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ORIGINAL PAPER

Diversity of estuarine and marine hydroids (Cnidaria, Hydrozoa) from subtropical ecosystems of Brazil

Larissa Ajala-Batista[1] · Daniel de Miranda Lins[1] · Maria Angélica Haddad[1]

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Abstract

The subtropical coastal waters of Brazil have been surveyed regarding their hydroid fauna since 1941. However, a comprehensive compilation of all hydroid records with detailed information has not yet been published for these waters. Besides filling this knowledge gap, we provide an updated species list, along with the biogeographic status (native, introduced, or cryptogenic) of each hydroid species for the area between Ilha Comprida municipality and the state of Rio Grande do Sul. We also present the distribution patterns of hydroid morphotypes, a sampling sufficiency analysis, and spatial-temporal progress of their research. The dataset was compiled by conducting a thorough bibliographical survey, accessing data of zoological collections, and performing field surveys with experimental settlement panels. This work provides an update for new hydroid records for a large number of localities within the study area. We listed 27 families, 59 genera, 129 morphotypes, and 95 unique species. Regarding the unique species, ~ 3% were classified as introduced, ~ 2% as native, and ~ 95% as cryptogenic. The 3% of introduced species include the first record of the non-indigenous *Podocoryna loyola* on natural substrata and new records of this species for São Paulo. The 95 unique species also represent ~ 19% and ~ 52% of the hydroid fauna recorded in South America and Brazil, respectively. Sampling effort is still not sufficient and therefore continuing research on the hydroid fauna is required, especially for the detection of new introduced species.

Keywords Anthoathecata · Benthos · Database · Leptothecata · Species list · Sampling sufficiency

Introduction

The term hydroid refers to the polypoid life history stage of Leptothecata and Anthoathecata hydrozoans (Oliveira et al. 2006). The presence or absence of a chitinous exoskeleton or theca, which surrounds and protects the polyp body (or hydranth), constitutes the main difference between these two orders (Leclère et al. 2009). Leptothecata's polyps are commonly known as "thecate hydroids" due to the presence of the theca, whereas Anthoathecata's as "athecate" because of the lack of this feature (Oliveira et al. 2006).

Hydroids display a great phenotypic diversity and a wide distribution (Gili and Hughes 1995). A considerable challenge for accurate and consistent hydroid species identification has been posed by their metagenetic life cycle, which led to a dual classification system: one for the medusa stage and another for the polyp stage (Maronna et al. 2016). In the complete life cycle, medusae and polyps commonly display extreme morphological dimorphism, adding complexity to taxonomic identification (Maronna et al. 2016; Miglietta et al. 2019). Knowing the complete life cycle is essential to avoid misidentification, especially for species with planktonic medusae, and cultivation experiments could therefore be of great value in this regard (Schuchert 2016).

Hydrozoans occur from tropical to polar seas (Schuchert 2010; Ronowicz et al. 2011) and from shallow to deep waters (Fernandez and Marques 2018). Most of the species are marine, but some live in fresh and/or brackish water (Grohmann 2009; Schuchert 2010; Belz et al. 2016). Hydroids grow mainly on rocky shores, where they join benthic communities, but

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✉ Larissa Ajala-Batista
lari.bio1@gmail.com

[1] Zoology Department, Universidade Federal do Paraná, Centro Politécnico Campus, Biological Science Sector, Curitiba, Paraná, Brazil

they are also found on artificial substrates (Bumbeer and Rocha 2012, 2016), soft bottoms (Di Camillo et al. 2017), and floating in the water column (Cabral et al. 2015). In addition, a great number of species grow as epibionts on algae, seagrasses, and various invertebrates (Oliveira and Marques 2011; Montano et al. 2015; Maggioni et al. 2020a, 2020b), including other hydroids (Miranda et al. 2011; Montano et al. 2020). Some hydroids (i.e., Milleporidae, Stylasteridae, and some hydractiniids) are calcareous and known as hydrocorals, contributing to coral assemblages (Lewis 1989; Cairns 2007; Di Camillo et al. 2017) and functioning as living substrates for other invertebrates (Lewis 2006; Pica et al. 2012; Hoeksema and García-Hernández 2020).

The great potential of hydroids for asexual reproduction, plasticity, and modular anatomy has been compared to that of vascular plants and therefore they are known as forest formers in zoobenthic communities (Di Camillo et al. 2017). They are important components of the ecosystems as pioneer organisms, providing shelter for many other invertebrates (Ronowicz et al. 2013), serve as a food source for several animals (Di Camillo et al. 2017), and have been studied as environmental indicators (Da Silveira and Migotto 1991; Grohmann 2009; Castellanos-Iglesias et al. 2018).

Although these animals confer great advantages for their ecosystems, some (e.g., Tubulariidae species) are frequently reported to cause harmful effects on aquaculture systems by adding extra weight to the equipment, decreasing the growth rate of the cultivated organisms and preying on their larvae (Guenther et al. 2009; Fitridge and Keough 2013). Due to their metagenetic life cycle, hydroids can be transported to areas outside their native range as polyps and medusa by both natural (e.g., carried by ocean currents, attached to nektonic vertebrates) and artificial means (e.g., ship hulls, ballast water, and anthropogenic debris) (Calder et al. 2014). In this scenario, non-indigenous species can become invaders, thus negatively affecting the biota of the invaded sites (Lowry et al. 2013; Bumbeer and Rocha 2016; Bumbeer et al. 2016; Bettim and Haddad 2017; Marques et al. 2017).

Studies have already recorded three introduced hydroid species in subtropical marine and estuarine waters of Brazil: *Podocoryna loyola* Haddad et al., 2014 *Calyptospadix cerulea* Clarke, 1882, and *Turritopsis dohrnii* (Weismann, 1883) (e.g., Bumbeer and Rocha 2012, 2016; Bumbeer et al. 2016; Schuchert 2016; Bettim and Haddad 2017; Miglietta et al. 2019). Moreover, many hydroids from this area are cryptogenic (Neves and Rocha 2008; Altvater 2009; Bumbeer et al. 2016; Felippe 2016), indicating a feasible previous introduction of non-native species (Neves and Rocha 2008).

Brazilian subtropical waters comprise a great variety of coastal ecosystems, such as rocky shores, estuaries, sandy beaches, and mangroves (Calliari et al. 2006; Bardi 2011; Miranda et al. 2011; Bettim and Haddad 2017), providing habitat for a wide array of hydroid species (Miranda et al. 2015; Oliveira et al. 2016). In addition, urban development and associated activities in the region offer artificial substrates for fouling adhesion and growth, such as aquaculture equipment, piers, marinas, and port structures (Bumbeer and Rocha 2012; Altvater and Coutinho 2015).

Although subtropical waters of Brazil have already been provided with meaningful and relevant surveys of their hydroid fauna, such as inventories (Altvater 2009; Bardi 2011; Bumbeer and Rocha 2012, 2016; Bumbeer et al. 2016; Felippe 2016), biogeography and endemicity (Miranda et al. 2015), list of taxa by state (Migotto et al. 2002), and hydroid records by coastal segments (Oliveira et al. 2016), a compilation of all hydroid records with detailed information about them (e.g., geographic position, date of record, and depth) has not yet been published. Hence, besides filling this knowledge gap, we provide an updated species list of the hydroid fauna, along with the biogeographic status (native, introduced, or cryptogenic) of each species from Ilha Comprida municipality (state of São Paulo—SP) to the state of Rio Grande do Sul (RS). In addition to this, we present the distribution patterns of hydroid morphotypes as well as a sampling sufficiency analysis, and the spatial-temporal progress of investigations.

We hypothesized that hydroid communities from the study area were not sufficiently sampled, principally those from RS since they have been receiving little attention (prior own observations). In addition to this, it has been proposed that the hydrozoan (e.g., Bouillon et al. 2004) and the global (marine) biodiversity in general (e.g., Bini et al. 2006; Appeltans et al. 2012) are probably underestimated.

The aims of this research are related to the objective number 14 of The Sustainable Development Goals, from the United Nations (Conserve and sustainably use the oceans, seas and marine resources) (United Nations 2020a) and to the objectives of UN Decade of Ocean Science for Sustainable Development (UN 2020b), since their results will help the scientific community to better understand different aspects (e.g., taxonomic diversity, geographic distribution patterns) of the hydroid fauna from the studied area, supporting future research and to further address conservation issues.

Material and methods

Study area

The study area (Fig. 1a, b) covers ~1.270 km of coast line, and it lies between Ilha Comprida municipality (25° 01′ 32.6″ S, 47° 54′ 53.1″ W), located in the southern area of the state of São Paulo (SP), and the state of Rio Grande do Sul (RS) (33° 44′ 35.8″ S 53° 22′ 13.7″ W), the southernmost state of Brazil. The area comprises Ecoregion 47 (WarmTemperate

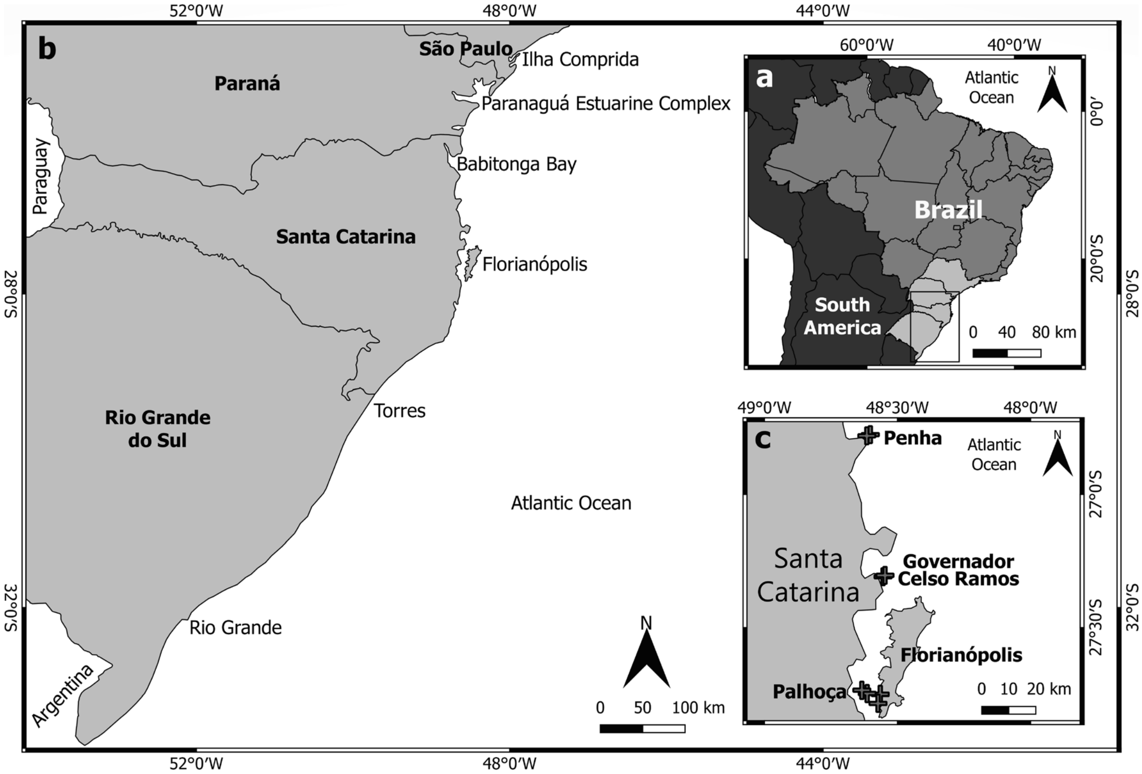

Fig. 1 Map of the study area. **a** Location of the study area in Brazil; **b** details of the study area, including the northern (Ilha Comprida) and southern (Rio Grande do Sul) limits, as well as some localities for reference only; **c** sampling sites (crosses) within mussel culture sites along the coast of Santa Catarina

Fig. 2 Experimental sets. **a** A schematic drawing of the sets across a mussel culture structure, and the side (**b**) and front (**c**) appearances of a plate occupied by the fouling community

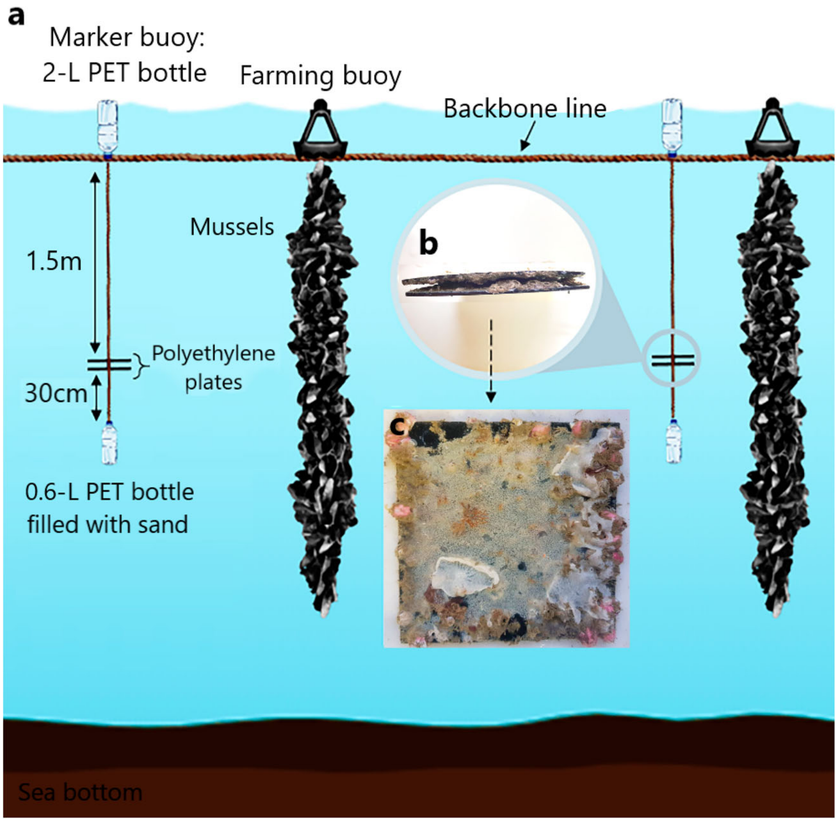

Table 1 List of morphotypes recorded for the study area alongside with their number of records, and status of each unique species with its reference. *C*, cryptogenic; *I*, introduced; *N*, native; 1, this study; 2, Rocha et al. (2013); 3, Marques et al. (2013); 4, Bettim and Haddad (2017); 5, Felippe (2016); 6, Bornancin (2007); 7, Bumbeer and Rocha (2012); 8, Miglietta et al. (2019); 9, Schuchert (2016); 10, Haddad et al. (2014)

Scientific name	Number of records	Status	Reference
Order Anthoathecata Cornelius, 1992			
Family Bougainvilliidae Lütken, 1850			
Bimeria sp.	1		
Bimeria vestita Wright, 1859	15	C	1
Bougainvillia muscus (Allman, 1863)	155	C	2
Bougainvillia rugosa Clarke, 1882	3	C	2
Bougainvillia sp.	16		
Calyptospadix cerulea Clarke, 1882	56	I	2
Parawrightia robusta Warren, 1907	2	C	1
Rhizorhagium sp.	13		
Family Cladocorynidae Allman, 1872			
Cladocoryne floccosa Rotch, 1871	2	C	1
Family Corynidae Johnston, 1836			
Coryne eximia Allman, 1859	2	C	2
Coryne pusilla Gaertner, 1774	20	C	2
Coryne sp.	2		
Stauridiosarsia reesi (Vannucci, 1956)	15	C	1
Family Eudendriidae L. Agassiz, 1862			
Eudendrium capillare Alder, 1856	1	C	2
Eudendrium caraiuru Marques & Oliveira, 2003	3	N	3
Eudendrium carneum Clarke, 1882	111	C	2
Eudendrium merulum Watson, 1985	1	C	1
Eudendrium sp.	20		
Family Hydractiniidae L. Agassiz, 1862			
Hydractinia sp.	26		
Podocoryna loyola Haddad et al., 2014	57	I	4,10
Stylactis sp.	1		
Family Oceaniidae Eschscholtz, 1829			
Corydendrium parasiticum (Linnaeus, 1767)	6	C	2
Turritopsis dohrnii (Weismann, 1883)	1	I	8, 9
Turritopsis nutricula McCrady, 1857	17	C	2
Turritopsis sp.	3		
?*Turritopsis* sp.	1		
Family Pandeidae Haeckel, 1879			
Amphinema sp.	15		
Leuckartiara sp.	1		2
Family Pennariidae McCrady, 1859			
Pennaria disticha Goldfuss, 1820	42	C	2
Pennaria sp.	2		
Family Porpitidae Goldfuss, 1818			
Porpita porpita (Linnaeus, 1758)	16	C	1
Velella velella (Linnaeus, 1758)	19	C	1
Family Sphaerocorynidae Prévot, 1959			
Sphaerocoryne sp.	2		
Family Tubulariidae Goldfuss, 1818			
Ectopleura crocea (Agassiz, 1862)	272	C	2

Table 1 (continued)

Scientific name	Number of records	Status	Reference
Ectopleura dumortierii (Van Beneden, 1844)	19	C	2
Ectopleura sp.	18		
Zyzzyzus warreni Calder, 1988	2	C	2
Order Leptothecata Cornelius, 1992			
Family Aglaopheniidae Marktanner-Turneretscher, 1890			
Aglaophenia latecarinata Allman, 1877	27	C	3
Aglaophenia rhynchocarpa Allman, 1877	1	C	1
Aglaophenia sp.	1		
Lytocarpia tridentata (Versluys, 1899)	1	C	1
Macrorhynchia philippina Kirchenpauer, 1872	13	C	2
Macrorhynchia sp.	6		
Family Campanulariidae Johnston, 1836			
Campanularia hincksii Alder, 1856	3	C	1
Campanularia sp.	1		
Clytia arborescens Pictet, 1893	1	C	1
Clytia elsaeoswaldae Stechow, 1914	5	C	1
Clytia cf. *gracilis* (Sars, 1850)	91	C	3
Clytia gracilis (Sars, 1850)	165	C	3
Clytia hummelincki (Leloup, 1935)	2	C	2
Clytia linearis (Thorneley, 1900)	86	C	2
Clytia noliformis (McCrady, 1859) sensu Calder, 1991	7	C	2
Clytia sp.	55		
Obelia bidentata Clark, 1875	206	C	2
Obelia dichotoma (Linnaeus, 1758)	222	C	2
Obelia geniculata (Linnaeus, 1758)	59	C	2
Obelia sp.	3		
Orthopyxis caliculata (Hincks, 1853)	34	C	1
Orthopyxis crenata (Hartlaub, 1901)	6	C	1
Orthopyxis mianzani Cunha et al., 2015	3	C	1
Orthopyxis sargassicola (Nutting, 1915)	29	C	1
Orthopyxis sp.	10		
Family Campanulinidae Hincks, 1868			
Calycella gabriellae (Vannucci, 1951)	1	C	1
Cuspidella sp.	2		
Lafoeina sp.	1		
Lafoeina tenuis Sars, 1874	32	C	1
Family Cirrholoveniidae Bouillon, 1984			
Cirrholovenia tetranema Kramp, 1959	16	C	2
Family Haleciidae Hincks, 1868			
Halecium bermudense Congdon, 1907	1	C	2
Halecium dichotomum Allman, 1888	1	C	1
Halecium dyssymetrum Billard, 1929	20	C	5
Halecium lightbourni Calder, 1991	1	C	1
Halecium nanum Alder, 1859	1	C	1
Halecium sp.	3		
Halecium tenellum Hincks, 1861	3	C	3
Nemalecium lighti (Hargitt, 1924)	1	C	3
Family Halopterididae Millard, 1962			
Antennella secundaria (Gmelin, 1791)	2	C	1

Table 1 (continued)

Scientific name	Number of records	Status	Reference
Halopteris carinata Allman, 1877	1	C	1
Halopteris diaphana (Heller, 1868)	4	C	2
Halopteris glutinosa (Lamouroux, 1816)	1	C	1
Halopteris polymorpha (Billard, 1913)	5	C	2
Halopteris sp.	1		
Monostaechas quadridens (McCrady, 1859)	6	C	1
Family Hebellidae Fraser, 1912			
Hebella scandens (Bale, 1888)	7	C	1
Scandia mutabilis (Ritchie, 1907)	5	C	1
Family Kirchenpaueriidae Stechow, 1921			
Kirchenpaueria halecioides (Alder, 1859)	24	C	2
Pycnotheca mirabilis (Allman, 1883)	8	C	1
Family Lafoeidae Hincks, 1868			
Acryptolaria conferta (Allman, 1877)	2	C	1
Acryptolaria sp. 1	1		
Acryptolaria sp. 2	1		
Filellum serratum (Clarke, 1879)	4	C	1
Filellum sp.	20		
Lafoea dumosa (Fleming, 1820)	1	C	1
Lafoea sp.	11		
Family Lovenellidae Russell, 1953			
Lovenella gracilis Clarke, 1882	1	C	1
Lovenella grandis Nutting, 1901	2	C	1
Family Plumulariidae McCrady, 1859			
Dentitheca bidentata (Jäderholm, 1905)	3	C	1
Dentitheca sp.	1		
Nemertesia ramosa (Lamarck, 1816)	1	C	1
Plumularia floridana Nutting, 1900	12	C	2
Plumularia margaretta (Nutting, 1900)	23	N	6
Plumularia setacea (Linnaeus, 1758)	3	C	2
Plumularia strictocarpa Pictet, 1893	2	C	2
Family Sertularellidae Maronna et al., 2016			
Sertularella areyi Nutting, 1904	1	C	2
Sertularella conica Allman, 1877	2	C	1
Sertularella leiocarpa (Allman, 1888)	3	C	1
Sertularella rugosa (Linnaeus, 1758)	1	C	1
Sertularella sp.	1		
Sertularella tenella (Alder, 1857)	8	C	1
Family Sertulariidae Lamouroux, 1812			
Amphisbetia distans (Lamouroux, 1816)	46	C	2
Amphisbetia operculata (Linnaeus, 1758)	1	C	2
Diphasia digitalis (Busk, 1852)	2	C	2
Diphasia tropica Nutting, 1904	1	C	1
Dynamena crisioides Lamouroux, 1824	26	C	2
Dynamena dalmasi (Versluys, 1899)	8	C	7
Dynamena disticha (Bosc, 1802)	36	C	2
Dynamena quadridentata (Ellis & Solander, 1786)	6	C	2
Dynamena sp.	2		
Idiellana pristis (Lamouroux, 1816)	7	C	3

Table 1 (continued)

Scientific name	Number of records	Status	Reference
Salacia desmoides (Torrey, 1902)	5	C	1
Sertularia loculosa Busk, 1852	5	C	2
Sertularia marginata (Kirchenpauer, 1864)	51	C	2
Sertularia rugosissima Thornely, 1904	6	C	2
Sertularia sp.	4		
Sertularia tumida Allman, 1877	2	C	1
Sertularia turbinata (Lamouroux, 1816)	37	C	2
Family Symplectoscyphidae Maronna et al., 2016			
Symplectoscyphus ?subdichotomus (Kirchenpauer, 1884)	1	C	1
Symplectoscyphus sp.	4		
Family Syntheciidae Marktanner-Turneretscher, 1890			
Hincksella cylindrica (Bale, 1888)	2	C	1
Family Zygophylacidae Quelch, 1885			
Zygophylax geniculata (Clarke, 1894)	1	C	1

Southwestern Atlantic) of the Marine Ecoregions of the World (MEOW) system (Spalding et al. 2007).

Different categories of protected territories can be found throughout the studied area, such as federal- and state-protected sites, world heritage sites, biosphere reserves, and ultra-humid territories of international importance. The area harbors one of the most well-preserved estuarine areas of Brazil (Cananéia Research Institute-IPeC 2018): the Estuarine-Lagoon Complex of Iguape-Cananéia-Paranaguá (LAGAMAR), a highly productive region, which extends from Southern São Paulo to the Paranaguá Estuarine Complex (PEC), in Paraná (PR).

Despite the fact that the LAGAMAR is recognized as a Biosphere Reserve (since 1991) by the UNESCO, intense anthropogenic activities such as high vessel traffic (Altvater and Coutinho 2015) are present in the region. Additionally, artificial structures like piers, boat hulls, and concrete pills are also found, especially by the PEC, because of the presence of marinas and the international ports of Paranaguá and Antonina (Altvater and Coutinho 2015).

Another large estuary is present on the southernmost coast of the state of Paraná: the Guaratuba Bay, which is partially protected by both national and international organizations such as the Ramsar Convention and Brazilian federal and state governments. Although this area may be considered well-preserved compared to other Brazilian bays, its marine biodiversity is under threat as a result of human activities (e.g., occupation of mangrove areas, pollution, overfishing, and unregulated tourism) (Ramsar Sites Information Service-RSIS 2017).

The state of Santa Catarina presents the longest coastline within the study area and contains the most continuous portion of rocky formations, offering much substrate for the development of benthic communities (Carraro 2012). Furthermore, the state holds approximately 98% of the national production of malacoculture (Brazilian Institute of Geography and Statistics-IBGE 2018), and artificial substrates are increasing as coastal urbanization grows. The large Babitonga Bay occurs on this coast, with an extension of 22.5 km, harboring two international ports (São Francisco do Sul and Itapoá), an extensive area of mangroves (principally in the inner portion) as well as several islands and beaches (Truccolo and Schettini 1999). In Brazil, mangroves and estuaries occur southward up to Laguna (a city of Santa Catarina near the neighboring state, Rio Grande do Sul), which is also the southernmost latitude of mangrove occurrence in the Southwest Atlantic (do Vale and Schaeffer-Novelli 2018). Santa Catarina also presents many coastal federal conservation units (Alves and Hanazaki 2015). The coast of RS mainly consists of sand with rock formations restricted to the northern limit of the state, forming the southern limits of rocky shores in Brazil, in Torres municipality (Calliari et al. 2006).

Bibliographical survey

A bibliographical survey was conducted to encounter hydroid records, including detailed information about sampling locality, date and depth of the record, and substrate. We compiled information from both white literature (articles and book chapters) and gray literature (academic documents, annals of scientific events, and personal communications) containing much unpublished data on the hydroid fauna.

Surveys were conducted mainly in electronic databases, such as Google Scholar, Web of Science, Portal de Periódicos da Coordenação de Aperfeiçoamento de Pessoal

Table 2 Some new hydroid records and insights on hydroid distribution provided by this study. *SP*, São Paulo; *PR*, Paraná; *SC*, Santa Catarina; *DZoo-UFPR*, Invertebrate Collection of the Department of Zoology from the Universidade Federal do Paraná

State	Localities	Morphotype	Source	Year of registration	Importance
SP	Ilha Comprida and Cananéia	*Calyptospadix cerulea*	DZoo-UFPR	2016, 2017	First georeferenced record of the species for both municipalities
SP	Ilha Comprida and Cananéia	*Podocoryna loyola*	DZoo-UFPR	2017	First record of the alien species for Ilha Comprida, first georeferenced record for Cananéia, and first record of the species in natural substrate (found in Cananéia)
SP	Ilha Comprida	*Cirrholovenia tetranema*	DZoo-UFPR	2017	First record of the genus and species for Ilha Comprida
SP	Ilha Comprida	*Eudendrium carneum*	DZoo-UFPR	2017	First record of the species for Ilha Comprida
SP	Cananéia	*Filellum* sp.	DZoo-UFPR	2016	First morphotype of the genus for Cananéia
SP	Cananéia	*Halecium* sp.	DZoo-UFPR	2017	First morphotype of the genus for Cananéia
PR	Paranaguá	*Stauridiosarsia reesi*	DZoo-UFPR	2010	Oldest record of the genus and species for the study area
PR	Currais Islands	*Filellum* sp.	DZoo-UFPR	2018	First morphotype of the genus recorded in the Currais Islands and fourth record for PR (last recorded in 2010)
PR	Currais Islands	*Macrorhynchia philippina*	DZoo-UFPR	2018	Second record for the Currais Islands and third for PR (last recorded in 2003 in both areas)
PR	Currais Islands	*Sertularia rugosissima*	DZoo-UFPR	2018	First record for the Currais Islands and third for PR (last recorded in 1983)
SC	Itapoá	*Orthopyxis caliculata*	DZoo-UFPR	2018	Third and fourth records for Itapoá (last recorded in 2003)
SC	Itapoá	*Sertularia rugosissima*	DZoo-UFPR	2018	Second record for Itapoá (last recorded in 2003) and third for SC (last recorded in 2006)
SC	Itapoá	*Sertularia loculosa*	DZoo-UFPR	2018	Second record for Itapoá (last recorded in 2006) and fourth for SC (last recorded in 2008)
SC	Penha	*Bimeria vestita*	This study	2017	First record for Penha, first record after 2008 for SC and first record for the study area after 2009
SC	Penha	*Dynamena dalmasi*	This study	2018	First record for Penha, first record after 2009 for the study area and extension of the most boreal distribution limit of the species in SC
SC	Penha and Governador Celso Ramos	*Coryne pusilla*	This study	2018	First record for both municipalities, first records of the species for SC and extension of the most austral distribution limit of the species for Brazil
SC	Governador Celso Ramos	*Halecium dyssymetrum*	This study	2017	First record for Governador Celso Ramos and first record for SC after 2008
SC	Governador Celso Ramos	*Ectopleura* sp., *Bougainvillia* sp. and *Filellum* sp., *Clytia linearis*, *Clitya* cf. *gracilis* and *Bougainvillia muscus*	This study	2017, 2018	First morphotypes of their genus recorded in Governador Celso Ramos
SC	Governador Celso Ramos and Florianópolis	*Amphimena* sp.	This study	2017, 2018	First morphotype of the genus recorded in both municipalities and first records for the study area after 2011
SC	Governador Celso Ramos, Florianópolis and Palhoça	*Obelia bidentata*	This study	2017	First record of the species for the municipalities
SC	Governador Celso Ramos and Palhoça	*Obelia dichotoma*	This study	2017	First record of the species for both municipalities
SC	Governador Celso Ramos and Palhoça	*Lafoeina tenuis*	This study	2017	First record for both municipalities, first record for the study area after 2008 and extension of the most austral distribution limit of the species for Brazil
SC	Palhoça	*Ectopleura crocea* and *Kirchenpaueria halecioides*	This study	2017, 2018	First record of the species for both municipalities
SC	Palhoça	*Plumularia floridana*	This study	2017	First record for the municipality and extension of the most austral distribution limit of the genus and species for Brazil

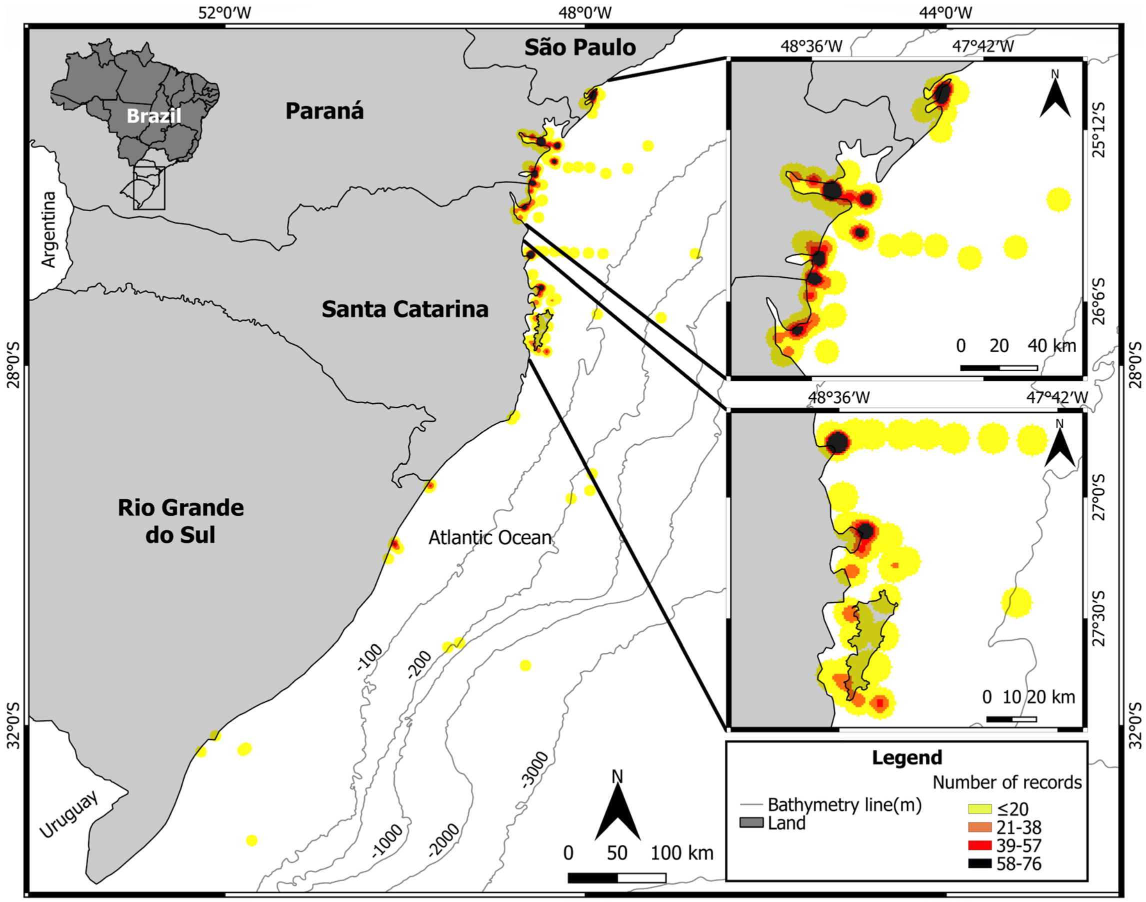

Fig. 3 Heatmap of hydroid records from estuarine and marine subtropical waters of Brazil between 1941 and 2018

de Nível Superior (CAPES), and university library websites. We also used the metasearch engine Google with the aim of expanding the likelihood of encountering studies.

The review was targeting documents in English and Portuguese by grouping multiple terms (e.g., hydroid, hidroide, Hydrozoa, hidrozoários, Paraná, Santa Catarina, and Cnidaria) and search operators (e.g., by using Boolean operators, wildcard, and truncation symbols). Non-electronic means of information were also surveyed, such as books, reports, and theses.

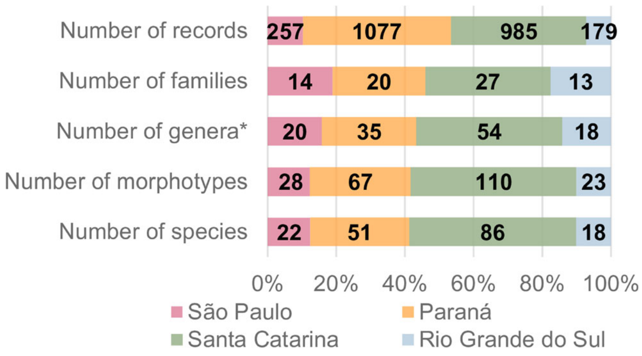

Fig. 4 Number of records, families, genera, morphotypes, and unique species per state. *, *Turritopsis* + ?*Turritopsis*

Only records of hydroids identified to genus or species level were computed. When a study did not describe the precise geographic location of the record(s), but presented a map indicating the sampling point(s), the coordinates were estimated through it. In the absence of a map, the locations were estimated according to the information available in the text or, when possible, the respective authors were contacted. Furthermore, the sampling point (i.e., coordinates) of some records was adjusted when we encountered inconsistency between the given coordinates and the sampling locality specified in the text (e.g., the text discusses that the work was conducted in the Paranaguá Yacht Club, but the given coordinates indicate a nearby inland point).

For records lacking the year of registration, when possible, we either estimated it through information in the text (i.e., the last year of sampling mentioned in the paper) or contacted the author(s). Any further necessary information about the records and worksheets was requested to the author(s) whenever possible. Additional records obtained after personal communications were also included in the dataset.

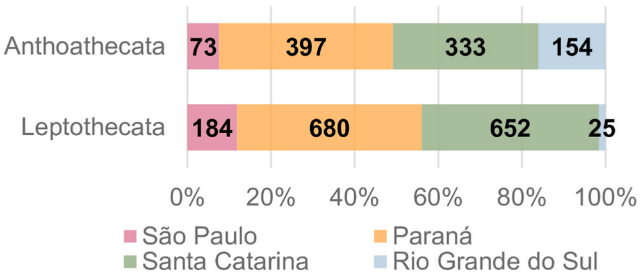

Fig. 5 Number of records for each order, by state

Zoological collection survey

We accessed recording information of hydroid samples deposited in the following institutions: (i) Invertebrate Collection of the Department of Zoology from the Universidade Federal do Paraná (DZoo-UFPR), (ii) Invertebrate Collection of the Department of Zoology from the Universidade Positivo (DZoo-UP), and (iii) the Hydrozoa Collection of the Museum of Zoology from the Universidade de São Paulo (MZUSP). Hydroid identification of some samples from the DZoo-UFPR and the DZoo-UP was performed when necessary.

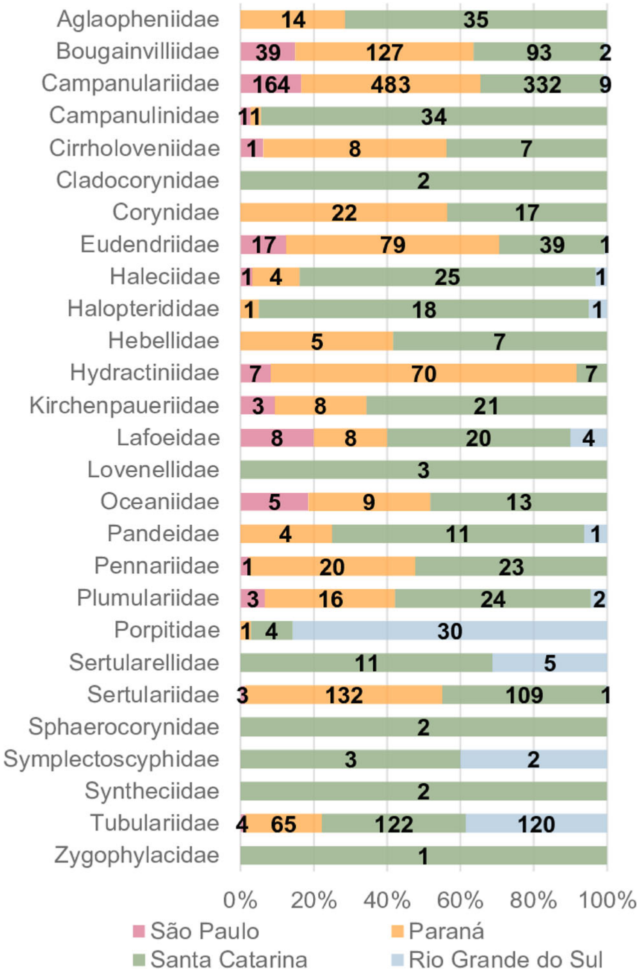

Fig. 6 Number of records for each family, by state (presented in alphabetical order)

Field survey

We identified and recorded hydroids from the coast of Santa Catarina growing on artificial panels. Recruitment plates made of polyethylene (12 × 12 cm^2) were installed in mussel farming structures from the municipalities of Penha, Governador Celso Ramos, Florianópolis, and Palhoça (Fig. 1c).

The plates were deployed in October/2017 and January/2018. After 1 month of submersion, they were removed from the water and labeled, and the adherent organisms were anesthetized with a menthol solution and then fixed with a 4% formaldehyde solution for further identification.

Plates were joined in parallel two by two, forming a “sandwich,” spaced 1.5 cm apart with the aid of rubber spacers. Each sandwich ($n = 12$ per period in each sampling site) was attached to a rope with a 0.6-L PET bottle filled with sand at one end to keep the structure submerged. Each set of plates (Fig. 2) was tied up perpendicularly to the backbone line of the mussel crop, and an empty 2-L PET bottle was attached to serve as a signal buoy. Samples of each observed morphotype were deposited in the Invertebrate Collection of the DZoo-UFPR.

Data standardization

With the aim of facilitating communication, the study area from the southern portion of the state of São Paulo was treated as a state (state of São Paulo) henceforth. We checked for duplicate records and standardized the nomenclature using the World Register of Marine Species (WoRMS Editorial Board 2020). A list of synonyms for South American hydroids is provided by Oliveira et al. (2016).

Throughout the whole study, any entry in the dataset was considered to be a morphotype (i.e., any hydroid classified to genus level), whereas unique species were considered to be recognized as singular (different) species for the studied area. Thus, a morphotype can either be a unique species or any hydroid entry assigned as “cf.,” “?,” or “sp.” (e.g., *Clytia* sp., ?*Turritopsis* sp.). Moreover, a morphotype assigned with “cf.” or “?” can be considered a unique species if it is (i) classified to species level and (ii) the unique representative of that species for the studied area (i.e., *Symplectoscyphus ?subdichotomus* (Kirchenpauer, 1884)).

In some graphs and analyses, the morphotypes “*Turritopsis* sp.” and “?*Turritopsis* sp.” were grouped together as well as “*Clytia gracilis*” and “*Clytia* cf. *gracilis*” aiming to minimize bias. When we conducted such a grouping, a note was added.

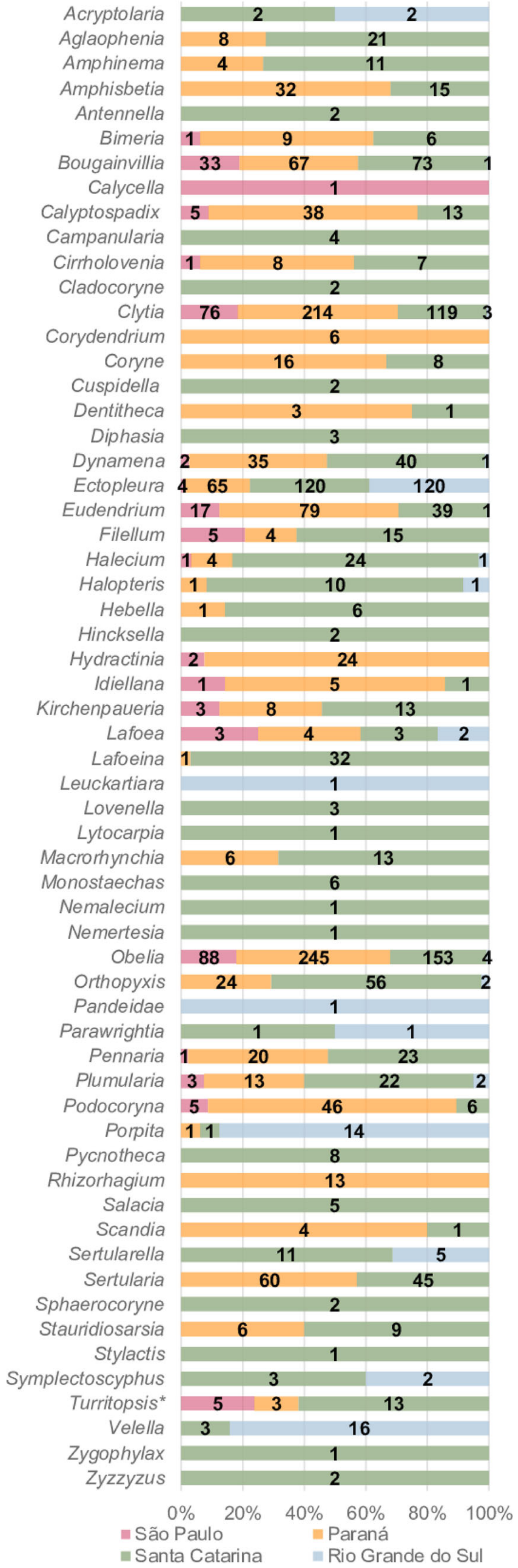

Fig. 7 Number of records of each genus, by state (presented in alphabetical order). *, *Turritopsis* + ?*Turritopsis*

Unique species were classified as cryptogenic, introduced, or native (Chapman and Carlton 1991; Carlton 1996). For status inferences, a literature review was conducted in the same way as that of the bibliographical survey. When a species status was not found in the literature, it was inferred following the criteria described by Chapman and Carlton (1991) and Carlton (1996).

Statistical analysis and figure production

To test whether the hydroid communities were sampled sufficiently, accumulation curves were drawn using four nonparametric richness estimators: Bootstrap, Chao2, and first- and second-order Jackknife estimators. These estimators were chosen because they are based on species incidence (presence/absence for a given location) to infer about community richness (Hortal et al. 2006; Canning-Clode et al. 2009). In other words, they indicate how much the observed species richness may agree with the actual species richness (Hoeksema and Koh 2009).

The dependent variable "number of morphotypes" was estimated from the independent variable "number of samples". In this analysis, one sample refers to the collection of one or more hydroid morphotypes in the same month, year, and locality (same latitude + longitude). Therefore, for estimating the sufficiency of hydroid sampling, only georeferenced records with information on month and year of the sampling were used. We could not use the day of collecting instead because many records did not present this. Besides presenting the accumulation curves for the total area, we also provide these curves for each state separately with the aim of allowing interregional comparisons.

The matrices (Online Resource 1) of the species accumulation curves were obtained using the PRIMER-E program (999 permutations) and, later, processed in Microsoft Excel® to generate the graphs. All maps and graphs were created with Q-gis (version 2.18.22) and Microsoft Excel®, respectively. Some figures were created and/or edited in Microsoft PowerPoint®.

Results

In total, 46.9% of the references are from the white literature and 53.1% from the gray literature. A total of 49 references were accessed, including articles ($n = 21$), academic documents ($n = 19$), biological collections ($n = 3$), annals of scientific events ($n = 2$), book chapters ($n = 2$), and personal communications ($n = 2$).

We listed 27 families, 59 genera, 129 morphotypes, and 95 unique species (Table 1) occurring in the study area between 1941 and 2018 (all of them being non-calcified). Regarding the unique species, 3.2% ($n = 3$: *Podocoryna loyola*,

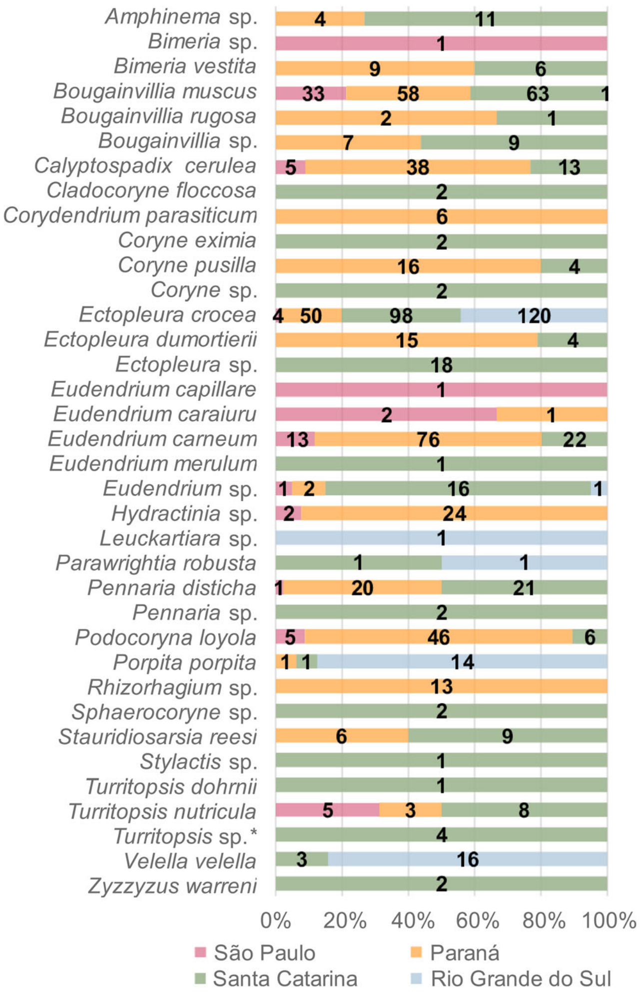

Fig. 8 Number of records for each Anthoathecata morphotype, by state (presented in alphabetical order). *, *Turritopsis* sp. + ?*Turritopsis* sp.

Calyptospadix cerulea, and *Turritopsis dohrnii*) were classified as introduced, 2.1% (*n* = 2: *Eudendrium caraiuru* and *Plumularia margaretta*) as native, and 94.7% (*n* = 90) as cryptogenic (Table 1). The recruitment plates deployed in Santa Catarina in 2017 and 2018, and the unpublished data from the DZoo-UFPR provided new records and insights on the hydroid distribution (Table 2).

A total of 2498 records refer to the absolute entries (i.e., entries comprising all morphotypes) and 2158 to the entries of unique species. Detailed information for each record as well as hydroid taxonomic classification can be found in Online Resource 2, and a heatmap of hydroid records in Fig. 3.

Regarding the number of records per state, Paraná displayed the highest number (*n* = 1077; 43.1%) followed by Santa Catarina (*n* = 985; 39.4%), São Paulo (*n* = 257; 10.2%), and Rio Grande do Sul (*n* = 179; 7.2%) (Fig. 4). Santa Catarina displayed the greatest number of families (*n* = 27; 100%), genera (*n* = 54; 91.5%), morphotypes (*n* = 110; 85.3%), and unique species (*n* = 86; 90.5%) (Fig. 4).

The most numerous order, families, genera, and morphotypes were Leptothecata (*n* = 1541; 61.7%; Fig. 5), Campanulariidae (*n* = 988; 39.6%) followed by Tubulariidae (*n* = 311; 12.4%) (Fig. 6), *Obelia* (*n* = 490; 19.6%) followed by *Clytia* (*n* = 412; 16.5%) and *Ectopleura* (*n* = 309; 12.4%) (Fig. 7), and *E. crocea* (*n* = 272; 10.9%; Fig. 8) followed by *O. dichotoma* (*n* = 222; 8.9%; Fig. 9), respectively. The distribution maps of the most common *Obelia*, *Clytia*, and *Ectopleura* morphotypes are available in Fig. 10.

Concerning the ecological distribution of the recorded morphotypes, we compiled the available information about depth and substrate type (artificial/natural). Although hydroids are typically benthic organisms, the two common pleustonic species (i.e., *Velella velella* and *Porpita porpita*) have been registered in the study area along with the less common planktonic *Clytia* spp.

Hydroids were recorded from the intertidal zone to 402 m depth (Online Resource 3), but the majority (*n* = 86; 66.7%), corresponding with 2070 records (82.9%), occurred up to a depth of 5 m (Fig. 11). *Acryptolaria* sp. 2 and *Symplectoscyphus* sp. displayed the deepest records (402 m), and *Plumularia setacea*, the greatest bathymetric range (5–387 m) (Online Resource 3). Other eurybathic hydroids such as *Filellum serratum*, *Lafoea dumosa*, *Sertularella leiocarpa*, *Symplectoscyphus ?subdichotomus*, and *Zygophylax geniculata* were also found within the study area (Online Resource 3).

Considering only the benthic records, 43.4% (*n* = 1084) corresponds to hydroids growing on artificial substrates (Fig. 12). The majority of Leptothecata morphotypes were recorded on natural substrates and that of Anthoathecata on artificial substrates (Fig. 12).

Research interest focusing on hydroids from the study area has increased, mainly after the year 2001, and the oldest hydroid record dates back to 1941 (Fig. 13). The number of records was raised by 284% from 2001 to 2011, the number of morphotypes by 73% from 1991 to 2001, and by 59% from 2001 to 2011, and the number of studies almost doubled from 2001 to 2011 and was increased by 145% from 2001 to 2018. Despite this increment, the accumulation curves indicate that sampling effort is still not sufficient in the different scenarios tested for total area and by state (Fig. 14, Online Resource 4). These curves demonstrated that the states of Santa Catarina and Paraná were sampled more thoroughly than their counterparts.

Discussion

This research provides new hydroid records from the recruitment plates deployed in Santa Catarina as well as unpublished

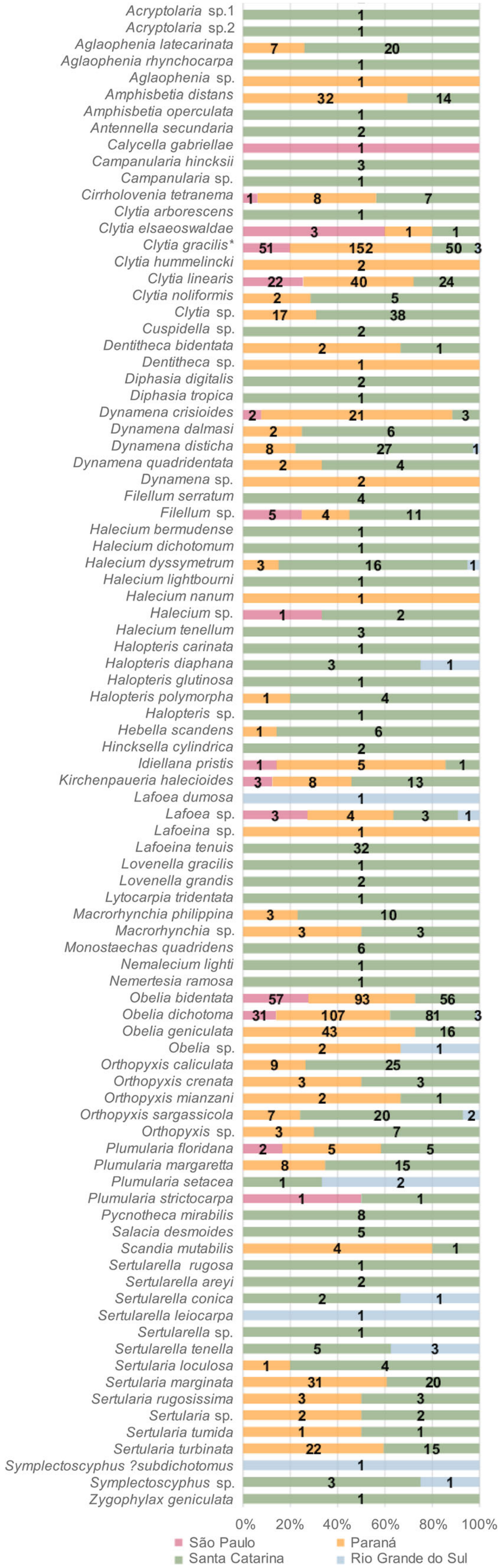

Fig. 9 Number of records per state for each Leptothecata morphotype (presented in alphabetical order). *, *Clytia gracilis* + *Clytia* cf. *gracilis*

data from the Department of Zoology of the Universidade Federal do Paraná. We recorded, for the first time, the hydroid fauna of Governador Celso Ramos (12 morphotypes, 8 unique species) and updated records for many localities (Table 2). The assessment of the Invertebrate Collection of the DZoo-UFPR allowed us to identify two new morphotypes for the Currais islands (*Filellum* sp. and *Sertularia rugosissima*), and *Macrorhynchia philippina* was recorded for the first time in the area since 2003. This collection also permitted us to officially present the first record of the introduced *P. loyola* on natural substrata (see Bettim and Haddad 2017) and new records of this alien species in Cananéia and Ilha Comprida (state of São Paulo).

The 95 unique species represent 18.9% and 52.2% of the hydroid species recorded in South America and Brazil, respectively (Oliveira et al. 2016, this study). Even though calcareous hydroids occur along the Brazilian coast (Amaral et al. 2008; Oliveira et al. 2016; De Souza et al. 2017), we did not find any in our study area. In Brazil, the state of São Paulo has been recorded as the southernmost locality for hydrocorals, but there have been reports of calcified hydroids southward up to Tierra del Fuego, southern Argentina (Oliveira et al. 2016). Taking this information into account and considering that hydrocorals occur from shallow to deep waters, and in both cold and warm waters (Lindner et al. 2008; Cairns 2011), we suppose that these animals can be present in marine subtropical waters of Brazil, but have not yet been recorded.

A prior study focusing on hydroid records from the coast of Paraná compiled 695 records, 18 families, 31 genera, and 44 morphotypes (Miranda 2017). Thus, the present study enhances the knowledge of hydroid occurrence for this state, assembling 1.077 records, 20 families, 35 genera, and 67 morphotypes, an increment of 55, 11, 13, and 52%, respectively.

The great diversity of hydroid morphotypes found within the study area was already expected as these animals can grow on different substrates and survive under a wide variety of environmental conditions and depths (Gili and Hugues 1995; Fernandez and Marques 2018). Additionally, the study area presents singular habitats (e.g., marine areas, estuaries, sandy beaches, and mangroves) as well as different types of natural substrates (e.g., rocky shores, mangrove roots) and artificial ones (e.g., port and marina structures, artificial reefs, and aquaculture equipment) for fouling growth (Bardi 2011; Bumbeer and Rocha 2012, 2016; Altvater and Coutinho 2015). The salinity gradient of the estuarine regions, for instance, enables the growth and reproduction of taxa with different salinity tolerances. Thus, the subtropical waters of Brazil provide suitable habitats for the occurrence of hydroids.

Leptothecata displayed the greatest number of records, which was expected since it is the most speciose order of Medusozoa (Maronna et al. 2016).This order was the most recorded in all states except for Rio Grande do Sul, where

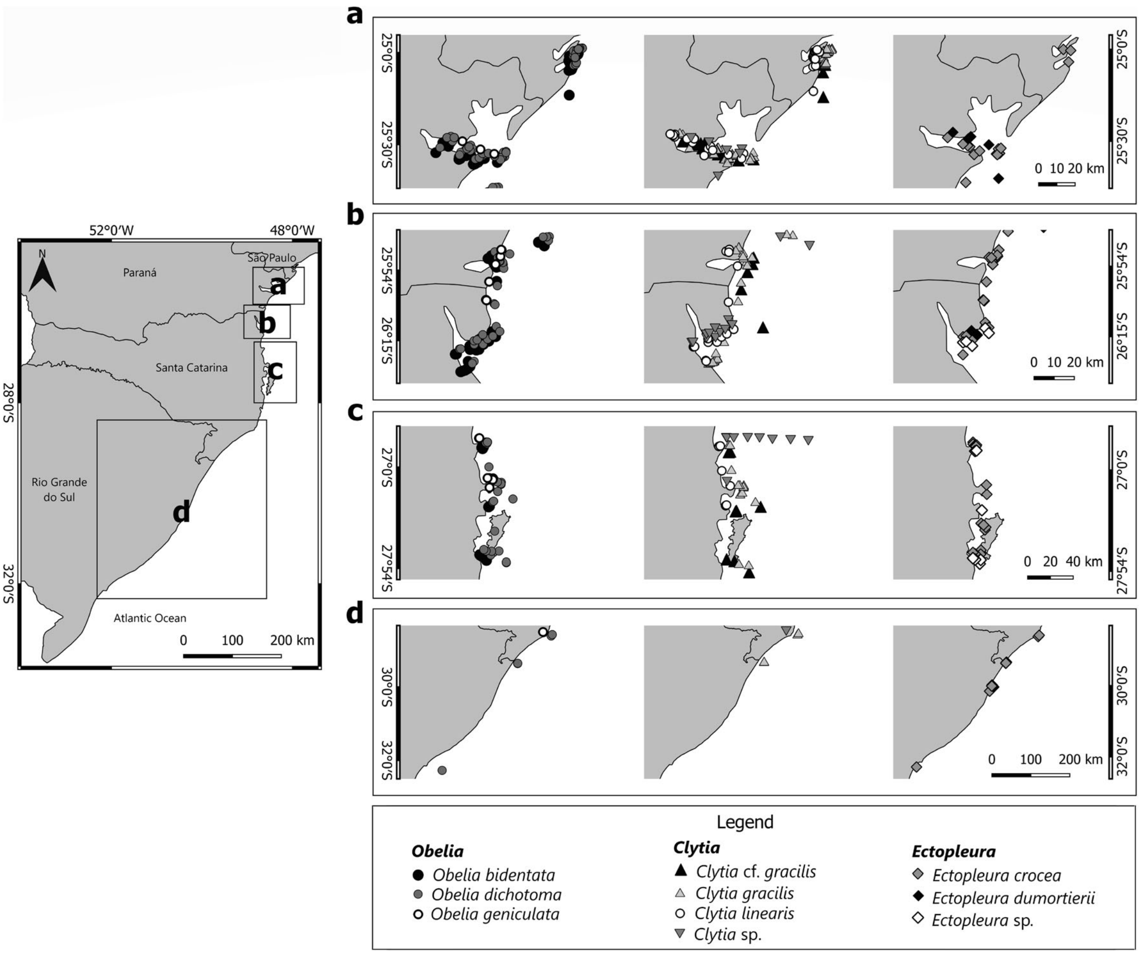

Fig. 10 Distribution map of the most common *Obelia* and *Clytia* morphotypes (left and middle columns, respectively), and of all *Ectopleura* morphotypes (right column)

records for Anthoathecata were 500% higher. The primary cause of the discrepancy is due to the high number of *Ectopleura* records, especially those from Agostini and Ozorio (2018), which corresponds to 63% of the total number of records for Rio Grande do Sul ($n = 178$).

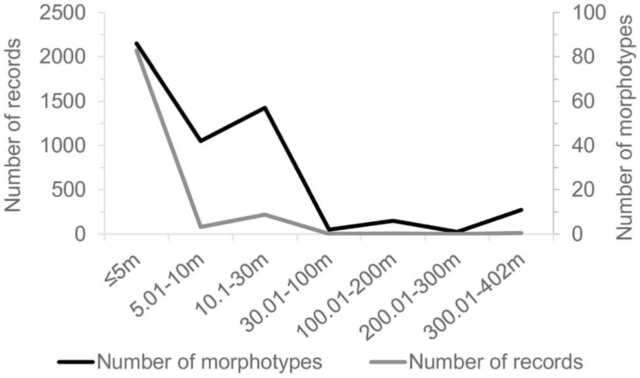

Fig. 11 Number of morphotypes and records per depth range. Only records presenting depth information were taken into account. *Clytia gracilis* and *Clytia* cf. *gracilis* were grouped together as well as *Turritopsis* sp. and ?*Turritopsis* sp.

The fact that hydroids were mainly recorded on artificial substrates and up to 5 m depth can be attributed to the different sampling methodologies. Many studies we accessed to create a dataset focused on the intertidal zone or on artificial substrates for fouling growth. Moreover, many hydroids were mostly found in the intertidal zone simply because hydroid richness rises towards the water surface (Fernandez and Marques 2018) and also because the intertidal zone is easier to access.

Some taxa such as *Cladocoryne floccosa* and *Sertularia tumida* are circumglobally distributed (Galea 2008), but were poorly reported. There are several possible explanations for this result, including insufficient of sampling and/or biological and ecological characteristics of each species that make them more difficult to become detected (e.g., life cycle, specializations, and seasonality in spatial distribution). Other scarcely reported taxa may also deal with the same issues, such as *Acryptolaria conferta*, *Monostaechas quadridens*, *Nemalecium lighti*, *Zygophylax geniculata*, and *Lytocarpia tridentata*.

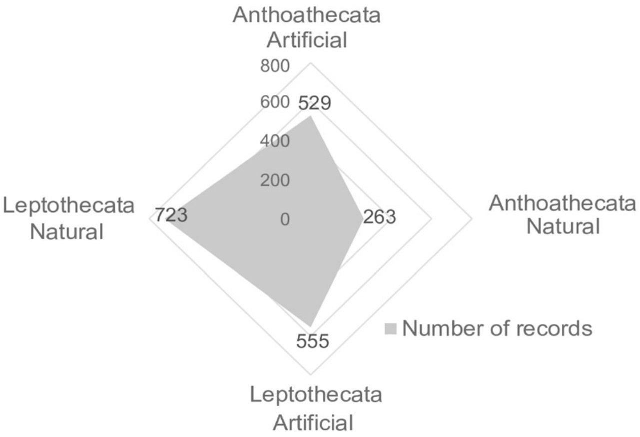

Fig. 12 Number of records per order according to the different nature of the sampled substrate(s). Only benthic hydroid records containing information about the nature of the substrates were taken into account

Concerning species status, the large proportion of cryptogenic species (95%) is due to the insufficient information regarding species status in the literature combined with the scarcity of historical distribution data, leading us to classify them as cryptogenic, therefore. The high number of cryptogenic species found in this study should be taken into consideration in ecological management plans since previous introductions of non-native species may have been masked (Neves and Rocha 2008), and introduced species can have a harmful impact on native communities (Neves and Rocha 2008). Therefore, we encourage future research focusing on the monitoring of the introduced species *P. loyola*, *C. cerulea*, and *T. dohrnii* as well as on an investigation of original species distributions since cryptogenic species may have been introduced at some time in the past and become more widespread afterward (Rocha 1999). Further works also need to be performed to confirm the identity of *Turritopsis* samples as recent studies (Schuchert 2016; Miglietta et al. 2019) on the taxonomic classification of this genus revealed the presence of the introduced *T. dohrnii* in the study area, which was previously misidentified as *Turritopsis nutricula* (voucher specimen #MZUSP4092 from Balneário Camboriú).

Our results demonstrated that this neglected fauna (Di Camillo et al. 2017) has gradually been receiving more attention since the beginning of the twenty-first century, but sampling effort on this fauna is still not sufficient. Because hydroid species richness is believed to be underestimated, as for all Hydrozoa (e.g., Bouillon et al. 2004) and the global (marine) biodiversity in general (e.g., Bini et al. 2006; Appeltans et al. 2012), non-recorded species are probably present within the studied area as well as non-descript species. The sizes of species-rage distributions are likely to be underestimated as well due to the cryptic nature of some hydrozoan taxa (e.g., Lindner et al. 2011; Montano et al. 2017a, b).

Considering that biological and ecological characteristics of species, as well as the sampling period, effort, and techniques, can influence the detectability of organisms (Thompson et al. 2003; Cunha and Jacobucci 2010), we propose that hydroids should be sampled in different months as well as on distinct substrates (e.g., rocky shores, artificial panels, port structures, soft bottoms, mangrove areas, living organisms such as large-multicellular algae, and benthic metazoans) and different depths to increase the likelihood of hydroid encounter. Planktonic sampling would improve the knowledge of the pelagic hydroids and those with medusa stages, which could help in solving taxonomic issues in addition to the use of molecular methods (e.g., Maggioni et al. 2016; Schuchert 2016; Miglietta et al. 2019).

Further research should be undertaken mainly in unsampled areas, such as beaches at the southern coast of Santa Catarina, on malacoculture areas, and in marine protected areas, but it is fundamental near the Port of Rio Grande and on its submerged structures since port areas are likely to shelter alien species (Bumbeer et al. 2016; Haddad et al. 2014).

For São Paulo and the northern region of the PEC (Guaraqueçaba and Pinheiros Bays), research on the hydroid fauna and other fouling species is still being carried out and will be published in future papers. Concerning the state of Rio Grande do Sul, although rocky formations are restricted to Torres municipality, the literature assembling hydroid data suggests that hydroids grow on many other natural (e.g., soft bottoms, mangrove roots) and artificial (e.g., artificial panels, port structures) substrata. For this latter state, we especially suggest the use of artificial panels since we did not find any study with this type of methodology for assessing the fouling community of its waters and because they are very useful to assess fouling species and evaluate their abundance and seasonal patterns of distributions (Bettim and Haddad 2017; Altvater and Coutinho 2015).

It is of great importance to maintain the dataset presented in this study updated. Lastly, we address some general considerations that occurred to us after this work. Firstly, we underscore that studies that provide the reader with the geographical coordinates of their sampling points can improve the data quality as well as facilitate processing for other researchers (e.g., the time needed for data compilation). Georeferenced records also allow researchers to better understand an organism's natural history (Clause et al. 2020) and are to be used in various kinds of ecological studies, supporting, for instance, the prediction of patterns of species richness and endemism (Foley et al. 2007). Secondly, we found many high-quality gray literature studies, which were crucial for improving our dataset. Finally, we recommend the application of a Standardized Integrative Taxonomy for describing marine benthic organisms, as proposed by Di Camillo et al. (2018).

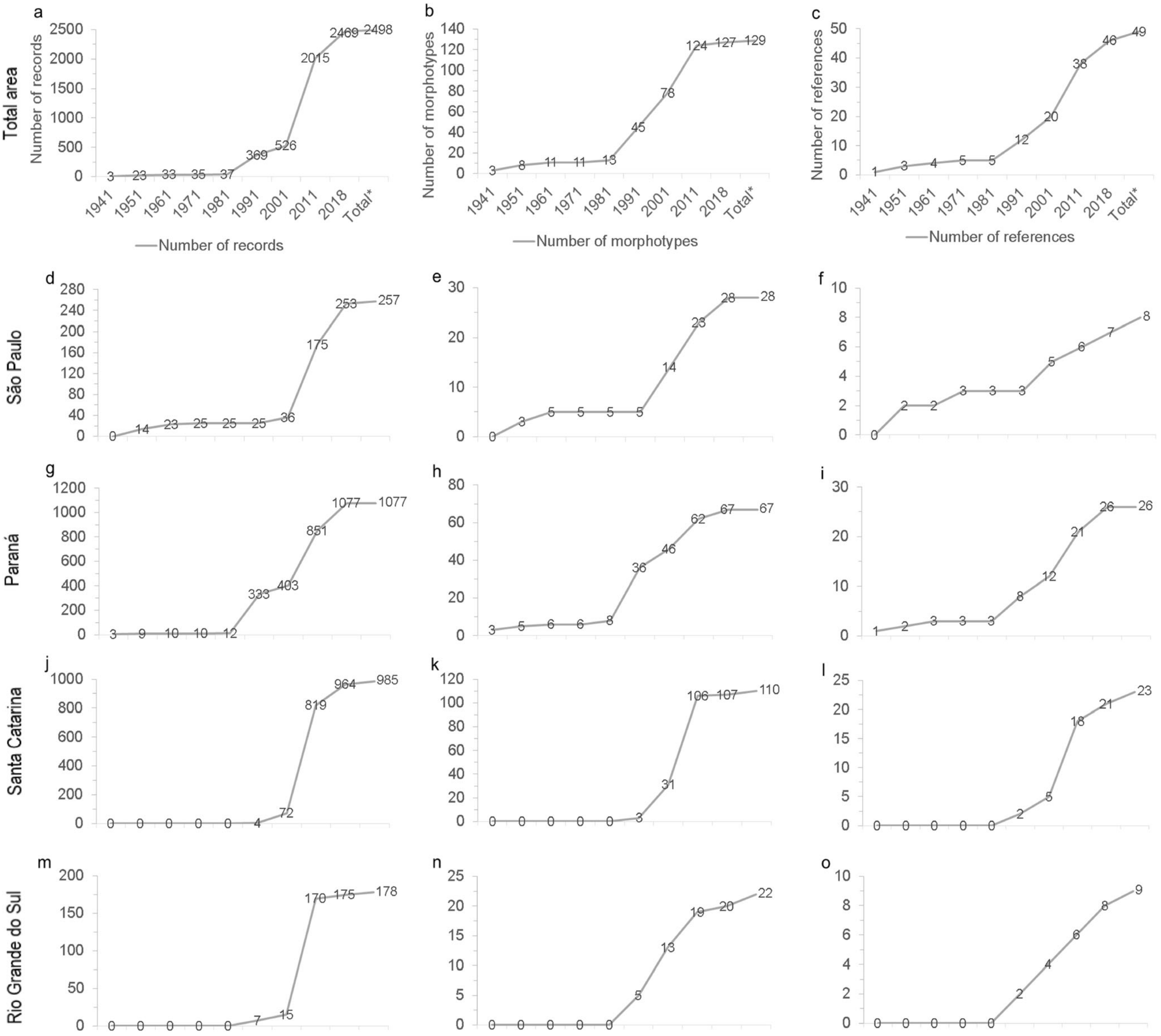

Fig. 13 Accumulation of the number of records, morphotypes, and references between 1941 and 2018. *, total number

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Compliance with ethical standards

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

Ethical approval No animal testing was performed during this study.

Sampling and field studies The license for data collection was issued based on Normative Instruction No. 03/2014 through the authentication code 0644940220200128. Any citizen can verify the authenticity or regularity of this document through the Sisbio/ICMBio website (www.icmbio.gov.br/sisbio).

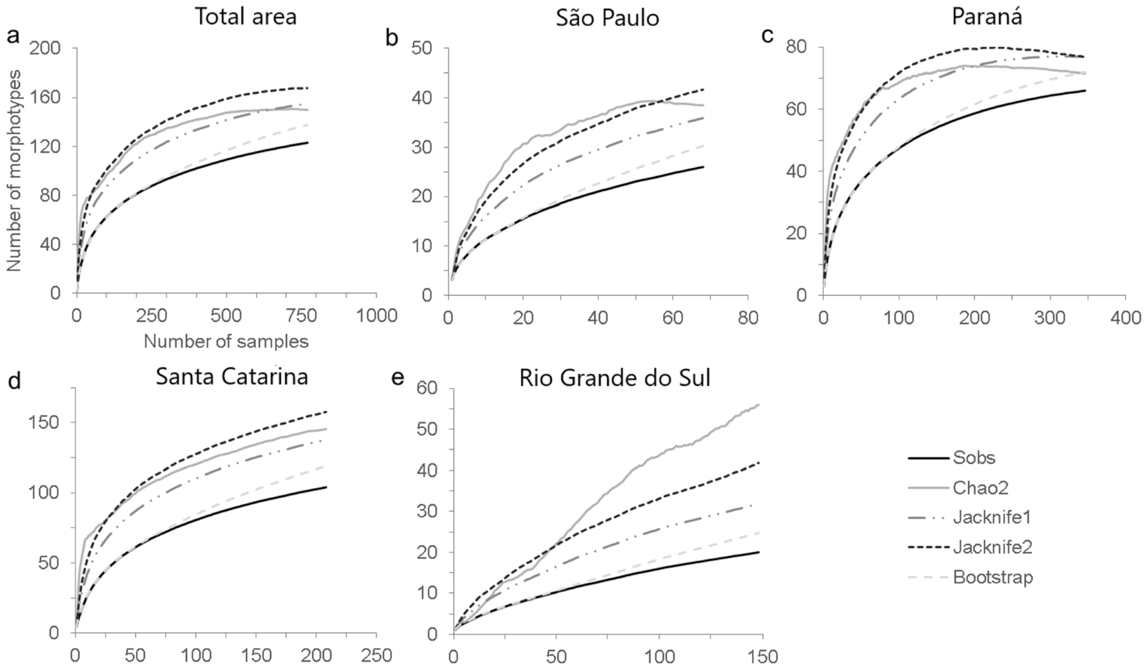

Fig. 14 Accumulation curves for hydroid sampling in different scenarios (total area and per state). Chao2, Jackknife1 and 2, and Bootstrap are the four non-parametric estimators of species richness, and Sobs is the observed richness. *Clytia gracilis* and *Clytia* cf. *gracilis* were grouped together as well as *Turritopsis* sp. and ?*Turritopsis* sp.

Data availability All data generated or analyzed during this study are included in this published article (and its supplementary information files).

Author contributions LAB and MAH conceived the main idea and compiled the data. LAB analyzed the data and led the writing. DML collected all the data from the mussel culture sites. All authors commented on drafts and approved the final version of the manuscript.

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