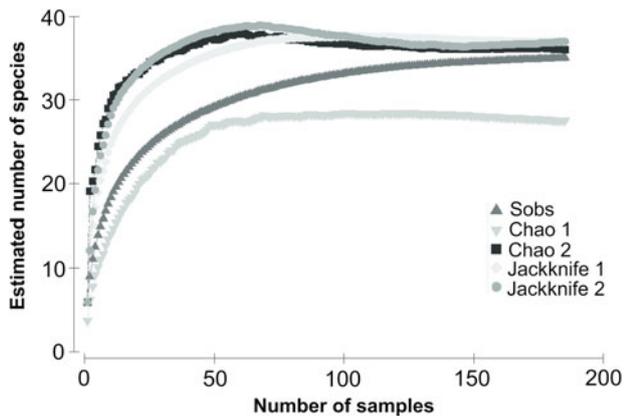


Fig. 15. Accumulation curves of richness estimators from planktonic hydrozoan species in Paranaguá Estuarine System, southern Brazil.

On the other hand, holoplanktonic hydrozoans from PES (i.e. Siphonophorae, Narcomedusae and Trachymedusae) represent only ~7 and 5% of all species from Brazil and the South Atlantic, respectively (Bouillon, 1999; Pugh, 1999; Oliveira *et al.*, 2016). With the exception of *Liriope tetraphylla*, present in 64% of the samples and representing 11% of all hydrozoans sampled, all other holoplanktonic species presented relatively low frequencies of occurrence and abundance. They were mostly found in the outer sectors of the estuary, in the inlets, mixing zone and outer stations of Pinheiros Bay (Table 1). These observations suggest their populations are not resident and were probably advected from adjacent shelf waters where they are common and abundant (Vannucci, 1957, 1963; Nagata *et al.*, 2014b; Nogueira Júnior *et al.*, 2014).

The additional records of *Dipurena* sp. (Bardi, 2011) and *Aglantha* sp. (Montú & Cordeiro, 1988) from PES were not considered, pending confirmation due to taxonomic uncertainties. The genus *Dipurena* is no longer accepted, and the species were moved either to the genus *Slabberia* or *Stauridiosarsia* (Schuchert, 2016). Moreover, Corynidae medusae are very similar to each other, particularly when juveniles, and Bardi (2011) does not state the reasons for identifying the three individuals only at the generic level (i.e. juveniles, damaged, not exactly fitting any known description). Since voucher, illustrations or descriptions of the studied individuals were not provided (Bardi, 2011) a critical re-analysis of the identification is not possible. Yet, we suspect that the *Dipurena* sp. record from PES may be juveniles and/or damaged *Stauridiosarsia reesii*, which is commonly found on South Brazilian Bight estuaries (Vannucci, 1957; Nogueira Júnior *et al.*, 2018) including PES (present study; Table 1) and not recorded by Bardi (2011). The record of *Aglantha* sp. (Montú & Cordeiro, 1988) is also doubtful (Nagata *et al.*, 2014a) because it is typically an oceanic genus (Bouillon, 1999) and is probably a misidentification of *Aglaurea hemistoma* (Figure 13), which is roughly similar and commonly found in the adjacent shallow shelf (Nagata *et al.*, 2014a, b), occasionally with a few individuals entering the estuary, as found here (Table 1).

Cnidostoma fallax (Figure 2) was the most numerous species, with 19,455 individuals sampled, followed by *Obelia* spp. (8285 individuals), *Clytia* spp. (7609), *Liriope tetraphylla* (Figure 14; 5547), *Corymorpha gracilis* (2739) and *Eucheilota*

duodecimalis (1628), all of them sampled both in summer and winter campaigns and in all PES sectors (Table 1). Some other species were frequently captured (>15% of samples), but were not so abundant (<1000 individuals), such as *Ectopleura dumortierii*, actinula larvae, *Bougainvillia muscus* and *Podocoryna loyola* (Figure 3).

The high dominance of *C. fallax* in the present study is noteworthy. This is in contrast to results from the PES in the 1980s (Montú & Cordeiro, 1988), 1990s (Lopes, 1997; Lopes *et al.*, 1998) and 2000s (Bardi, 2011) when *L. tetraphylla* was the dominant hydromedusa, followed by *Obelia* spp., *Clytia* spp. or *C. gracilis*, and *C. fallax* was not present at all (Figure 16). In fact, *L. tetraphylla*, *Obelia* and *Clytia* have historically been the dominant hydromedusae in open shallow coastal and estuarine environments from the South Brazilian Bight (Vannucci, 1957, 1963; Teixeira *et al.*, 1965; Navas-Pereira, 1980; Bardi, 2011; Nogueira Júnior, 2012; Nagata *et al.*, 2014a, b; Nogueira Júnior *et al.*, 2014, 2018). It is difficult to explain the reasons for such a replacement in the dominant species, particularly due to the poor historical knowledge of the Brazilian hydromedusan fauna, but unexpected high abundances of *C. fallax* have also recently been recorded at Patos Lagoon (Teixeira-Amaral *et al.*, 2017). Considering that the presence of *C. fallax* in the south-western Atlantic has only recently been detected, and now is known to occur in many estuaries along Brazilian coast between ~24 and 34°S (Teixeira-Amaral *et al.*, 2017; Nogueira Júnior *et al.*, 2018; present study), two mutually excluding hypotheses may be proposed:

- C. fallax* may have been overlooked in the few previous studies of these estuaries, either due to taxonomic uncertainties and/or to the low abundances of the species. Although most of these historical estuarine studies focused on the zooplankton as a whole and the most abundant taxa such as copepods, some focused on or attempted to identify the estuarine Brazilian hydromedusae including a few with relatively satisfactory spatial and temporal coverage (Vannucci, 1957; Teixeira *et al.*, 1965; Montú & Cordeiro, 1988; Lopes, 1997; Bardi, 2011), and none has recorded *C. fallax* which is a very peculiar and easily identifiable species.
- C. fallax* appeared recently, perhaps introduced from tropical Atlantic African coastal estuaries which are the

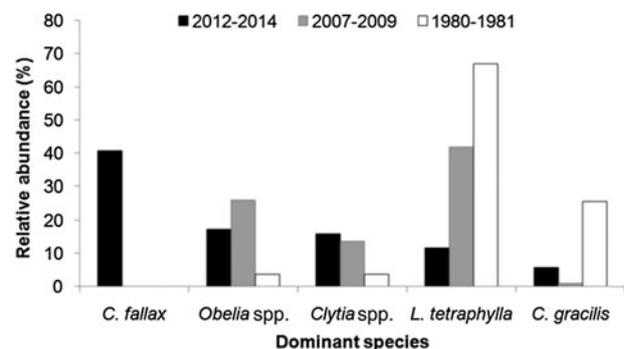


Fig. 16. Comparisons of the relative abundance (%) of dominant hydromedusae species from Paranaguá Estuarine System, southern Brazil from different periods. Data source: (a) 1980–1981 – taken from Montú & Cordeiro, 1989; (b) 2007–2009 – taken from Bardi, 2011; (c) 2012–2014 – present study. Lopes *et al.* (1998) did not provide quantitative data on hydromedusae but comment that *Liriope tetraphylla* was the dominant species.

location of all historical records of the species (Vanhöffen, 1911; Picard & Rahm, 1954 as *Archaeoceania tournieri*; Kramp, 1959). The evidence for this hypothesis would be the lack of previous records in spite of studies (albeit few) on these very same estuaries (e.g. Teixeira *et al.*, 1965; Montú & Cordeiro, 1988; Lopes, 1997; Bardi, 2011) where the species is currently known to occur (see references above). Although speculative, it is not unlikely that *C. fallax* is an introduced species considering that along with its recent discovery, all sites with known populations are brackish water environments near ports (e.g. Vanhöffen, 1911; Picard & Rahm, 1954; Kramp, 1959; Teixeira-Amaral *et al.*, 2017; this study), and the high national and international ship traffic in PES could be a potential vector, along with other cnidarian and non-cnidarian exotic species (e.g. Neves & Rocha, 2008; Van Ofwegen & Haddad, 2011; Haddad *et al.*, 2014; Bettim & Haddad, 2017).

Independently of the origin of the *C. fallax* population (hypothesis *i* or *ii* above), its massive presence during the present study is noteworthy and suggests a replacement of a historically dominant species. In the present study *C. fallax* dominated the total abundance and the typical previous dominant species *L. tetraphylla* ranks fourth, representing only 11% of all hydromedusae. This contrasts with previous studies where *L. tetraphylla* has always been dominant, representing between 42 and 67% of the population (Figure 16). Considering that *C. fallax* and *L. tetraphylla* probably have different roles in the ecosystem – the former is meroplanktonic small-sized (<1 mm) and probably eats very small organisms and the latter is holoplanktonic larger-sized (>5 mm) and eats larger organisms like copepods (Figure 14), this shift in the dominance of these species could change the energy pathways of local food webs and the planktonic assemblage structure.

Species which produce medusa buds such as *C. fallax* can rapidly increase their population levels by asexual reproduction, typically under warm and specific temperature conditions (Carré & Carré, 1990; Kawamura & Kubota, 2008). Thus, we question which environmental factors may have contributed to *C. fallax* population increase and what impacts it may cause. It occurred over three consecutive summers in the present study, but was mainly captured in summer 2012 (>16,000 medusae), which coincides with the swarm recorded from Patos Lagoon, ~500 km south (Teixeira-Amaral *et al.*, 2017); also suggesting that the changes reported here may not be restricted to PES. A hypothesis for the simultaneous occurrence of *C. fallax* swarms in these Brazilian estuaries may be related to large inter-annual variations in river discharge, circulation and salinization processes associated with ENSO events. March 2012 was at the end of a La Niña event (NOAA, 2017). On the southern Brazilian coast, these events are usually associated with lower precipitation and freshwater outflow, and higher salinity values (Grimm *et al.*, 1998; Möller & Fernandes, 2010; Nascimento Júnior & Sant'Anna Neto, 2015) and maybe this condition favoured a *C. fallax* outburst.

Although *C. fallax* abundance diminished from summer 2012 to the summer of 2014, it remained among the dominant species (Table 1), maintaining high levels and apparently persistent populations inside PES. Indeed, specimens of different sizes and development were observed every summer. We do

not know if this change in assemblage structure is permanent or if it is part of an erratic and intermittent massive occurrence commonly registered for jellyfish around the world (e.g. Buecher *et al.*, 1997; Malej & Malej, 2004; Boero *et al.*, 2008; Licandro *et al.*, 2012; Van Walraven *et al.*, 2015), including some invasive species (Greve, 1994; Riisgård *et al.*, 2012; Yilmaz, 2015). Thus, further monitoring programmes would be welcome to check if this peculiar hydrozoan species will maintain high population levels in the medium- to long-term. Moreover, future studies assessing the biology and ecology of *C. fallax* (e.g. genetics and evolution, life cycle constraints, preferential temperature and salinity ranges, effects of climatic events, reproductive potential and feeding rates) will be important to assess which environmental factors contributed to its population outburst as reported here, and what impacts it may cause. The life cycle of *C. fallax* is not known and its taxonomy is arguable and it was suggested to belong to the families Oceaniidae (Picard & Rahm, 1954), Cytaeidae (Kramp, 1961) and Hydractiniidae where it is currently placed (Schuchert, 2016). In any case, it probably has a polyp stage (e.g. Bouillon *et al.*, 2006) and therefore life-cycle studies and factors affecting its potential benthic stage should also be considered.

CONCLUSIONS

The present study constitutes a comprehensive survey of planktonic hydrozoans from PES, a Natural World Heritage site. Currently, a total of 39 species have been recorded from PES, 35 of them studied here. Given the high sampling effort employed (185 samples analysed and >49,000 organisms examined), it can be considered that the planktonic hydrozoan fauna from PES is relatively well represented in the present study, as also suggested by the species accumulation curves (Figure 15), although a few further species are likely to be found. The high biodiversity observed herein indicates that the estuary harbours a diverse aquatic fauna, being important for regional biodiversity conservation. The most abundant species (~40% of all specimens) was unexpectedly *Cnidostoma fallax*, indicating changes in the assemblage structure compared to previous decades when *L. tetraphylla* has always been dominant. It is difficult to deduce the reasons for these changes in the planktonic hydrozoan assemblage structure due to the low number of historical studies for Brazilian estuaries. The complete absence of *C. fallax* from these previous studies from PES and nearby estuaries may suggest it has been recently introduced, although it may have been overlooked. Further studies including molecular analysis (see for instance Harrison *et al.*, 2013 for *Blackfordia virginica*) could help to clarify the origins of such populations. In any case, changes in the structure of the hydromedusae assemblage were clear when compared to previous decades when *L. tetraphylla* has always dominated. Such replacement may lead to changes in the local pelagic assemblage and food chain. Although *C. fallax* was abundantly sampled through three consecutive years, future surveys are important to check the permanency and the abundance levels of this population.

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