

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/325991964>

# Diversity, Species Composition and Assemblage Dynamics of Estuarine Gelatinous and Semi-Gelatinous Zooplankton from Brazil

Chapter · June 2018

DOI: 10.1007/978-3-319-77869-3\_18

CITATIONS

4

READS

64

5 authors, including:



**Miodeli Nogueira Júnior**

Universidade Federal da Paraíba

54 PUBLICATIONS 311 CITATIONS

[SEE PROFILE](#)



**Lorena Silva Nascimento**

Universidade Federal do Paraná

4 PUBLICATIONS 7 CITATIONS

[SEE PROFILE](#)



**Livia Oliveira**

Universität Bremen

1 PUBLICATION 4 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Diversity and dynamics of non-crustacean estuarine zooplankton [View project](#)



Diversidade e ecologia de cnidários Medusozoa da Paraíba [View project](#)

# Diversity, Species Composition and Assemblage Dynamics of Estuarine Gelatinous and Semi-Gelatinous Zooplankton from Brazil



Miodeli Nogueira Jr., Lorena Silva do Nascimento, Pedro Vieira Maciel, Sebastião Tilbert, and Livia Dias Oliveira

**Abstract** The literature on gelatinous (Cnidaria, Ctenophora, Tunicata) and semi-gelatinous (Chaetognatha) zooplankton from 32 Brazilian estuaries is reviewed. Altogether 104 species have been recorded, 70 cnidarians, 2 ctenophores, 14 chaetognaths, 13 appendicularians and 5 thaliaceans. All groups are understudied with only few detailed data available. Most of these gelatinous and semi-gelatinous taxa are typically oceanic, and thus the low diversity in estuarine systems was expected and is not probable to increase much with increasing sampling effort. Contrary, the meroplanktonic hydromedusae from the orders Anthoathecata and Leptothecata are diversified in estuarine ecosystems and the respectively 29 and 19 species currently reported from Brazilian estuaries are an underestimation and certainly will increase considerably with increased sampling effort. The best-studied taxa are the chaetognaths, followed by appendicularians, and very little is known about the other taxa, particularly concerning ctenophores and thaliaceans. We summarize the main tendencies of each taxon regarding diversity, abundance, temporal and spatial variations, species composition, and the most abundant species. In addition, we also provide general guidelines for future research on gelatinous and semi-gelatinous zooplankton taxa from Brazilian estuaries.

**Keywords** Cnidaria · Ctenophora · Chaetognatha · Tunicata · Brazilian estuaries

---

M. Nogueira Jr. (✉) · P. V. Maciel · L. D. Oliveira  
Departamento de Sistemática e Ecologia,  
Universidade Federal da Paraíba, João Pessoa, PB, Brazil

L. S. do Nascimento  
Centro de Estudos do Mar, Universidade Federal do Paraná, Paraná, Brazil

S. Tilbert  
Departamento de Sistemática e Ecologia,  
Universidade Federal da Paraíba, João Pessoa, PB, Brazil

Laboratório de Meiofauna, Centro de Educação e Saúde,  
Universidade Federal de Campina Grande, Cuité, PB, Brazil

## 1 Introduction

Zooplankton is highly diversified and a paramount component of aquatic ecosystems mainly due to their trophic role as link between the primary producers and higher trophic levels. Thus, understanding the factors influencing its abundance, biomass, assemblage composition and dynamics is fundamental to the general comprehension of the functioning of these ecosystems (e.g., Boltovskoy 1999). Many zooplankton taxa, not directly related phylogenetically, have aqueous tissues in different degrees, such as cnidarians, ctenophores, polychaetes, chaetognaths and tunicates, in addition to the larvae of other groups such as echinoderms (Hamner et al. 1975; Larson 1986). These watery tissues are an evolutive convergence with advantages such as:

- (i). Higher sizes may be achieved with relatively little carbon investments and consequently the metabolism can be relatively low (Larson 1986; Acuña et al. 2011).
- (ii). Rapid individual and population growth and production (Paffenhöfer and Lee 1987; Hopcroft and Roff 1998; Acuña et al. 2011).
- (iii). Larger sizes increase the possibility of encounters as well as the size range of a possible prey and, in addition, reduce the chances of predation by smaller organisms (Larson 1986; Arai 1997; Kremer 2002).
- (iv). Greater corporal plasticity, allowing them to grow, shrink, and grow again depending on the environmental conditions and food availability (Arai 1997).
- (v). They are frequently transparent and invisible to visual predators which is a way to hide in the tridimensional and relatively homogeneous pelagic habitat (Hamner et al. 1975; Johnsen 2001).
- (vi). Large amount of water in the tissues results in a better buoyancy (Larson 1986).

Thus, among the many functional zooplankton classifications, such as according to the life-cycle strategy or to the body size, the relative amount of water in the tissues can be used to classify zooplankton taxa as gelatinous, semi-gelatinous, or non-gelatinous organisms (Larson 1986).

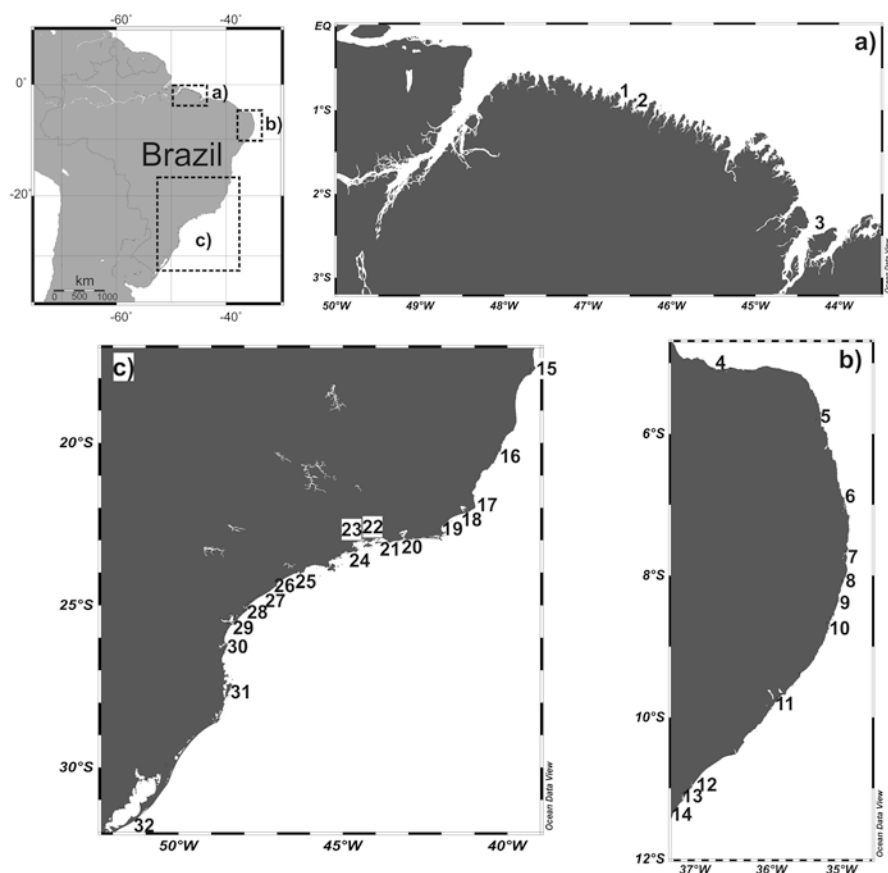
These watery organisms are often understudied, in part due to their body fragility that frequently hinders their sampling and preservation in conditions to allow accurate taxonomic classification and sometimes even to enumerate them (Hamner et al. 1975; Esnal and Daponte 1999a, b; Mianzan 1999). However, they represent an important fraction of the marine zooplankton biodiversity and may reach high densities, typically having an important ecological role in the pelagic realm and energy flow (Boltovskoy 1999). Both carnivores (mainly cnidarians, ctenophores, and chaetognaths) and herbivores (mainly tunicates) commonly have high feeding rates, with crucial role as consumers in the pelagic domain. It is not uncommon for gelatinous and semi-gelatinous zooplankton to negatively affect populations of other organisms, including those with commercial value, either through direct predation or competition for food (Mills 1995; Kremer

2002). In this way, it can usually be expected that these organisms are relevant to the diversity, dynamics, and community structuring of the pelagic ecosystems and also affect several human activities at the sea such as tourism and fisheries (e.g., Nagata et al. 2009).

Estuaries can generally be defined as coastal water bodies, usually semi-enclosed, which are permanently or intermittently connected to the sea and where marine and freshwater from continental runoff interact (Potter et al. 2010; Whitfield and Elliot 2011). These ecosystems have high ecological, economic and cultural importance. Their biological productivity is typically very high, harboring an abundant, diversified and characteristic biota which includes many important fishing resources (Daily et al. 1997; Lana et al. 2001; Cremer et al. 2006). Additionally, human occupation for habitation commercial and recreational purposes is historic and massive nearby estuaries worldwide, posing a great threat to these environments.

Since estuaries are transitional ecosystems, spatial gradients are typical particularly regarding the salinity (Potter et al. 2010; Whitfield and Elliot 2011). Physical conditions of an estuary are vital in determining its biological components such as primary production, biomass, diversity, trophic pathways and species composition. This may be particularly true for zooplankton assemblages which are under direct influence of the hydrography and are commonly sensitive to changes in the physical structure of the water column. Features such as salinity, tides, temperature, rainfall and continental runoff are typically the most important ones. These parameters change horizontally and/or vertically mainly influenced by the mixing, circulation and stratification processes of the estuarine systems (Daily et al. 1997), as well as seasonally, when it is mostly controlled by local rainfall regime and general latitudinal climatic patterns.

The Brazilian coast is enormous with over 8,000 km spanning from the tropics ( $\sim 2^{\circ}\text{N}$ ) to almost temperate areas ( $\sim 33.7^{\circ}\text{S}$ ) and embraces countless estuarine/brackish-water ecosystems, most of them with high ecological, economic, cultural importance and under high human pressure (e.g., Lana et al. 2001; Cremer et al. 2006; Mahiques et al. 2013). Gelatinous and semi-gelatinous zooplankton taxa are primarily marine. Yet, representatives of all major groups can be found inside estuaries where they may reach high abundances, biomass, and/or production rates and have a significant role in the trophic chains (Dagg et al. 1996; Dagg and Brown 2005; Sato et al. 2008; Spinelli et al. 2009; Marques et al. 2017). Most of the (few) information available on these estuarine gelatinous and semi-gelatinous zooplankton taxa from Brazil is superficial and scattered through general zooplankton publications. In this study, we made an effort to summarize all the available data on gelatinous (cnidarians, ctenophores, and tunicates) and semi-gelatinous (chaetognaths) zooplankton from Brazilian estuaries, focusing on species composition, diversity, abundance and assemblage structure trends. We were able to gather data for at least one major gelatinous/semi-gelatinous taxon from 32 estuaries (Fig. 1, Table 1), spanning a wide latitudinal range ( $0\text{--}32^{\circ}\text{S}$ ). Not all estuaries and/or taxa are known at the same depth, but we tried to include all information available and summarize the general tendencies of each taxon.



**Fig. 1** Map of the Brazilian coast showing the location of the estuaries considered in the present review (1–32). For codes of the numbers and data sources, please see Table 1

## 2 Cnidaria

There are quite few studies dealing with estuarine planktonic cnidarians from Brazil (e.g., Navas-Pereira 1980; Montú and Cordeiro 1988; Mesquita et al. 2006). A total of 70 species have been recorded (Table 2); most of them are meroplanktonic hydro-medusae, particularly those from the orders Anthoathecata (29 spp.) and Leptothecata (19 spp.) which commonly are highly diversified in shallow coastal waters. This number is probably underestimated considering that most Brazilian estuaries have not been studied adequately or at all, along with the inability to properly identify down to species level the medusae of some genera such as *Clytia* and *Obelia*; at least three different medusa species of the former have been reported from Brazilian estuaries (Mesquita et al. 2006; Nogueira Júnior 2012, Table 2); however we pulled all together as *Clytia* spp. since we cannot exactly determine which species each

**Table 1** Summary of the Brazilian estuaries included in this study showing their minimum and maximum recorded temperature (Temp, in °C) and salinity (Sal), data availability for each taxa (Cnid, Cnidaria; Cten, Ctenophora; Chae, Chaetognatha; Tun, Tunicata) along with the source of the information. N°, number of the estuary in the Fig. 1; nda, no data available

Estuary	N°	Cnid	Cten	Chae	Tun	Temp	Sal	Data source
Taperaçu River (0°45'S/46°44'W)	1			X	X	25.9–30.1	9.1–40	Costa et al. (2008)
Caeté River (0°55'S/45°36'W)	2	X		X	X	25.7–28.3	0–37	Krumme and Liang (2004), Mesquita et al. (2006)
São Marcos Bay (2°32'S/44°36'W)	3			X	X	22.7–28.9	16.4–24.1	Bonecker and Dias (2009)
Conceição and Casqueira Rivers (5°06'S/36°35'W)	4			X	X	27.5–31	31–43.5	Sankarankutty et al. (1997)
Potengi River (5°45'S/35°12'W)	5			X	X	25.5–30	26.8–37.5	Sankarankutty et al. (1979, 1995, 1996), Esnal et al. (1985)
Paraíba River (6°58'S/34°51'W)	6	X	X	X	X	25–30	2.5–36.8	Singarajah (1978), MNJ unpublished
Santa Cruz Channel and Itamaracá estuarine system (7°42'S/34°54'W)	7			X	X	25–31	17.4–35.5	Porto Neto et al. (1999), Silva et al. (2003), Freire et al. (2014)
Capibaribe and Jiquiá Rivers (8°05'S/34°51'W)	8	X				26.8–29.5	2.2–36	Freire et al. (2014)
Barra das Jangadas estuarine system (8°14'S/34°56'W)	9	X		X	X	25.2–29.6	0.3–33.4	Paranaguá (1963), Cavalcanti et al. (2008)
Suape Bay (8°22'S/35°05'W)	10	X		X	X	23.4–33	0.05–36	Neumann-Leitão and Matsumura-Tundisi (1998), Silva et al. (2004)
Mundaú/Manguaba estuarine system (9°35'S/35°42'W)	11			X		23–29	0.13–37	Magalhães et al. (1996)
Sergipe River (10°8'S/37°2'W)	12	X		X	X	23–29.9	8.6–32.6	Araújo et al. (2008), Freire et al. (2014)

(continued)

**Table 1** (continued)

Estuary	Nº	Cnid	Cten	Chae	Tun	Temp	Sal	Data source
Tabatinga River (11°32'S/37°29'W)	13	X		X		24.5–30	5.9–26.3	Marcolin (2008), Marcolin et al. (2010)
Itapicuru River (11°47'S/37°30'W)	14	X		X	X	25–31	8.6–36.3	Marcolin (2008), Marcolin et al. (2010)
Caravelas River (17°44'S/39°04'W)	15				X	nda	nda	Carvalho and Bonecker (2010)
Vitória Bay estuarine system (20°18'S/40°20'W)	16			X	X	21–28	12–38	Loureiro Fernandes et al. (2005), Sterza and Loureiro Fernandes (2006)
Macaé River (22°22'S/41°46'W)	17				X	23–24.5	18.5–22.5	Carvalho et al. (2016)
Imboassica Lagoon (22°24'S/44°42'W)	18				X	18.1–31.1	0–34	Branco et al. (2007)
São João River (22°36'S/41°59'W)	19				X	22.5–26	21–23.5	Carvalho et al. (2016)
Guanabara Bay (22°45'S/43°08'W)	20			X		22–26	12–31.2	Marazzo and Nogueira (1996), Mendes et al. (2012)
Sepetiba Bay (22°55'S/43°40'W)	21	X		X	X	20–29.9	0.003–33.9	Navas-Pereira (1980), Coelho-Botelho et al. (1999)
Bracuí River (22°57'S/44°23'W)	22				X	21–29	20–28.5	Carvalho et al. (2016)
Ribeira Bay (22°59'S/44°25'W)	23			X	X	21–36.4	29–36	Dias and Bonecker (2008)
Perequê-Açu River (23°12'S/44°42'W)	24				X	21.5–30	17.5–22	Carvalho et al. (2016)
Santos estuarine system (23°50'S/46°25'W)	25	X		X		19.2–32.5	4.2–35.8	Pereira (2011), Nogueira Júnior and Silva Nascimento (2018), MNJ unpublished

Una do Prelado River (24°S/47°03'W)	26	X		X	X	20–31	0–34.4	Lansac-Tôha and Lima (1993)
Guaraú River (24°22'S/7°06'W)	27			X	X	17–29	0.5–35.4	Lopes (1994)
Cananéia estuarine system (25°S/47°46'W)	28	X	X	X	X	18.6–32.6	4.5–33	Vannucci (1954, 1956, 1957), Teixeira et al. (1965), Morandini (2003), Liang et al. (2003), Bardi and Marques (2009), Bardi (2011), Martinez et al. (2015), Nogueira Júnior and Silva Nascimento (2018), MNJ unpublished
Paranaguá estuarine system (25.5°S/48°17'W)	29	X	X	X	X	16.9–30.5	0–34	Montú and Cordeiro (1988), Lopes et al. (1998), Nogueira Júnior and Oliveira (2006), Bardi and Marques (2009), Bardi (2011), Miyashita et al. (2012), Haddad et al. (2014), Nascimento (2016), Nogueira Júnior and Silva Nascimento (2018), L.K. Miyashita, personal communication, MNJ unpublished
Babitonga estuarine system (26.2°S/48.6°W)	30	X	X	X	X	19.2–27	10.1–33.6	Bardi and Marques (2009), Oliveira (2007), Bardi (2011), Nogueira Júnior (2012), Nogueira Júnior et al. (2015b), Nogueira Júnior and Silva Nascimento (2018), MNJ unpublished
North and South Bays (27°30'S/48°32'W)	31	X	X	X	X	17.5–28	29.3–37.8	Resgalla (2001), Nogueira Júnior et al. (2010), MNJ unpublished
Patos lagoon (31°50'S/52°2'W)	32	X		X		8.4–31	0–35	Montú (1980), Teixeira-Amaral et al. (2017)



**Table 2** List of gelatinous and semi-gelatinous estuarine zooplankton species recorded from Brazil. N = 104 spp. See Table 1 and Fig. 1 to see data source, estuary codes and locations. To avoid artificial inflation of the number of species due to taxonomic problems, only unique morphotypes were considered in the total species count. The interrogation indicates doubtful taxa, probably misidentifications which were disregarded from the total species count (see text)

Taxa	Estuary	Taxa	Estuary
<b>Phylum Cnidaria</b>		<b>Order Narcomedusae</b>	
<b>Class Hydrozoa</b>		<b>Family Cuninidae</b>	
Actinula larvae	25, 28–30	<i>Cunina octonaria</i> McCrady, 1859	21, 25, 28–30
<b>Subclass Hydroidolina</b>		<b>Family Solmarisidae</b>	
<b>Order Anthoathecata</b>		<i>Solmaris</i> sp.	28, 29
<b>Suborder Filifera</b>		<b>Order Trachymedusae</b>	
<b>Family Bougainvilliidae</b>		<b>Family Geryoniidae</b>	
<i>Bougainvillia muscus</i> Allman, 1863	12–14, 21, 25, 28, 29	<i>Liriope tetraphylla</i> Chamysso and Eyesenhardt, 1821	1, 12–14, 21, 25, 28–32
<i>Bougainvillia pagesi</i> Nogueira et al. 2013	30	<i>Geryonia proboscidalis</i> Forskål, 1775	29
<i>Bougainvillia frondosa</i> Mayer, 1900	29	<b>Family Rhopalonematidae</b>	
<i>Bougainvillia carolinensis</i> McCady, 1859	25, 29–30	<i>Aglaura hemistoma</i> Péron and Lesueur, 1810	28, 29
<b>Family Hydractiniidae</b>		? <i>Aglantha</i> sp.?	29
<i>Cnidostoma fallax</i> Vanhöffen, 1911	25, 28–30, 32	<i>Crossota</i> sp.	1
<i>Hydractinia</i> sp.	30	<i>Rhopalonema velatum</i> Gegenbaur, 1857	21
<i>Podocoryna loyola</i> Haddad, Bettim and Miglieta, 2014	25, 28–30	<b>Class Scyphozoa</b>	
<i>Podocoryna</i> sp.	26	<b>Subclass Discomedusae</b>	
<b>Family Oceaniidae</b>		<b>Order Semaestomeae</b>	
<i>Turritopsis nutricula</i> McCrady, 1857	25, 28–30	<b>Family Pelagiidae</b>	
<b>Family Pandeidae</b>		<i>Chrysaora lactea</i> Eschscholtz, 1829	6, 25, 28–31
<i>Amphinema australis</i> Mayer, 1900	21	<b>Family Ulmaridae</b>	
<i>Amphinema dinema</i> Perón and Lesueur, 1810	28–30	<i>Aurelia</i> sp.	28, 31
<i>Amphinema</i> sp.	1, 25	<b>Order Rhizostomeae</b>	
<b>Family Proboscidactylidae</b>		<b>Family Lychnorhizidae</b>	
<i>Proboscidactyla ornata</i> McCrady, 1859	28–30	<i>Lychnorhiza lucerna</i> Haeckel, 1880	6, 25, 28–31
<b>Family Protiaridae</b>		<b>Family Rhizostomatidae</b>	
<i>Halitiara formosa</i> Fewkes, 1882	30	? <i>Rhizostoma pulmo</i> (Macri, 1778)?	6
<i>Protiaara</i> sp.	30	<b>Family Mastigiidae</b>	

(continued)

**Table 2** (continued)

Taxa	Estuary	Taxa	Estuary
<b>Family Rathkeidae</b>		<i>Phyllorhiza punctata</i> Lendenfeld, 1884	28–31
<i>Podocorynoides minima</i> Trinci, 1903	21, 28, 30	<b>Family Stomolophidae</b>	
<i>Lizzia blondina</i> Forbes, 1848	28, 29	<i>Stomolophus meleagris</i> Agassiz, 1862	28, 29
<b>Suborder Capitata</b>		<b>Class Cubozoa</b>	
<b>Family Calycopsidae</b>		<b>Order Carybdeida</b>	
<i>Heterotiar</i> sp.	1	<b>Family Tamoyidae</b>	
<b>Family Corymorphidae</b>		<i>Tamoya haplonema</i> Müller, 1859	28, 31
<i>Corymorpha gracilis</i> Brooks, 1883	21, 28–30	<b>Order Chirodropida</b>	
<i>Corymorpha forbesii</i> Mayer, 1894	21, 25, 28–30	<b>Family Chiropsalmidae</b>	
<i>Corymorpha januarii</i> Steenstrup, 1854	25, 29, 30	<i>Chiropsalmus quadrumanus</i> Müller, 1859	28–31
<b>Family Corynidae</b>		<b>Phylum Ctenophora</b>	
<i>Stauridiosarsia reesi</i> Vannucci, 1956	25, 28–30	<b>Class Nuda</b>	
<i>Coryne eximia</i> Allman, 1859	25, 28, 29	<b>Order Beroida</b>	
<i>Sarsia</i> sp.1	1	<b>Family Beroidae</b>	
<i>Sarsia</i> sp.2	1	<i>Beroe ovata</i> Bruguière, 1789	6, 25, 28–31
<b>Family Halimedusidae</b>		<b>Class Tentaculata</b>	
<i>Tiaricodon</i> sp.**	28	<b>Order Cydippida</b>	
<b>Family Moerisiidae</b>		<b>Family Pleurobrachiidae</b>	
<i>Moerisia inkermanica</i> Paltshikowa–Ostroumova, 1925	9, 28, 29, 30	? <i>Pleurobrachia</i> sp.?	6
<b>Family Tubulariidae</b>		<b>Order Lobata</b>	
<i>Ectopleura dumortieri</i> van Beneden, 1844	21, 25, 28–30	<b>Family Bolinopsidae</b>	
<b>Capitata incertae sedis</b>		<i>Mnemiopsis leidyi</i> A. Agassiz, 1865	6, 25, 28–31
<i>Paulinum</i> sp.	30	<b>Phylum Chaetognatha</b>	
<b>Family Zancleopsidae</b>		<b>Class Sagittoidea</b>	
<i>Zancleopsis dichotoma</i> Mayer, 1900	21	<b>Order Apheragmophora</b>	
<i>Zanclea costata</i> Gegenbaur, 1857	29	<b>Family Sagittidae</b>	
<b>Order Leptothecata</b>		<i>Caecosagitta macrocephala</i> Fowler, 1904	6, 23
<b>Family Aequoreidae</b>		<i>Decipisagitta decipiens</i> Fowler, 1905	16, 23

(continued)

**Table 2** (continued)

Taxa	Estuary	Taxa	Estuary
<i>Rhacostoma atlanticum</i> L. Agassiz, 1851	30, 31	<i>Ferosagitta hispida</i> Conant, 1895	3, 16, 20, 21, 23, 25, 28, 31
<i>Aequorea</i> sp.	31	<i>Flaccisagitta enflata</i> Grassi, 1881	5, 6, 11–14, 16, 21, 23, 25, 28–32
<b>Family Blackfordiidae</b>		<i>Flaccisagitta hexaptera</i> d’Orbigny, 1836	23
<i>Blackfordia virginica</i> Mayer, 1910	7–9, 25, 28–30	<i>Mesosagitta minima</i> Grassi, 1881	16, 23
<b>Family Cirrholovenidae</b>		<i>Parasagitta friderici</i> Ritter–Záhony, 1911	1, 2, 7, 9, 16, 20, 21, 23, 25–32
<i>Cirrholovenia tetranema</i> Kramp, 1959	28–30	<i>Parasagitta tenuis</i> Conant, 1896	3–5, 7, 9, 10, 12–14, 21, 28–31
<b>Family Eirenidae</b>		<i>Sagitta helenae</i> Ritter– Záhony, 1911	5
<i>Eirene</i> sp.	28, 30	<i>Sagitta bipunctata</i> Quoy and Gaimard, 1827	6, 23
<i>Eutima mira</i> McCrady, 1859	25, 28–30	<i>Serratosagitta serratodentata</i> Krohn, 1853	6, 23
<i>Eutima</i> sp.	12	<b>Family Krohnittidae</b>	
<i>Helgicirrha</i> sp.	25, 28–30	<i>Krohnitta pacifica</i> Aida, 1897	23, 28
<b>Family Laodiceidae</b>		<i>Krohnitta subtilis</i> Grassi, 1881	6, 23
<i>Laodicea minuscula</i> Vannucci, <a href="#">1957</a>	25, 28–30	<b>Family Pterosagittidae</b>	
<b>Family Lovenellidae</b>		<i>Pterosagitta draco</i> Krohn, 1853	23
<i>Eucheilota duodecimalis</i> A. Agassiz, 1862	21, 25, 28–30	<b>Phylum Chordata</b>	
<i>Eucheilota maculata</i> Hartlaub, 1894	25, 28–30	<b>Subphylum Tunicata</b>	
<i>Eucheilota paradoxa</i> Mayer, 1900	21, 25, 28–30	<b>Class Appendicularia</b>	
<b>Family Malagazziidae</b>		<b>Order Copelata</b>	
<i>Malagazzia carolinae</i> Mayer, 1900	21, 25, 28–30	<b>Family Oikopleuridae</b>	
<i>Malagazzia</i> sp.	1	<i>Oikopleura (Coecaria)</i> <i>cornutogastra</i> Aida, 1907	23
<i>Octophialucium haeckeli</i> Vannucci and Moreira, 1966	30	<i>Oikopleura (Coecaria)</i> <i>fusiformis</i> Fol, 1872	15, 16, 21, 22
? <i>Octophialucium funerarium</i> (Quoy and Gaimard, 1827)?	6	<i>Oikopleura (Coecaria)</i> <i>gracilis</i> Lohmann, 1896	21, 23
<b>Family Tiaropsidae</b>	1	<i>Oikopleura (Coecaria)</i> <i>intermedia</i> Lohmann, 1896	21

(continued)

**Table 2** (continued)

Taxa	Estuary	Taxa	Estuary
<i>Tiaropsidium</i> sp.	1	<i>Oikopleura</i> ( <i>Coecaria</i> ) <i>longicauda</i> Vogt, 1854	7, 9, 10, 12, 15–19, 22, 23, 25, 28–30
<b>Suborder Proboscoida</b>		<i>Oikopleura</i> ( <i>Vexillaria</i> ) <i>albicans</i> Leuckart, 1853	21
<b>Family Campanulariidae</b>		<i>Oikopleura</i> ( <i>Vexillaria</i> ) <i>cophocerca</i> Gegenbaur, 1855	15, 23
<i>Obelia</i> spp.	10, 21, 25, 26, 28–30	<i>Oikopleura</i> ( <i>Vexillaria</i> ) <i>dioica</i> Fol, 1872	1–4, 7, 10, 12, 13, 15–17, 19, 21–31
<i>Clytia hemisphaerica</i> Linnaeus, 1767	21	<i>Oikopleura</i> ( <i>Vexillaria</i> ) <i>parva</i> Lohmann, 1896	31
<i>Clytia</i> spp. (1–3 spp. on each location)	1, 21, 25, 28–30	<i>Oikopleura</i> ( <i>Vexillaria</i> ) <i>rufescens</i> Fol, 1872	3, 7, 10, 15, 16, 23
<b>Order Siphonophora</b>		<i>Oikopleura</i> spp.	13, 14, 31
<b>Suborder Calyophora</b>		<b>Family Fritillariidae</b>	
<b>Family Abylidae</b>		<i>Appendicularia sicala</i> Fol, 1874	28
<i>Abylopsis tetragona</i> Otto, 1823	29, 30	<i>Fritillaria haplostoma</i> Fol, 1872	17, 23
<b>Family Diphyidae</b>		<i>Fritillaria tenella</i> Lohmman, 1896	23
<i>Diphyes bojani</i> Eschscholtz, 1825	30	<i>Fritillaria</i> spp.	10, 25, 29
<i>Lensia</i> sp.	10	<b>Class Thaliacea</b>	
<i>Muggiaea kochii</i> Will, 1844	28–30	<b>Order Doliolida</b>	
<b>Suborder Physonectae</b>		<b>Family Doliolidae</b>	
<b>Family Agalmatidae</b>		<i>Dolioletta gegenbauri</i> Uljanin, 1884	23, 28
<i>Nanomia bijuga</i> delle Chiaje, 1844	25, 28–30	<i>Doliolina</i> sp.	6
<b>Subclass Trachylina</b>		<i>Doliolum nationalis</i> Borgert, 1893	3, 23, 28, 30
<b>Order Limnomedusae</b>		<i>Doliolum</i> sp.	12
<b>Family Olindiasidae</b>		<b>Order Salpida</b>	
<i>Gossea brachymera</i> Bigelow, 1909	29, 30	<b>Family Salpidae</b>	
<b>Family Olindiidae</b>		<i>Salpa</i> sp.	6
<i>Aglauroopsis kawari</i> Moreira and Yamashita, 1972	25, 29, 30	<i>Thalia democratica</i> Forskål, 1775	12, 23, 25, 28–31
<i>Olindias sambaquiensis</i> Müller, 1861	25, 28–31		

record refers to; three species of *Obelia* polyps have been recorded from coastal Brazilian waters (Oliveira et al. 2016) and probably medusae of all of them can be found inside estuaries. Also, the distribution of these studies is highly uneven through the Brazilian coast. Except for Paranaguá (1963) and Mesquita et al. (2006), and from general zooplankton studies which mention a few cnidarian species (e.g., Singarajah 1978; Araújo et al. 2008; Marcolin 2008; Marcolin et al. 2010), studies are concentrated at South Brazilian Bight (~23–28°S) subtropical estuaries (e.g., Montú and Cordeiro 1988; Navas-Pereira 1980; see Table 1), reflecting the proximity of historically consolidated research groups studying cnidarians (Haddad and Marques 2009).

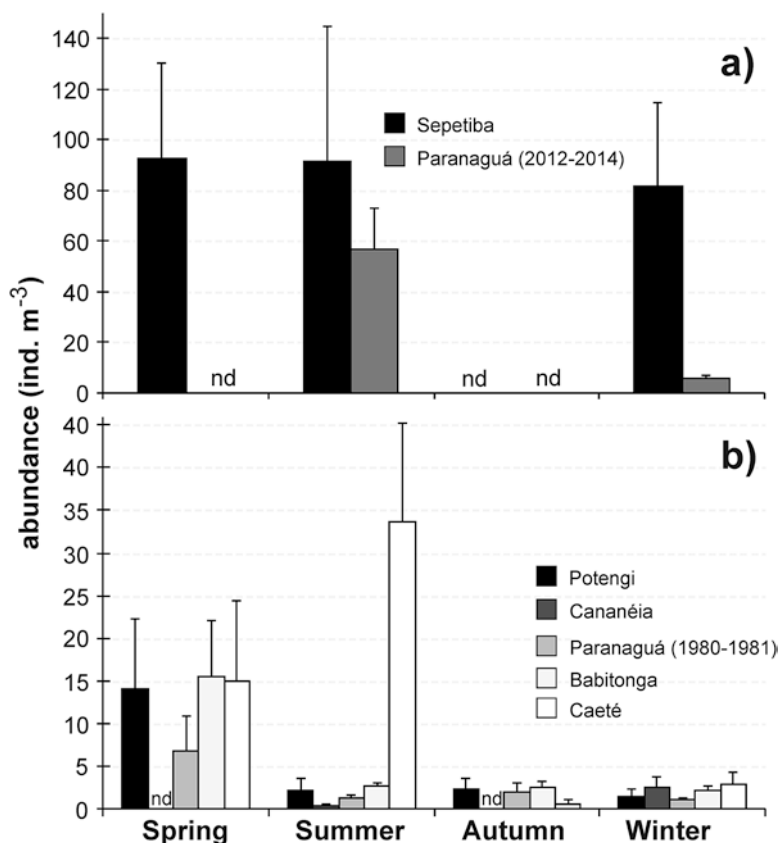
The records of *Octophialucium funerarium* (as *Octocanna funeraria*) and *Rhizostoma pulmo* from the Paraíba River estuary (Singarajah 1978) were considered doubtful since the former species has no other record from the South Atlantic (Bouillon 1999) and *R. pulmo* has only been found at the African coast (Mianzan and Cornelius 1999). We suspect that the record of *R. pulmo* is a misidentification with *Lychnorhiza lucerna*, which is relatively similar and known to commonly occur throughout the Brazilian coast (Oliveira et al. 2016) including inside the Paraíba estuary (MNJ personal observations). The record of *Aglantha* sp. from Paranaguá (Montú and Cordeiro 1988) also is considered doubtful, probably a misidentification with *Aglaura hemistoma* (see Nagata et al. 2014a). These doubtful records were retained in the species list (marked with an interrogation) but were not included in the total species count. The records of *Dipurena* sp. from Santos (Pereira 2011), Paranaguá and Babitonga (Bardi 2011) were considered as *Stauridiosarsia reesi*. The genus *Dipurena* is no longer accepted with the species being moved either to *Slabberia* or *Stauridiosarsia* (Schuchert 2011). *S. reesi* is common and the unique species of these genera reported (Table 2) from these fairly well-studied subtropical estuaries (Vannucci 1956; Nogueira Júnior 2012; Martinez et al. 2015; MNJ unpublished).

Among the few relatively well-known Brazilian estuaries regarding species composition, 36 hydromedusae species have been recorded at Babitonga (Nogueira Júnior 2012) and 34 at Paranaguá (Nascimento 2016) and Cananéia (Martinez et al. 2015). These values are typically higher than the adjacent shelf (16–27 spp., Vannucci 1957, 1963; Nagata et al. 2014a), highlighting the high estuarine hydromedusae diversity and the necessity of thorough sampling and analysis of other Brazilian estuaries, particularly those from tropical latitudes which are less studied and potentially harbor high diversity. Lower number of hydromedusae species recorded from some estuaries (e.g., Navas-Pereira 1980; Mesquita et al. 2006; Marcolin et al. 2010; Bardi 2011, Table 2) is not conclusive due to the small sampling and/or analysis effort (only aliquots analyzed and/or from a reduced number of samples), particularly considering that most species are not common. For instance, in tens of thousands of individuals analyzed from hundreds of samples, 17 and 18 species were represented by <10 individuals at Paranaguá and Babitonga bays, respectively (Nogueira Júnior 2012; Nascimento 2016). This number of rare species alone is larger than the 12–15 total hydromedusae species recorded by Navas-Pereira (1980) and Mesquita et al. (2006), highlighting the need of comprehensive efforts to fully depict the estuarine planktonic cnidarian diversity.

Holoplanktonic cnidarians are considerably less diversified on Brazilian estuaries and 12 species have been reported thus far, 5 trachymedusae, 5 siphonophores, and 2 narcomedusae (Table 2). This relatively low species richness is a regular feature, since these holoplanktonic cnidarians are typically oceanic and more common, abundant and diversified in offshore open waters (Bouillon 1999; Pugh 1999; Nogueira Júnior et al. 2014). This may be particularly true for the South Brazilian Bight estuaries since the continental shelf in this region is large, reaching up to 200 km wide, which may be difficult for these oceanic species to reach coastal waters. Yet, species such as *Abylopsis tetragona* and *Diphyes bojani*, more typical from mid- to outer shelf on this area (Nogueira Júnior et al. 2014, 2015a), may occasionally enter estuaries (Table 2) in low abundances. The short shelf from the Northeastern Brazil may allow species with more oceanic affinities reach the coast and even penetrate estuaries occasionally, such as the occurrence of the siphonophore *Lensia* sp. at Suape (Neumann-Leitão and Matsumura-Tundisi 1998).

There are few quantitative data available. Higher hydromedusae densities (Fig. 2a) were reported from Sepetiba and Paranaguá (early 2010s) and considerably lower at Cananéia ( $<15$  ind.  $m^{-3}$ , Bardi 2011). The seasonality and succession of planktonic cnidarian assemblages from Brazilian estuaries apparently are less predictable (Nagata et al. 2014b) than in high-latitude estuaries (e.g., Zamponi and Genzano 1994; Ballard and Myers 2000; Primo et al. 2012) and temporal variations seem to differ between years (Fig. 2a, b), species and populations (see below). At Sepetiba, high hydromedusae densities (80–90 ind.  $m^{-3}$ ) occur throughout most of the year (Fig. 2a), while at Paranaguá peaks were observed during spring or summer, with high abundance differences between the early 1980s and early 2010s (Fig. 2a, b). Spring/summer peaks, associated with the dry season and higher salinities, have also been observed for the tropical Caeté estuary (Mesquita et al. 2006). Abundance peaks at Babitonga and Potengi were reported during spring, averaging  $\sim 15$  ind.  $m^{-3}$  on both, while at Cananéia hydromedusae typically peak during winter (Fig. 2b), but in 2007 summer peaks were recorded (Bardi 2011). Such longer temporal variations may be associated with large-scale climatic events in some cases, as already observed for these organisms in other estuaries worldwide (e.g., Purcell 2005; Primo et al. 2012); however it is not known their effects in the community on Brazilian estuaries.

The holoplanktonic *Liriope tetraphylla* is ubiquitous, occurring in nearly all the few estuaries with available data, typically being the most common and abundant species from subtropical Brazilian estuaries reaching up to 117 ind.  $m^{-3}$  (Teixeira et al. 1965; Navas-Pereira 1980; Nogueira Júnior et al. 2015b). Its direct holoplanktonic development, lacking a hydroid stage (Russell 1953), associated with its high adaptability to environmental variables and ability to take advantage of food available, results in fast population responses (Purcell 2005; Yilmaz 2015) and is probably the reason why this species is so ubiquitous in these estuaries. These medusae may have a variable seasonal pattern; at Babitonga and Paranaguá, higher abundances have been reported during spring, when young medusae predominated followed by the dominance of adults during summer (Montú and Cordeiro 1988; Pukanski 2011; Nogueira Júnior et al. 2015b). However, winter



**Fig. 2** Mean seasonal variation of hydromedusae abundance (ind. m<sup>-3</sup>) from different Brazilian estuaries. (a) Sepetiba (data from Navas-Pereira 1980) and Paranaguá (2012–2014, data from Nascimento 2016), (b) Potengi (data from Sankarankutty et al. 1995), Cananéia (data from Bardi 2011), Paranaguá (1980–1981, data from Montú and Cordeiro 1988), Babitonga (data from Nogueira Júnior et al. 2015b), and Caeté (data from Mesquita et al. 2006) estuaries. The bars indicate the standard error. nd, no available data

peaks from these estuaries have also been reported (Bardi 2011), similar to the observed for Sepetiba (Navas-Pereira 1980). In the tropical Caeté estuary (Mesquita et al. 2006), *L. tetraphylla* peaked during summer but reached considerably lower densities (<4 ind. m<sup>-3</sup>) and ranked in fifth, with hydromedusae abundance being dominated by *Clytia* spp. (up to ~32 ind. m<sup>-3</sup>) and *Sarsia* spp. (up to ~15 ind. m<sup>-3</sup>).

Other abundant and/or frequent hydromedusae from Brazilian estuaries are the meroplanktonic *Clytia* spp., *Obelia* spp., *Bougainvillia* spp., *Corymorpha gracilis*, *Blackfordia virginica*, *Malagazzia carolinae*, *Podocoryna loyola* and *Cnidostoma fallax* (Navas-Pereira 1980; Mesquita et al. 2006; Bardi 2011; Nogueira Júnior 2012; Martinez et al. 2015; Nascimento 2016; Teixeira-Amaral et al. 2017; Nogueira

Júnior and Silva Nascimento 2018). Polyps from *Clytia*, *Obelia*, *P. loyola*, and *B. muscus* are frequently captured in these estuaries (Bardi 2011; Haddad et al. 2014; Oliveira et al. 2016; Bettim and Haddad 2017); however polyps from *C. gracilis*, *B. virginica*, *M. carolinae* and *C. fallax* have never been found. *Blackfordia virginica* polyps are probably very difficult to find in the field, probably due to its short benthic life and very small size (Moore 1987; Mills and Rees 2000), while polyps of the other three species have not been described yet and perhaps are also small and/or cryptic or short-lived. The presence and abundance of these meroplanktonic medusae is largely controlled by factors affecting polyp growth and medusae production (e.g., Boero et al. 2008) and may occur in seasonal pulses, as the summer peak of *C. fallax* (Nascimento 2016; Teixeira-Amaral et al. 2017), *P. loyola*, *T. nutricula* and *B. virginica* or late autumn peak of *Corymorpha gracilis* and *Proboscoidactyla ornata* (Nogueira Júnior et al. 2015b). The factors controlling such peaks have not been evaluated, and differences between the estuaries and different years are expected (see below).

With a few exceptions, only scant punctual nonquantitative records are available for Scyphomedusae. The most common and abundant species are *Chrysaora lactea* and *Lychnorhiza lucerna* which are known to typically occur year-round on subtropical estuaries, reaching densities of up to ~60 and ~40 ind. ha<sup>-1</sup>, respectively, at Babitonga bay (MNJ, unpublished). Both medusa species usually are less abundant during summer; *L. lucerna* abundance typically peaks during spring, reaching higher biomass during winter when most medusae are large, while *C. lactea* may peak during spring or autumn (Morandini 2003; Nogueira Júnior et al. 2010; Nogueira Júnior and Souza-Conceição 2010).

*Phyllorhiza punctata* is a typical estuarine species (e.g., Rippingale and Kelly 1995) widely distributed on Brazilian coastal and estuarine waters (Oliveira et al. 2016). This medusa has intermittent periods of abundant occurrence, such as those observed between the mid-1950s and early 1960s and between the 1990s and early 2000s, followed by disappearance few years later on both periods (Silveira and Cornelius 2000; Haddad and Nogueira Júnior 2006; Nagata et al. 2013). Since *P. punctata* has a well-documented history of invasions (e.g., González-Duarte et al. 2016), it is not clear whether these fluctuations are (ir)regular populational variations or recurrent invasions (Nagata et al. 2013). When present, *P. punctata* medusa has a well-marked seasonal cycle on subtropical estuaries, growing from late spring/early summer reaching larger sizes in late summer or early autumn, later becoming senescent and disappearing from the water column (Haddad and Nogueira Júnior 2006). Populations of *Stomolophus meleagris* may be in decline since large quantities of this medusa have been recorded in the 1950s from Cananéia, Paranaguá, and Guaratuba estuaries (Vannucci 1954; Prof. Dr. Jayme de Loyola-e-Silva 2005 personal communication), while in more recent evaluations only a few specimens have rarely been found (Morandini 2003; Nogueira Júnior and Haddad 2006).

There is no detailed information regarding the Cubomedusae, but both species are not common, and only a few individuals have been occasionally recorded inside subtropical estuaries (Morandini 2003; Nogueira Júnior et al. 2010; Nogueira Júnior 2012). These species are typical from the open shallow waters where *Chiropsalmus*



*quadrumanus* may reach high concentrations and *Tamoya haplonema*, though not abundant, is commonly found (Nogueira Júnior and Haddad 2008). Both are known stingers that often cause accidents in fishermen and bathers.

*Muggiaea kochii* is typically the most common and abundant siphonophore, reaching densities of up to 5 col. m<sup>-3</sup> and found in salinities down to 21 (Nogueira Júnior et al. 2015b; Nascimento 2016). This is considered one of the few typical neritic siphonophores (Mackie et al. 1987; Pugh 1999), being common and abundant over the shallow shelf mostly under influence of the Coastal Water (Nogueira Júnior et al. 2014; Nogueira Júnior and Brandini, [this volume](#)). Although not particularly abundant, the frequent presence of the physonect *Nanomia bijuga* is noteworthy both inside estuaries such as Babitonga, Paranaguá, Cananéia, and Santos Bays (Table 2) in salinities down to 11.5 (MNJ unpublished observations) and over the shelf more than a 100 km offshore in salinities >36 (Nogueira Júnior et al. 2014, 2015a), suggesting a large habitat plasticity of this species.

Exotic species in Brazilian estuaries are all meroplanktonic; between them, *P. punctata* (see above) and *Blackfordia virginica* are the best known. The latter is known to have established populations in some estuaries of tropical (Freire et al. 2014) and subtropical Brazil (Nogueira Júnior and Oliveira 2006; Bardi and Marques 2009; Nogueira Júnior 2012). Although recurrently found, it is not abundant being mainly found during summer, reaching densities up to 1.2 ind. m<sup>-3</sup> at Babitonga and commonly lower (<1 ind. m<sup>-3</sup>) in other estuaries (Nogueira Júnior and Oliveira 2006; Bardi and Marques 2009; Nascimento 2016). *Blackfordia virginica* can tolerate a wide salinity range (2–35, Moore 1987), being more frequent and abundant in inner and intermediate estuarine portions (Pukanski 2011; Nascimento 2016) in brackish water with intermediate salinities (~20–30) both on Brazilian (e.g., Bardi 2011) estuaries and elsewhere (e.g., Genzano et al. 2006; Chícharo et al. 2009; Marques et al. 2017). Moreover, polyps are known to recruit in salinities between 15 and 22 (Wintzer et al. 2011) and medusae production seems to be stimulated under low salinity conditions (Moore 1987).

The hydromedusae *Moerisia inkermanica* (Paranaguá 1963; Nogueira Júnior and Oliveira 2006), *Podocoryna loyola* (Haddad et al. 2014), and more recently *Cnidostoma fallax* (Nascimento 2016) have also been appointed as probably nonindigenous species. In spite of local studies since the 1980s, *P. loyola* hydroids were detected in 2007 growing on artificial substrata, and subsequently both polyps and medusae have been recurrently found on Brazilian subtropical estuaries (Nogueira Júnior 2012; Haddad et al. 2014; Nogueira Júnior et al. 2015b; Bettim and Haddad 2017), suggesting it has been introduced. *Cnidostoma fallax* has only recently been detected in Brazilian estuaries, but it seems widespread between ~24 and 34°S, occasionally dominating estuarine assemblages with recorded abundances up to 11,369 and 3,542 ind. m<sup>-3</sup> at Patos Lagoon (Teixeira-Amaral et al. 2017) and Paranaguá Bay (Nascimento 2016), respectively. Considering the absence of *C. fallax* in the previous studies on these estuaries (Montú 1980; Montú and Cordeiro 1988; Lopes et al. 1998; Bardi 2011), it seems that this medusa appeared recently.

Although the species richness tends to be highest in portions of high and more stable salinity, most of these estuarine medusae species are euryhaline, occurring in

a wide salinity range (Navas-Pereira 1980; Mesquita et al. 2006; Bardi 2011; Nogueira Júnior 2012; Nascimento 2016), with few species being considered exclusively estuarine or oceanic. Exceptions are *Halitiara formosa* and *Moerisia inkermanica* which occurred only in salinities <20 and are typically brackish-freshwater species, the latter commonly occurring in salinities down to 0 (Nogueira Júnior and Oliveira 2006; Bardi 2011). On the other hand, *Bougainvillia frondosa*, *Amphinema australis*, *Protiara* sp., *Rhopalonema velatum*, *Clytia hemisphaerica*, *Aglauropsis kawari*, and *Aglaura hemistoma* were only captured in salinities >30, and most of them are more common in shelf waters (Vannucci 1957, 1963; Nagata et al. 2014b), corroborating the hypothesis that they are nonresident species that can enter the estuary under specific conditions. *Rhopalonema velatum* and *Aglaura hemistoma*, for instance, are typical from the Tropical Water (Vannucci 1957, 1963, Navas-Pereira 1973; Nogueira Júnior and Brandini [this volume](#)) and reported inside estuaries only during winter (Navas-Pereira 1980; Bardi 2011; Nascimento 2016). The typical conditions for this season at these subtropical latitudes, such as low precipitation rates, high salinities, and frequent incidence of south winds favor their higher abundance in the inner shelf (Nagata et al. 2014b) and occasional entries into estuaries.

Some frequent euryhaline species are *Obelia* spp., *P. ornata*, and *L. tetraphylla*, the three occurring in lower salinities down to 10 and higher up to 37 for the latter species and to 34 for the two others (Bardi 2011; Nogueira Júnior 2012). *Obelia* spp. and *P. ornata* were very tolerant to diluted seawater in laboratory (Moreira 1978), showing decrease of the swimming movement only at salinity 20; at 15 they moved only after mechanical stimulation, and at salinity 10 the movements of the medusae stopped completely, but some of them were able to recover when placed again in appropriated conditions (Moreira 1978). In contrast, *L. tetraphylla* did not tolerate very low salinities, surviving well only in salinities above 20 (Moreira 1978). *Obelia* spp. have established populations in Brazilian estuaries, commonly occurring in all estuarine portions but often being more abundant in salinities >20 (Nascimento 2016). In the adjacent shelf, medusae from *Obelia* are also common and abundant, mostly associated with the Coastal Water (Nagata et al. 2014b; Nogueira Júnior et al. 2014). *Proboscycydactila ornata* is a shelf water mass indicator (Vannucci 1957), occurring in the shelf more than 150 km far from the coast (Nogueira Júnior et al. 2014), although it is also found in coastal waters after strong winds or vertical mixing (Vannucci 1963), only occurring in outer portions of the estuary (Nascimento 2016). Similarly, *L. tetraphylla* is typically most abundant in intermediate and outer sectors with higher marine influences, being less abundant in inner portions (Pukanski 2011; Nascimento 2016).

### 3 Ctenophora

The study of the ctenophores is challenging mostly due to their large fragility and consequent difficulties for identification and quantification (Mianzan 1999). Nondestructive specific sampling techniques are highly recommended, but not

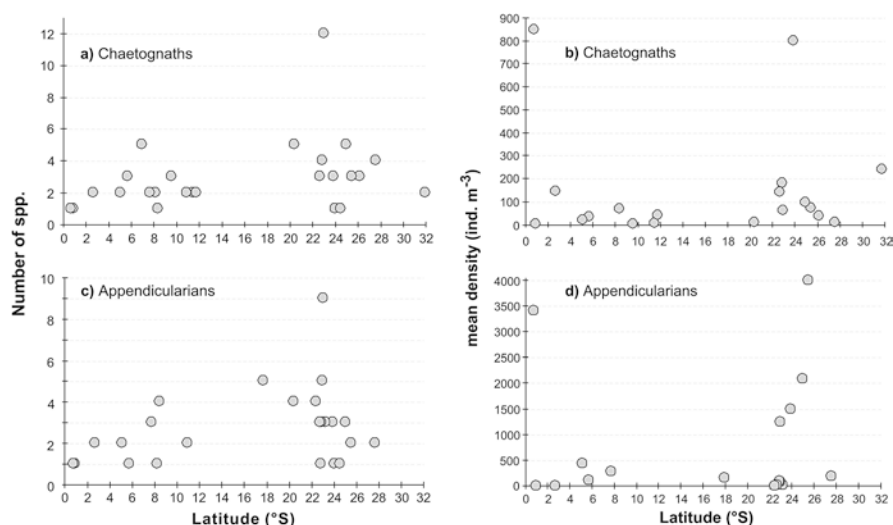
always possible to perform. Consequently, ctenophores are commonly understudied worldwide, which is particularly true for Brazilian waters where less than ten studies dealing with the phylum have been published (Oliveira et al. 2007, 2016). Regarding estuarine ecosystems, there are few scattered records of *Mnemiopsis leidyi* and *Beroe ovata* from tropical ( $\sim 7^{\circ}\text{S}$ , Singarajah 1978) and subtropical latitudes ( $\sim 23\text{--}26^{\circ}\text{S}$ , e.g., Montú and Cordeiro 1988, see Tables 1 and 2). Yet, these two species are expected to dwell in the majority, if not all, Brazilian estuarine environments, considering both their wide distribution on southwestern Atlantic ( $0\text{--}>40^{\circ}\text{S}$ ) and the wide environmental conditions they can withstand (Mianzan 1999; Costello et al. 2012). *Pleurobrachia* sp. has been recorded exclusively in the tropical Paraíba river estuary (Singarajah 1978), what may be a misidentification since in the southwestern Atlantic this genus is only known to occur in temperate Argentina ( $37\text{--}47^{\circ}\text{S}$ , Mianzan 1999; Oliveira et al. 2016). Moreover, larvae of lobate ctenophores (e.g., *M. leidyi*) are morphologically similar to the adults of the cydippids as *Pleurobrachia* sp. (Oliveira et al. 2007), particularly for non-experts on the phylum.

Distributional and quantitative ecological data are almost completely nonexistent for Brazilian ctenophores whether they are estuarine or not. Summer densities between  $<1$  and  $14 \text{ ind. } 10 \text{ m}^{-3}$  were reported for *M. leidyi* at different subtropical estuaries ( $25\text{--}26^{\circ}\text{S}$ , Oliveira 2007). Between November 2007 and August 2008 at Babitonga, *M. leidyi* peaked during early summer (January) and winter (August), with average densities in the main channel around  $1.1\text{--}1.2 \text{ ind. } 10 \text{ m}^{-3}$  in both seasons; its biomass (wet weight), on the other hand, was considerably higher during winter (mean  $\sim 11 \text{ g } 10 \text{ m}^{-3}$ ) than summer (mean  $\sim 0.4 \text{ g } 10 \text{ m}^{-3}$ ) due to differences in the population structure, dominated by small juveniles during summer and larger individuals during winter (MNJ unpublished data). Detailed studies on Brazilian estuarine ctenophores such as population dynamics and biological parameters such as growth, reproduction and predation rates, including their relationship with the environment and other organisms, are lacking and strongly encouraged.

## 4 Chaetognatha

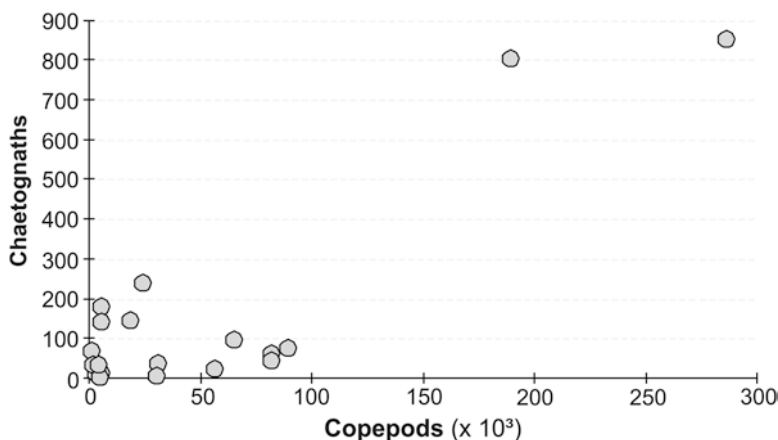
Only a few studies provide detailed quantitative accounts on Brazilian estuarine chaetognaths (Magalhães et al. 1996; Marazzo and Nogueira 1996; Liang et al. 2003; Loureiro Fernandes et al. 2005; Mendes et al. 2012), apart from studies that dealt with the entire zooplankton community and presented brief additional information on the group (e.g., Krumme and Liang 2004; Araújo et al. 2008). Altogether, 14 chaetognath species have been recorded from Brazilian estuaries (Table 2), which represents 56% of the 25 species recorded from the whole Brazilian coast (Bonecker et al. 2017). This is a relatively high value, considering that most chaetognaths are regarded as typically oceanic and not expected to dwell in brackish waters (see below).

Species richness did not have any latitudinal tendency (Fig. 3a). This is not surprising considering chaetognath diversity remains relatively constant between  $40^{\circ}\text{N}$



**Fig. 3** Latitudinal trends of Brazilian estuarine chaetognath (a, b) and appendicularian (c, d) species richness (a, c) and mean density (b, d). See Table 1 for data sources

and 40°S in the Atlantic (Macpherson 2002). Moreover, even though up to 12 species have been recorded in a single estuary (Dias and Bonecker 2008), 79% of the estuaries harbor  $\leq 3$  species (Fig. 3a). However, it is important to emphasize that most, if not all, of the Brazilian estuaries, with a single chaetognath species recorded, have not been comprehensively studied and the records are from studies that focused mostly on crustaceans and analyzed only small aliquots of the samples (Lansac-Tôha and Lima 1993; Lopes 1994; Neumann-Leitão and Matsumura-Tundisi 1998; Cavalcanti et al. 2008; Costa et al. 2008). Hence, these studies may have missed scarce species. Furthermore, taxonomic confusion with the two *Parasagitta* species may also have occurred (see below). In any case, this low species richness is in general accordance with what is normally found at different tropical or subtropical brackish-water ecosystems worldwide, such as those from India (Srinivasan 1971, 1980), Pacific side of Costa Rica (Hossfeld 1996), Mexican Caribbean (Hernández et al. 2005), or subtropical China (Du et al. 2011; Liu et al. 2013). This reflects both the low diversity and the typical oceanic affinities of the phylum, with only a few species able to tolerate lower and variable salinities of estuaries (Srinivasan 1971, 1980; Boltovskoy 1975; Pierrot-Bults and Nair 1991; Hossfeld 1996; Hernández et al. 2005). The relatively high diversity reported from the Ribeira Bay (12 spp., Dias and Bonecker 2008, Table 2, Fig. 3a) is an exception, probably related to the high openness and sea influence on this ecosystem where salinities are always  $>29$  (Dias and Bonecker 2008). Most of these species are typical from outer shelf and oceanic waters (Liang 2002; Liang and Vega-Pérez 2001, 2002; Souza et al. 2014) and thus are not expected in most of the other less saline estuaries.



**Fig. 4** Scatterplot between mean chaetognath and maximum copepod abundances (ind.  $m^{-3}$ ) from 19 Brazilian estuaries (see Table 1 for data source). Whenever possible, data was taken from the same study or year for both chaetognaths and copepods. Both variables have a significant positive correlation (Pearson,  $r = 0.85$ ,  $n = 19$ ,  $p < 0.05$ )

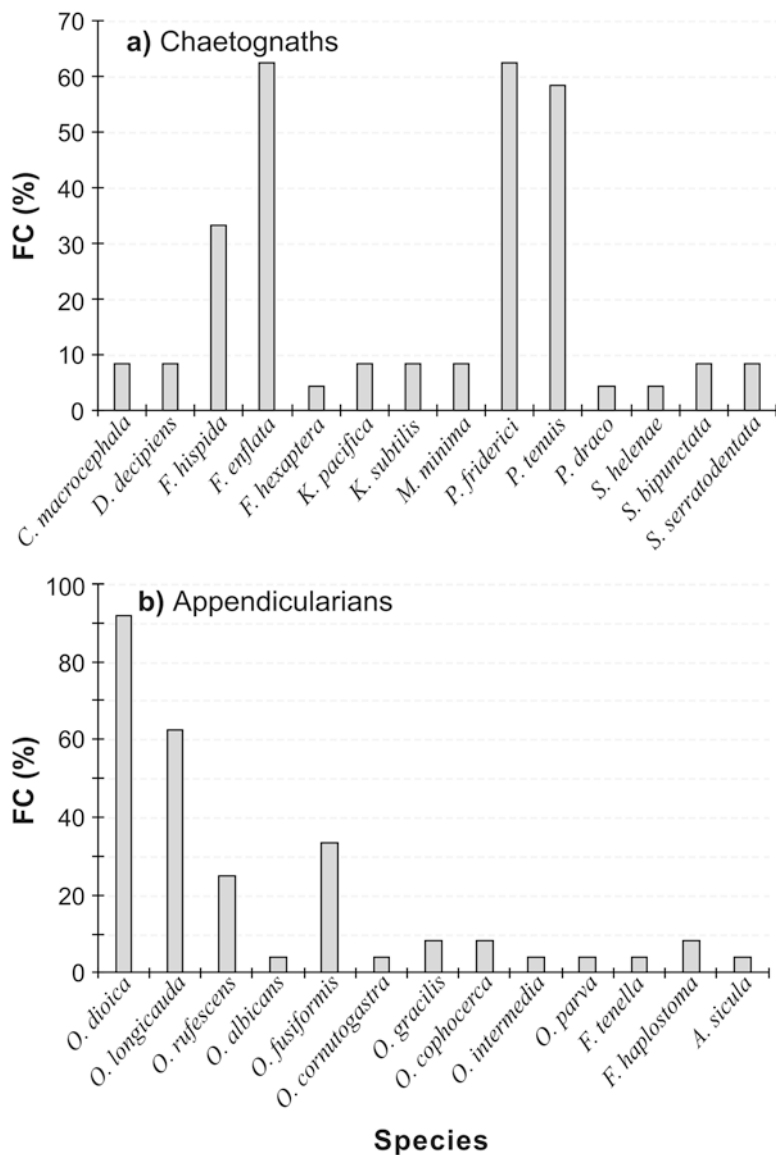
Chaetognath densities from different Brazilian estuaries vary a lot, without any clear latitudinal trend (Fig. 3b). In most ecosystems, maximum and mean densities are lower than 800 and 200 ind.  $m^{-3}$  respectively (Fig. 3b). The lowest densities are from Mundaú-Manguaba, with chaetognath triennial mean of 0.75 ind.  $m^{-3}$  and maximum values of  $\sim 5$  ind.  $m^{-3}$  (Magalhães et al. 1996). Highest abundances were reported from Taperaçu and Santos estuaries with maximum chaetognath densities between 5,200 and 5,750 ind.  $m^{-3}$  and mean densities between 800 and 850 ind.  $m^{-3}$  (Fig. 3b, Costa et al. 2008; Pereira 2011). Due to data scarcity, it is difficult to determine the factors controlling such huge density differences, in some cases in ecosystems close to each other (see Fig. 3b), but food availability certainly plays an important role.

Copepods, typically the main prey item of chaetognaths (Vega-Pérez and Liang 1992; Liang and Vega-Pérez 1995; Sato et al. 2011), have very high abundances (maximum densities  $> 190,000$  ind.  $m^{-3}$ , Costa et al. 2008; Pereira 2011) in the two estuarine systems with higher chaetognath abundances (Taperaçu and Santos). On the other hand, in most of the estuaries with lower chaetognath abundances such as Caeté, Potengi, Itamaracá, Suape, Vitória and Sepetiba, copepod densities are also considerably lower, rarely exceeding 5,000 ind.  $m^{-3}$  (Sankarankutty et al. 1979, 1995; Navas-Pereira 1980; Neuman-Leitão and Matsumura-Tundisi 1998; Silva et al. 2003, 2004, Krumme and Liang 2004; Sterza and Loureiro Fernandes 2006). Indeed, mean and maximum chaetognath densities have a relatively high positive ( $r = 0.85$  and  $0.83$ , respectively) and significant ( $p < 0.05$ ) correlation to maximum copepod abundance (Fig. 4). Yet, this trend must be seen with caution considering that the two ecosystems with very high abundances of both chaetognaths and copepods may bias the analysis and the tendency is not always valid. For instance, Tabatinga and Casqueira and Conceição estuaries sustain mid-to-high copepod densities (up to 30,000 and 56,000 ind.  $m^{-3}$ , respectively) and relatively low chaeto-

gnath abundance levels (Sankarankutty et al. 1997; Marcolin 2008; Marcolin et al. 2010), suggesting that other factors are also important. Geomorphology of the estuary (e.g., degree of openness, depth), physical and biological characteristics (salinity variations, tidal circulation, temperature, quality of food, parasites, abundance of predators, etc.), and the intricate interactions between all of these factors have been shown to be important (Srinivasan 1971, 1980; Mulkana and McIlwain 1973; Grant 1977; Nair and Sankarankutty 1988; Hossfeld 1996; Tse et al. 2008), but data is mostly missing from Brazilian estuaries.

*Parasagitta friderici*, *Flaccisagitta enflata* and *Parasagitta tenuis* are the most common and widespread chaetognaths, reported between 60 and 64% of the 25 Brazilian estuaries with data available (Table 2, Fig. 5a). In addition, these species are also the most abundant ones; most sites are dominated by *P. friderici* and/or *P. tenuis* and a few by *F. enflata* (Fig. 6a). The two *Parasagitta* species have a wide distribution (Srinivasan 1971, 1980; McLelland 1980, 1989; Pierrot-Bults and Nair 1991) on coastal tropical to mid-temperate east Pacific and east and west Atlantic coasts, including the Mediterranean (*P. friderici*) or Indian estuaries and coastal open waters (*P. tenuis*). They are among the few chaetognath species restricted to and abundant at coastal waters (Srinivasan 1971, 1980; Boltovskoy 1975; Pierrot-Bults and Nair 1991; Hossfeld 1996; Casanova 1999), including brackish-water ecosystems. Indeed, they have been commonly found in salinities <15 (Montú and Cordeiro 1988; Magalhães et al. 1996; Marazzo and Nogueira 1996; Loureiro Fernandes et al. 2005) and even in salinities <5 for *P. friderici* (Montú 1980; Liang et al. 2003), supporting the hypothesis that they are well-adapted to the brackish-water condition of estuaries maintaining permanent populations in many of them.

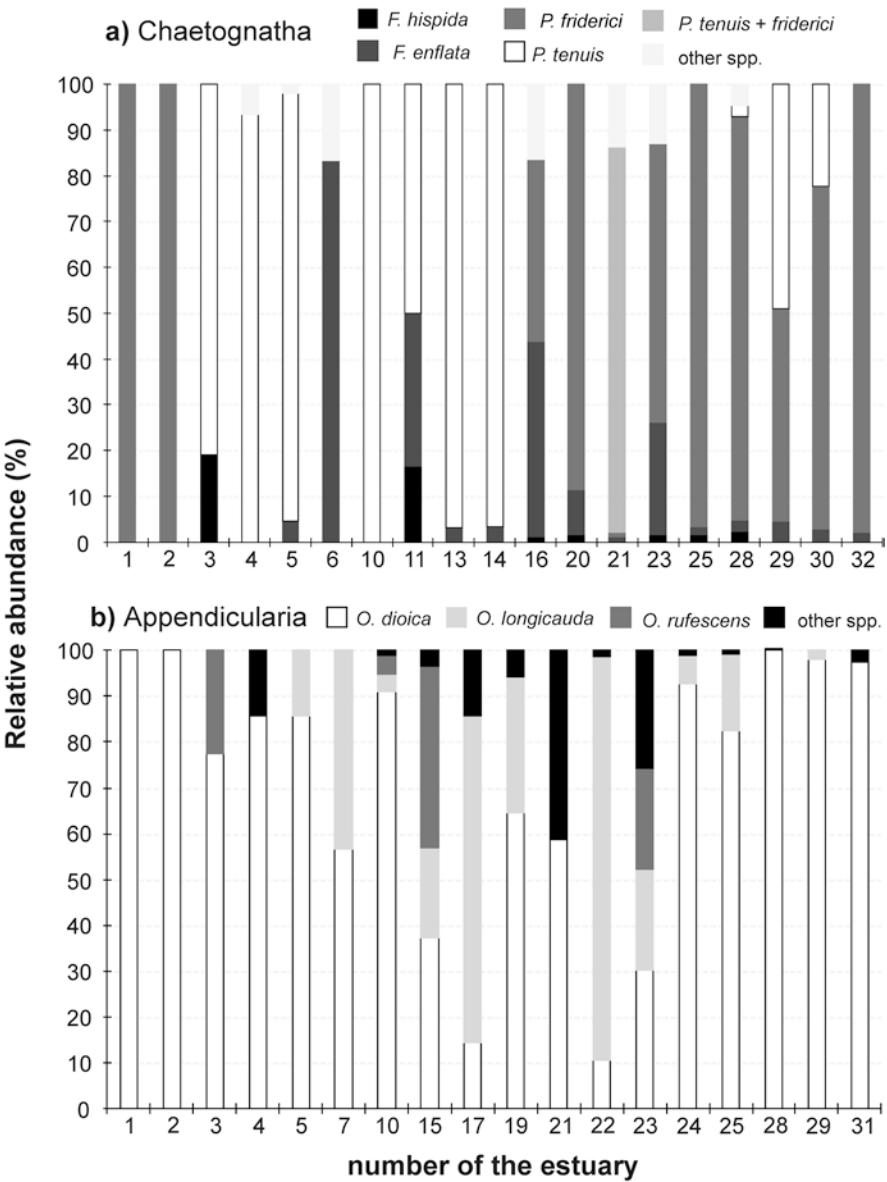
It is noteworthy that most estuaries in latitudes <11.5°S are dominated by *P. tenuis*, while most of those in latitudes >22°S are dominated by *P. friderici* (Fig. 6a). Exceptions are Paranaguá and Taperaçu and Caeté estuaries; in the former, both species are nearly equivalent in abundance (Miyashita et al. 2012; L.K. Miyashita personal communication), but *P. friderici* may dominate in some years (Lopes et al. 1998). Concerning the two latter estuaries, only *P. friderici* has been recorded (Fig. 6a, Table 2, Krumme and Liang 2004; Costa et al. 2008). It is difficult to determine the factors leading to such latitudinal shift, but a taxonomic caution is necessary here. These two species are morphologically very similar and their validity has been greatly discussed even with the proposition for their synonymization in the past (e.g., Pierce 1951; Furnestin 1957; Almeida-Prado 1961; Boltovskoy 1981). Currently, there is a relatively long-lasting consensus that both are valid separated species (e.g., McLelland 1980, 1989; Casanova 1999; Thuesen 2009). Yet, in some of the Brazilian studies, both species were explicitly considered synonyms (Coelho-Botelho et al. 1999; Resgalla 2010), probably following the identification guide of Boltovskoy (1981). This may have been the case of other studies that did not disclose this particular piece of information. Therefore, this latitudinal shift may be an artifact of taxonomic problems. Detailed taxonomic studies, including morphological and molecular analyses from as many estuaries as possible, are recommended to test the validity of this latitudinal dominance shift from *P. tenuis* in tropical (~2–12°S) to *P. friderici* in subtropical (22–32°S) Brazilian estuaries (Fig. 6a).



**Fig. 5** Relative (%) number of Brazilian estuaries each chaetognath (a) and appendicularian (b) species have been recorded. 100% = 25 estuaries for chaetognaths and 24 for appendicularians

*Flaccisagitta enflata* is distributed worldwide between ca. 40°N and 40°S including both coastal and oceanic waters. It usually is considered as a typical oceanic epipelagic species (Pierrot-Bults and Nair 1991; Casanova 1999), more associated with shelf and offshore warm Tropical Water off Brazil (Souza et al. 2014;





**Fig. 6** Relative abundance (% of ind. m<sup>-3</sup>) of the dominant chaetognath (a) and appendicularian (b) species from different Brazilian estuaries. Numbers of the estuaries correspond to the numbers of Fig. 1 and Table 1. See the latter for data source. Coelho-Botelho et al. (1999) considered *P. friderici* as a junior synonym of *P. tenuis*, and thus it is not possible to know the contribution of each species



Nogueira Júnior and Brandini [this volume](#)). Nevertheless, *F. enflata* has frequently been reported from Brazilian brackish waters (Figs. 5a, 6a) and also from many brackish-water ecosystems worldwide (Srinivasan 1971, 1980; Mulkana and McIlwain 1973; Grant 1977; Hernandez et al. 2005; Du et al. 2011; Liu et al. 2013). It is the dominant species from Paraíba and Vitória estuaries, typically associated with the outer sectors and higher salinities (Singarajah 1978; Loureiro Fernandes et al. 2005).

Beyond these three abovementioned species, *Ferosagitta hispida* has been reported in ~36% of the Brazilian estuaries (Fig. 5a), usually in low densities (Fig. 6a). It is probably not resident from most of these estuaries but rather transported from open marine waters (Coelho-Botelho et al. 1999; Liang et al. 2003; Loureiro Fernandes et al. 2005; Pereira 2011). Yet, at São Marcos Bay (2.7°S) *F. hispida* reaches relatively high densities (up to ~89 ind. m<sup>-3</sup>, averaging 22 ± 34 ind. m<sup>-3</sup>) and can be found throughout the estuary (Bonecker and Dias 2009), representing ca. 20% of total chaetognath abundance (Fig. 6a) which seems in accordance with its tropical affinities (Casanova 1999). It is endemic from brackish, neritic, and oceanic Atlantic warm waters (Reeve 1970; Pierrot-Bults and Nair 1991; Casanova 1999).

All the other 10 chaetognath species have been reported only from 1–2 sites each (<9%, Fig. 5a, Table 2), sporadically found near the mouth of the estuary in low abundances (<1 ind. m<sup>-3</sup>, e.g., Singarajah 1978; Coelho-Botelho et al. 1999; Liang et al. 2003; Loureiro Fernandes et al. 2005). These data indicate that they probably do not sustain permanent estuarine populations. Indeed, all these species typically have oceanic affinities (Pierrot-Bults and Nair 1991; Liang and Vega-Pérez 2001, 2002; Souza et al. 2014) and their occasional occurrence inside estuaries is probably related to tidal- and/or wind-driven transport from adjacent shelf (Nair and Sankarankutty 1988; Loureiro Fernandes et al. 2005).

Data on temporal dynamics of estuarine Brazilian chaetognaths is lacking for most ecosystems. The few available ones suggest that there is no clear general seasonal trend neither for total chaetognaths nor for dominant species, greatly varying between different environments and/or species. Seasonal variations were small or absent in some of the low-latitude (<7°S) estuaries, such as *P. friderici* from Taperaçu (Costa et al. 2008), *F. enflata* from Paraíba river (Singarajah 1978), and *P. tenuis* from Casqueira and Conceição rivers (Sankarankutty et al. 1997). Although, a slight peak in December was noticeable at the innermost stations but not in the others in the latter case (Sankarankutty et al. 1997). *Parasagitta tenuis* populations from other tropical estuaries may vary seasonally such as winter and/or summer peaks at Potengi estuary (Nair and Sankarankutty 1988; Sankaranutty et al. 1995, 1996), higher abundance during rainy (August) and dry (December) seasons at Tabatinga and Itapicurú rivers, respectively (Marcolin 2008), and October/November peaks at Mundaú-Manguaba (Magalhães et al. 1996). This latter ecosystem was sampled through three consecutive years and in spite of great interannual abundance variations, the seasonal trend was analogous (Magalhães et al. 1996).

All information from higher latitudes (20–32°S) indicate seasonal variations, more commonly with densities peaking between spring and/or summer such as reported for Patos Lagoon (Montú 1980), Paranaguá (Montú and Cordeiro 1988; Miyashita et al. 2012; Salvador and Bersano 2017), Cananéia (Liang et al. 2003)

and Santos bays (Pereira 2011). Some minor variations have also been reported, such as a winter smaller peak in Paranaguá (Montú and Cordeiro 1988; Miyashita et al. 2012). While abundance peaks of both *P. friderici* and *F. enflata* are common during spring and/or summer in the outer sector of Guanabara Bay, in the innermost areas, they peak during winter because of the low salinities during summer associated with higher rainfall (Marazzo and Nogueira 1996; Mendes et al. 2012). At Vitória Bay, differently, higher abundances for both *P. friderici* and *F. enflata* have been reported during winter and spring, with considerably lower densities during summer (Loureiro Fernandes et al. 2005).

Biomass and production of Brazilian estuarine chaetognaths have not been evaluated in details, with the exception of *P. friderici* populations from Cananéia, where mean annual biomass is ca. 30 mg DW m<sup>-3</sup>, reaching daily means of up to 57 mg DW m<sup>-3</sup> during summer, and mean annual production is of ~1 mg C m<sup>-3</sup> d<sup>-1</sup> reaching up to ~4.5 mg C m<sup>-3</sup> d<sup>-1</sup> (Liang et al. 2003). The few available data on reproductive dynamics show that all *P. friderici* developmental stages occur through the year at Guanabara and Cananéia, with dominance of adults and increased reproduction during spring followed by a recruitment peak mostly in summer (Mendes et al. 2012) or juvenile dominance throughout the year with three apparent annual cohorts (Liang et al. 2003) respectively. Three annual spawning peaks (May, September and December) have also been recorded for *P. tenuis* in the Potengi estuary, where juveniles and developing individuals can be found through the year and mature ones occur sporadically, mostly during winter (Nair and Sankarankutty 1988).

Apart from seasonal dynamics, small-scale temporal variations (e.g., lunar, nictemeral, tidal cycles) may be large (Sankarankutty et al. 1979; Liang et al. 2003; Mendes et al. 2012) and particularly important considering the high level of these short-scale variations in the estuarine physical environment, mainly controlled by the tidal patterns and ultimately by the salinity. In general, higher species richness and densities of chaetognaths have been found more typically during high tide (Sankarankutty et al. 1979; Nair and Sankarankutty 1988; Loureiro-Fernandes et al. 2005; Marcolin 2008) tending to positively correlate with tidal height (Liang et al. 2003). However, greater densities of *P. friderici* have been reported during ebb at Itapicuru estuary (Marcolin 2008).

Neither vertical nor horizontal distribution of Brazilian estuarine chaetognaths has been evaluated in details thus far, but the few data available indicate that abundance tend to be higher closer to the estuary mouth (Montú 1980; Pekala 1980; Montú and Cordeiro 1988; Marazzo and Nogueira 1996; Sankarankutty et al. 1997; Loureiro Fernandes et al. 2005), a pattern similar to other estuaries elsewhere (e.g., Grant 1977; Srinivasan 1980), probably associated with higher sea influence. Still, *P. friderici* is highly resistant to low salinities (see above) and commonly found in the inner portions, being probably a permanent resident in estuaries (Montú and Cordeiro 1988; Loureiro Fernandes et al. 2005). In addition, wind patterns (e.g., Hernández et al. 2005) along with tidal cycles can be particularly important in the horizontal distribution of estuarine chaetognaths probably increasing their extent (as well as abundance; see above) during flood and decreasing in the ebb, which obviously will also be influenced by the geomorphology of the estuary and the flow of the tidal current. Interactions between spatial and seasonal factors in the abun-

dances may occur (Marazzo and Nogueira 1996; Sankarankutty et al. 1997; Miyashita et al. 2012), resulting in different seasonal cycles for different parts of the estuary; for instance, as commented above, at Guanabara outer sector chaetognaths peak during summer and/or winter, but in the innermost areas, peaks have been recorded only during winter, apparently constrained by low salinities during summer (Marazzo and Nogueira 1996; Mendes et al. 2012).

## 5 Appendicularia

Similar to the previous taxa, information on Brazilian estuarine appendicularians is derived mostly from general zooplankton studies which provide variable and usually superficial information about the group (e.g., Bonecker and Dias 2009; Miyashita et al. 2012; Salvador and Bersano 2017). A total of 13 appendicularian species have been recorded from Brazilian estuaries (Table 2), which represents 37% of the 35 species recorded from Brazil (Rocha et al. 2017). Similar to the chaetognaths, no latitudinal trend in the appendicularian species richness can be noticed (Fig. 3c), which is in accordance with the relatively constant species richness of the group in the Atlantic Ocean between  $\sim 40^{\circ}\text{N}$  and  $40^{\circ}\text{S}$  (Macpherson 2002).

Appendicularian species richness from Brazilian brackish-water environments is usually low (Fig. 3c). Up to 9 species have been recorded from a single estuary, but 75% of them harbor 1–3 species (Fig. 3c), which is in general accordance to other estuaries worldwide (Brunetti et al. 1990; Spinelli et al. 2009; Du et al. 2011; Liu et al. 2013). Although deep temperate estuaries such as Toyama Bay, Japan, may harbor considerably higher number of species including the presence of many oceanic epipelagic and deepwater species (Tomita et al. 2003). Similar to the chaetognaths, most of the Brazilian estuaries with a single species recorded have not been comprehensively studied, and the records are derived from studies focusing on crustaceans that analyzed only small aliquots of the samples (e.g., Lopes 1994; Cavalcanti et al. 2008; Costa et al. 2008) and that may have missed rarer species. In any case, the class Appendicularia is not particularly diversified (Esna 1999; Rocha et al. 2017), and, in parallel to the observed for chaetognaths, highest species richness at Ribeira Bay probably reflects the higher openness and sea influence on this ecosystem (see above).

No latitudinal pattern has been observed for appendicularian densities (Fig. 3d). In most estuaries from Brazil, maximum and mean densities are lower than 1,000 and 280 ind.  $\text{m}^{-3}$ , respectively. The lowest densities are from São Marcos Bay, never exceeding 1 ind.  $\text{m}^{-3}$ , yet these estimates were made from a single sampling campaign (Bonecker and Dias 2009) and probably have missed the full extent of local abundance variability. Low appendicularian densities have also been reported from Caeté (mean of 0.65 and up to 4.5 ind.  $\text{m}^{-3}$ , Krumme and Liang 2004) and from Perequê-Açu, Sepetiba, Macaé, São João, and Itapicuru (mean densities between 5 and 20 ind.  $\text{m}^{-3}$ , Fig. 3d). Highest densities have been reported from Cananéia, Santos, Ribeira and Taperaçu, with mean densities between 1190 and 3400 ind.  $\text{m}^{-3}$  (Fig. 3d) and maximum between  $\sim 13,000$  and 31,550 ind.  $\text{m}^{-3}$ .

*Oikopleura dioica* and *Oikopleura longicauda* are the most common species, respectively, reported from 91.7 and 66.7% of the 24 estuaries considered for the group (Fig. 5b, Table 2). These two species also are by far the most abundant appendicularian, particularly the former which represent  $\geq 70\%$  of total appendicularian abundance in  $\sim 60\%$  of the estuaries (Fig. 6b). The latter species represented around 80 and 90% of all appendicularians at Macaé and Bracuí rivers, respectively, and 43% at Itamaracá (Fig. 6b). This is similar to the observed elsewhere in the world where *O. dioica* and/or *O. longicauda* are common and typically the dominant appendicularian species in brackish-water ecosystems from temperate (Brunetti et al. 1990 Spinelli et al. 2009), subtropical (Du et al. 2011; Liu et al. 2013) and tropical areas (Hopcroft and Roff 1998; Hoover et al. 2006). Both *O. dioica* and *O. longicauda* are abundant and widely distributed throughout South Atlantic up to  $\sim 55$  and  $60^\circ\text{S}$ , respectively (Esnal 1999). Both species have coastal affinities, but while the latter is neritic and oceanic (Esnal and Castro 1977), commonly being the dominant species at the inner shelf off Brazil (Tundisi 1970; Miyashita and Lopes 2011), *O. dioica* is more neritic/estuarine being usually the most abundant appendicularian in brackish-water ecosystems (Figs. 5b, 6b). Along Brazil, *O. dioica* is commonly found in salinities  $< 20$  (e.g., Lopes et al. 1998; Miyashita et al. 2012; Bonecker and Dias 2009) and occasionally even in salinities down to nearly zero (Coelho-Botelho et al. 1999), being rarely found in offshore waters under oceanic influence (Tundisi 1970; Esnal and Castro 1977).

Apart from these two abovementioned appendicularians, *Oikopleura fusiformis* has been found in 33% of the estuaries and *Oikopleura rufescens* in 25% (Fig. 5b). The last one contributed up to ca. 40% (Fig. 6b) to the total appendicularian abundance at Caravelas (mean of 26 and up to 242 ind.  $\text{m}^{-3}$ , Carvalho and Bonecker 2010) and around 20% at São Marcos and Ribeira Bays, reaching densities up to 1,990 ind.  $\text{m}^{-3}$  in the latter (Dias and Bonecker 2008; Bonecker and Dias 2009, Fig. 6b). *Oikopleura fusiformis* also can reach relatively high densities at Ribeira Bay (up to 849 ind.  $\text{m}^{-3}$ , Dias and Bonecker 2008); however its relative contribution to total appendicularian abundances is typically low ( $< 5\%$ ), and low densities (mean  $< 1$  ind.  $\text{m}^{-3}$ ) have been reported from all other estuaries this species has been recorded (Coelho-Botelho et al. 1999; Carvalho and Bonecker 2010; Carvalho et al. 2016). All the other nine appendicularian species have been reported only from 1–2 estuaries ( $< 9\%$ , Fig. 5b, Table 2), in lower abundances in the outer sectors, probably not maintaining permanent populations. These species typically have more oceanic affinities and are more common and abundant on salinities  $> 35$  (Tundisi 1970; Miyashita and Lopes 2011; Carvalho et al. 2016). Their eventual presence in estuaries probably is resultant of advective processes transporting them from the adjacent shelf.

With a few exceptions (e.g., Esnal et al. 1985), temporal dynamics of appendicularians from Brazilian estuaries have not been evaluated in details. The few data available suggest different patterns for different ecosystems and/or species. At Taperaçu, the unique available data very close to the Equator, *O. dioica* remain in similarly high densities ( $\sim 3,000$ – $3,800$  ind.  $\text{m}^{-3}$ ) both in the dry and rainy seasons (Costa et al. 2008). Southward ( $\sim 5$ – $11^\circ\text{S}$ ), at Casqueira and Conceição (Sankarankutty et al. 1997), Potengi (Esnal et al. 1985), and Tabatinga (Marcolin 2008), appendicular-

ians, mostly *O. dioica*, tend to be more abundant between September and March, corresponding to the summer-dry season. Yet, variations also occur such as (i) a smaller winter peak of *O. dioica* at Casqueira and Conceição (Sankarankutty et al. 1997) and Potengi (EsnaI et al. 1985), depending on the tide and/or the location within the estuary, (ii) *O. longicauda* peaking in the rainy season and no clear seasonal pattern for *O. dioica* at Itamaracá (Porto Neto et al. 1999), and (iii) *Oikopleura* spp. more abundant in the beginning of the rainy season at Itapicuru (Marcolin 2008). Further south at Caravelas, the dominant species *O. dioica* and *O. rufescens* also tended to peak during the dry season, which in this region correspond to the months between May and October; however the very high standard deviations observed (Carvalho and Bonecker 2010) clearly indicate a high variability between different sampling campaigns. Data from subtropical latitudes such as Santos (Pereira 2011), Guaraú (Lopes 1994), Paranaguá (Montú and Cordeiro 1988; Miyashita et al. 2012; Salvador and Bersano 2017) and Babitonga (MNJ unpublished) suggest higher appendicularian abundances typically during spring and/or summer, occasionally with a second smaller peak during winter.

Larger scales of temporal variability have not been addressed in details, but data from Salvador and Bersano (2017) suggest abundance variations of 1.5 to 2 times between 2 consecutive years at Paranaguá. Small-scale temporal variations have also not been evaluated in details, except for the Potengi estuary, where *O. dioica* reaches highest abundances during low tide, particularly at night, and *O. longicauda* only appear during high tide (EsnaI et al. 1985), supporting the estuarine affinities of the former species.

Biomass and secondary production of Brazilian estuarine appendicularians have not been evaluated at all but probably are significative considering the high abundances they may attain in some of these ecosystems (Fig. 3d) and the typical high production rates of appendicularians from warm waters (Hopcroft and Roff 1998). For instance, estimates from subtropical Brazilian shallow shelf indicate appendicularian secondary production represents 77% that of the copepods (Miyashita and Lopes 2011). Regarding population dynamics, the only data available is from Potengi, with the presence of both mature and juvenile *O. dioica* throughout the year, indicating a continuous reproductive period, but with mature individuals attaining smaller sizes during winter (EsnaI et al. 1985). It is interesting to note a consistent nictemeral pattern throughout the year, with mature individuals predominating at night, being nearly absent during day, and juveniles dominating during day and representing only around 10% of the nighttime population (EsnaI et al. 1985).

## 6 Thaliacea

Studies reporting thaliaceans from Brazilian estuaries are quite few and five species have been recorded thus far (Table 2), apart from some unidentified records (e.g., Sterza and Loureiro Fernandes 2006; Araújo et al. 2008). Although local studies on the group are quite scant, this low diversity is not expected to increase considerably, since thaliaceans are not particularly species-rich. There are only 81 species

currently recognized as valid worldwide (Purushothaman et al. 2017) and most of them are typical from outer shelf and oceanic areas, not tolerating brackish estuarine waters (Esnal and Daponte 1999a, b). *Doliolum nationalis*, *Dolioletta gegenbauri*, and *Thalia democratica* are among the few thaliaceans that thrive in coastal waters (e.g., Paffenhöfer and Lee 1987; Paffenhöfer et al. 1995; Menard et al. 1997; Nakamura 1998) and also are the most commonly reported from Brazilian estuaries. Aside from salinity variations, coastal and estuarine waters are particularly problematic for salps considering their filters clog under high concentrations of particulate organic matter (Bone 1998; Esnal and Daponte 1999a) which is common of estuarine high productive waters.

The salp *T. democratica* and the doliolids *D. gegenbauri* and *D. nationalis* are common and abundant in open coastal and offshore waters throughout most of the Brazilian coast (Tavares 1967; Esnal and Daponte 1999a, b; Nogueira Júnior and Brandini [this volume](#)) and also in many regions of the world (Purushothaman et al. 2017), mostly in open waters. Their presence inside Brazilian estuaries is quite occasional (Pereira 2011; Nogueira Júnior 2012), suggesting they do not maintain resident populations but are rather transported from adjacent shelf waters. Truly, they are mostly associated with the outer sectors of the estuaries where salinities are generally higher, but *T. democratica* and *D. nationalis* have occasionally been found in salinities down to ~21 and 26, respectively (Nogueira Júnior 2012; MNJ unpublished).

While both doliolid species have always been found in very low numbers, *T. democratica*, though not frequent, usually found in <15% of the samples, may represent a considerable fraction of the gelatinous zooplankton assemblage (Nogueira Júnior 2012; Martinez et al. 2015), reaching densities of up to 600 and 3,330 ind. 10 m<sup>-3</sup> at Babitonga and Cananéia estuaries respectively (MNJ unpublished). Such high concentrations are probably related with high rates of asexual reproduction (aggregate zooids asexually produced normally dominate these estuarine aggregations), along with its capacity to tolerate broad changes in environmental conditions (Bone 1998; Gibbons 1997; Esnal and Daponte 1999a). Their spatial and temporal dynamics have not been explored but are probably related to local wind and tide patterns along with geomorphological aspects, such as the degree of openness of the estuary. The fate of these estuarine aggregations justifies detailed investigation, to test whether these populations do not persist inside the estuaries because they perish (and then sink and enrich the estuarine benthos) or because they are transported back to open waters during ebb.

## 7 Conclusions

A total of 104 gelatinous and semi-gelatinous zooplankton species have been recorded from Brazilian estuaries, 70 cnidarians, 2 ctenophores, 14 chaetognaths, 13 appendicularians and 5 thaliaceans (Table 2). All major taxa are understudied, and detailed taxonomic and/or quantitative information is not available for most of the numerous Brazilian estuarine ecosystems. Despite this, the number of



siphonophores, ctenophores, chaetognaths, appendicularians, and thaliaceans species from Brazilian estuaries is not expected to increase considerably with increasing sampling effort since most of these taxa are not particularly species-rich and typically have oceanic affinities, with only a few species occurring in estuarine ecosystems. The same is not true for meroplanktonic hydrozoans, particularly those from the orders Anthoathecata and Leptothecata which are diversified in coastal environments with several species tolerating lower and variable salinities of estuaries, representing ~28 and 18%, respectively, of all species recorded here, and whose diversity is probably underestimated due to the lack of data and thus probably will increase considerably with increasing sampling effort, particularly from the less studied tropical estuaries.

For all higher taxa, higher abundances and diversity tend to occur in the outer sectors of the estuaries, because of the higher marine influence and sporadic occurrence of nonresident species, transported by tidal and/or wind processes from the adjacent shelf to inside the estuaries. Density peaks are more common between spring and summer, especially for estuaries from subtropical latitudes (20–32°S), probably due to the nutrient enrichment associated with higher rainfall in these seasons at those latitudes. However, a great variation has been reported from different years, locations, and/or species, which seems to be more related to specific environmental preferences, tolerances, and favorable conditions for their occurrence within estuaries. In lower latitudes (0 to ~11°S), patterns are even more variable, with absence of seasonal variations or peaks in the rainy or dry seasons, but they were less studied. Larger-scale temporal variations, such as interannual and interdecadal changes, have not been explored in details yet, although preliminary data (Nascimento 2016; Salvador and Bersano 2017; Teixeira-Amaral et al. 2017) suggest they may be large. Similarly, small-scale temporal analyses also have been only superficially evaluated. Most typically, chaetognaths tend to increase abundance with the high tide, while the unique available data for appendicularians indicate the opposite. There is no such data for the other gelatinous taxa.

Among cnidarians, the most abundant and ubiquitous species are the holoplanktonic *L. tetraphylla* and the meroplanktonic *Clytia* spp. and *Obelia* spp. along with *P. loyola* and *C. fallax* on subtropical estuaries which are considerably best studied. The Scyphomedusae *C. lactea* and *L. lucerna* also are common throughout Brazilian estuaries and may attain high biomass, but quantitative studies are lacking. Nearly nothing is known on ctenophores, but both *M. leidyi* and *B. ovata* are probably widespread and resident from most, if not all, Brazilian estuaries. No latitudinal trend was found for species richness or abundance neither for chaetognaths nor appendicularians, with most estuaries harboring between one and three species of each taxa. *Parasagitta friderici* and *Parasagitta tenuis* are the most widespread and abundant chaetognaths, and an apparent latitudinal shift in their dominance must be carefully tested since it may be resultant from taxonomic problems. *Oikopleura dioica* and *Oikopleura longicauda* are the most ubiquitous appendicularians, particularly the former species reported from >90% of the estuaries and most commonly being the dominant species. Thaliaceans have only a few scattered records and probably do not maintain permanent populations inside these estuaries, being trans-

ported from the adjacent shelf. Yet, *Thalia democratica* may reach dense aggregations apparently associated with high rates of asexual reproduction.

Basically, any future research on estuarine gelatinous and semi-gelatinous zooplankton from Brazil would be welcome. Species composition is the best-known aspect, but efforts are still necessary, particularly regarding the cnidarians, which are more species-rich, and tropical estuaries which have been less studied and potentially are highly diversified. Abundance data and its temporal variations in many different scales (e.g., tidal, nictemeral, seasonal, interannual, etc.), along with environmental data and prey and/or predator levels, are mostly available for a few subtropical estuaries. Long-term monitoring programs may be particularly interesting considering the presence of exotic species, some of them apparently well-established, in order to track possible changes in abundances and/or species composition and predict their effects on the ecosystem. Studies on any biological parameter (i.e., reproduction, population dynamics, life cycle, secondary production, feeding rates, trophic interactions, etc.) with rare exceptions are missing and should also be emphasized in the future, particularly associating field data with laboratory experiments.

**Acknowledgments** We are deeply indebted to Dras. Graciela Esnal and Tulia Aguilar Martinez for kindly providing important references and to Dr. Leonardo Kenji Miyashita and Dra. Catarina Marcolin for generously providing their original data abundances from different estuaries. Dra. Elena Guerrero read the text and provided useful suggestions. Dra. Monica Susana Hoffmeyer and Dr. Frederico Pereira Brandini are acknowledged for their invitation and patience during the development of this study. MNJ also acknowledges Dr. Renato Mitsuo Nagata for his friendship and encouragement.

## References

- Acuña JL, López-Urrutia Á, Colin S (2011) Faking giants: the evolution of high prey clearance rates in jellyfishes. *Science* 333:1627–1629
- Almeida-Prado MS (1961) Distribuição dos Chaetognatha no Atlântico Sul Ocidental. *Bol Inst Ocean* 12:15–49
- Arai MN (1997) A functional biology of Scyphozoa. Chapman and Hall, London. 316 pp
- Araújo HMP, Nascimento-Vieira DA, Neumann-Leitão S et al (2008) Zooplankton community dynamics in relation to the seasonal cycle and nutrient inputs in an urban tropical estuary in Brazil. *Braz J Biol* 68:751–762
- Ballard L, Myers A (2000) Observations on the seasonal occurrence and abundance of gelatinous zooplankton in Lough Hyne, Co. Cork, South-West Ireland. *Proc R Ir Acad* 100:75–83
- Bardi J (2011) Comunidades de hidrozoários (Cnidaria) estuarinos do sudeste e sul do Brasil. PhD thesis, Universidade de São Paulo
- Bardi J, Marques AC (2009) The invasive hydromedusae *Blackfordia virginica* Mayer, 1910 (Cnidaria: Blackfordiidae) in southern Brazil, with comments on taxonomy and distribution of the genus *Blackfordia*. *Zootaxa* 2198:41–50
- Bettim AL, Haddad MA (2017) Seasonal recruitment of the hydroid *Podocoryna loyola* (Hydractiniidae) in the Paranaguá Bay, South of Brazil. *Mar Biol Res* 13(5.) <https://doi.org/10.1080/17451000.2017.1307990>
- Boero F, Bouillon J, Gravili C et al (2008) Gelatinous plankton: irregularities rule the world (sometimes). *Mar Ecol Prog Ser* 356:299–310



- Boltovskoy D (1975) Some biometrical, ecological, morphological and distributional aspects of Chaetognatha. *Hydrobiologia* 46:515–534
- Boltovskoy D (1981) Chaetognatha. In: Boltovskoy D (ed) *Atlas del zooplancton del Atlántico Sudoccidental y métodos de trabajo con zooplancton marino*. INIDEP, Mar del Plata, pp 759–791
- Boltovskoy D (1999) *South Atlantic zooplankton*. Backhuys Publishers, Leiden
- Bone Q (1998) *The biology of pelagic tunicates*. Oxford University Press, New York
- Bonecker SLC, Dias CO (2009) Zooplankton composition in an estuarine area of State of Maranhão, Northeastern Brasil. *Animal Biol J* 1:69–79
- Bonecker SLC, Oliveira OMP, Carvalho PF (2017) Chaetognatha in Catálogo Taxonômico da Fauna do Brasil. PNUD. Available in: <http://fauna.jbrj.gov.br/fauna/faunadobrasil/140164>. Accessed 11 Sept 2017
- Bouillon J (1999) Hydromedusae. In: Boltovskoy D (ed) *South Atlantic zooplankton*. Backhuys Publishers, Leiden, pp 385–465
- Branco CWC, Kozłowski-Suzuki, B, Esteves FA (2007) Environmental changes and zooplankton temporal and spatial variation in a disturbed Brazilian coastal lagoon. *Braz J Biol* 67:251–262
- Brunetti R, Baiocchi L, Bressan M (1990) Seasonal distribution of *Oikopleura* (Larvacea) in the lagoon of Venice. *Boll Zool* 57:89–94
- Carvalho PF, Bonecker LC (2010) Seasonal and spatial variability of Appendicularian density and taxonomic composition in the Caravelas estuary (Northeastern Brazil) and adjacent coastal area. *Braz Arch Biol Technol* 53:161–169
- Carvalho PF, Bonecker SLC, Nassar CAG (2016) Analysis of the Appendicularia class (subphylum Urochordata) as a possible tool for biomonitoring four estuaries of the tropical region. *Environ Monit Assess*. <https://doi.org/10.1007/s10661-016-5616-5>
- Casanova JP (1999) Chaetognatha. In: Boltovskoy D (ed) *South Atlantic zooplankton*. Backhuys Publishers, Leiden, pp 1353–1374
- Cavalcanti EAH, Neumann-Leitão A, DAN V (2008) Mesozooplâncton do sistema estuarino de Barra das Jangadas, Pernambuco, Brasil. *Rev Brasil Zool* 25:436–444
- Chícharo A, Leitão T, Range P (2009) Alien species in the Guadiana Estuary (SEPortugal/SW–Spain): *Blackfordia virginica* (Cnidaria, Hydrozoa) and *Palaemon macrodactylus* (Crustacea, Decapoda): potential impacts and mitigation measures. *Aquat Invasions* 4:501–506
- Coelho-Botelho MJ, JBN M, Dias CO et al (1999) Aspectos do zooplâncton da Baía de Sepetiba (RJ, Brasil). *Oecologia Brasiliensis* 7:1–33
- Costa KG, Pereira LCC, Costa RN (2008) Short and long-term temporal variation of the zooplankton in a tropical estuary (Amazon region, Brazil). *Bol Mus Para Emílio Goeldi sér Ciências Naturais* 3:127–141
- Costello JH, Bayha KM, Mianzan HW (2012) Transitions of *Mnemiopsis leidyi* (Ctenophora: Lobata) from a native to an exotic species: a review. *Hydrobiologia* 690:21–46
- Cremer MJ, Morales PRD, Oliveira TMN (2006) *Diagnóstico Ambiental da baía da Babitonga*. Editora da Univille, Joinville
- Dagg MJ, Brown SL (2005) The potential contribution of fecal pellets from the larvacean *Oikopleura dioica* to vertical flux of carbon in a river dominated coastal margin. In: Gorsky G, Youngbluth MJ, Deibel D (ed) *Response of marine ecosystems to global change Ecological impact of Appendicularians*, pp 293–397
- Dagg MJ, Green EP, McKee BA et al (1996) Biological removal of fine-grained lithogenic particles from a large river plume. *J Mar Res* 54:149–160
- Daily GCS, Alexander PR, Ehrlich L et al (1997) Ecosystem services: benefits supplied to human societies by natural ecosystems. *Issues in Ecology* 2:1–16
- Dias CO, Bonecker SLC (2008) Long-term study of zooplankton in the estuarine system of Ribeira Bay, near a power plant (Rio de Janeiro, Brazil). *Hydrobiologia* 614:65–81
- Du P, Xu X, Liu J, Zeng J, Chen Q, Shou L, Liao Y, Zhou Q (2011) Distribution of zooplankton in the Jiaojiang Estuary and its response to environment factors in spring and autumn. *Chin J Appl Environ Biol* 17:486–494. (in Chinese with English abstract)

- Esnal GB (1999) Appendicularian. In: Boltovsakoy D (ed) South Atlantic zooplankton. Backhuys Publishers, Leiden, pp 1375–1399
- Esnal GB, Castro RJ (1977) Distributional and biometrical study of appendicularians from the west South Atlantic Ocean. *Hydrobiologia* 56:241–246
- Esnal GB, Daponte MC (1999a) Doliolida. In: Boltovsakoy D (ed) South Atlantic zooplankton. Backhuys Publishers, Leiden, pp 1409–1421
- Esnal GB, Daponte MC (1999b) Salpida. In: Boltovsakoy D (ed) South Atlantic zooplankton. Backhuys Publishers, Leiden, pp 1423–1444
- Esnal GB, Sankaranakutty C, Castro RJ (1985) Diurnal and seasonal fluctuations of *Oikopleura dioica* fol 1872 (Tunicata, Appendicularia) in the mouth of the River Potengi (North Brazil). *Physis*, Secc A 43:65–71
- Freire M, Genzano GN, Neumann-Leitão S (2014) The nonindigenous medusa *Blackfordia virginica* (Hydrozoa, Leptothecata) in tropical Brazil: 50 years of unnoticed presence. *Biol Invasions* 16:1–5
- Furnestin ML (1957) Chaetognathes et zooplancton du secteur Atlantique Marocain. *Revue des Travaux de l'Institut des Pêches Maritimes* 21:1–356
- Genzano GN, Mianzan H, Acha EM (2006) First record of the invasive medusa *Blackfordia virginica* (Hydrozoa: Leptomedusae) in the Río de la Plata estuary, Argentina–Uruguay. *Rev Chil Hist Nat* 79:257–261
- Gibbons MJ (1997) Vertical distribution and feeding of *Thalia democratica* on the Agulhas Bank during march 1994. *J Mar Biol Assoc UK* 77:493–505
- González-Duarte MM, Megina C, López-González PJ (2016) Cnidarian alien species in expansion. In: Goffredo S, Dubinsky Z (eds) *The Cnidaria, past, present and future*. Springer, Basel, pp 139–160
- Grant GC (1977) Seasonal distribution and abundance of the Chaetognatha in the lower Chesapeake Bay. *Estuar Coast Shelf Sci* 5:809–824
- Haddad MA, Marques AC (2009) Cnidaria. In: Rocha RM, Boeger WA (eds) *Zoologia. Estado da arte e perspectivas*. Editora da UFPR, Curitiba, pp 29–48
- Haddad MA, Nogueira Júnior M (2006) Reappearance and seasonality of *Phyllorhiza punctata* von Lendenfeld (Cnidaria, Scyphozoa, Rhizostomeae) medusae in southern Brazil. *Rev Brasil Zool* 23:824–831
- Haddad MA, Bettim AL, Miglietta MP (2014) *Podocoryna loyola*, n. sp. (Hydrozoa, Hydractiniidae): a probably introduced species on artificial substrate from southern Brazil. *Zootaxa* 3796:494–506
- Hamner WM, Madin LP, Alldredge AL et al (1975) Underwater observations of gelatinous zooplankton: sampling problems, feeding biology, and behavior. *Limnol Oceanogr* 20:907–917
- Hernández RM, Suarez-Morales E, Gasca R (2005) Seasonal distribution of Chaetognatha in a Mexican neotropical bay during a year cycle. *J Coast Res* 21:186–192
- Hoover RS, Hoover D, Miller M et al (2006) Zooplankton response to storm runoff in a tropical estuary: bottom-up and top-down controls. *Mar Ecol Prog Ser* 318:187–201
- Hopcroft RR, Roff JC (1998) Production of tropical larvaceans in Kingston Harbour, Jamaica: are we ignoring an important secondary producer? *J Plankton Res* 17:205–220
- Hossfeld B (1996) Distribution and biomass of arrow worms (Chaetognatha) in Golfo de Nicoya and Golfo Dulce, Costa Rica. *Rev Biol Trop* 44:157–117
- Johnsen S (2001) Hidden in plain sight: the ecology and physiology of organismal transparency. *Biol Bull* 201:301–318
- Kremer P (2002) Towards understanding of salp swarm dynamics. *CM* 12:1–15
- Krumme U, Liang TH (2004) Tidal-induced changes in a copepod-dominated zooplankton community in a macrotidal mangrove channel in Northern Brazil. *Zool Stud* 43:404–414
- Lana PC, Marone E, Lopes RM et al (2001) The subtropical estuarine complex of Paranaguá Bay, Brazil. In: Seeliger U, Lacerda LD, Kjerfve B (eds) *Coastal Marine ecosystems of Latin America*. Springer Verlag, Basel, pp 131–145
- Lansac Tôha FA, Lima AF (1993) Ecologia do zooplâncton do Estuário do Rio Una do Prelado (São Paulo, Brasil). *Acta Limnol Bras* 6:82–95

- Larson RJ (1986) Water content, organic content, and carbon and nitrogen composition of medusae from the Northeast Pacific. *J Exp Mar Biol Ecol* 99:107–120
- Liang TH (2002) Chaetognath seasonality and distribution at surface layers off Ubatuba, South Brazil Bight coastal waters. *Oceanides* 17:103–111
- Liang TH, Vega-Pérez LA (1995) Studies on chaetognaths of Ubatuba region, Brazil. II. Feeding habits. *Bol Inst Oceanogr* 43:27–40
- Liang TH, Vega-Pérez LA (2001) Diversity, abundance and biomass of epiplanktonic chaetognath off South Atlantic Western sector, from Cabo Frio (23°S, 42°W) to São Pedro and São Paulo rocks (01°N, 29°W). *Oceanides* 16:34–48
- Liang TH, Vega-Pérez LA (2002) Distribution, abundance and biomass of Chaetognaths off São Sebastião region, Brazil in February 1994. *Rev Bras Oceanogr* 50:1–12
- Liang TH, Ara K, Miranda LB, Bérnago AL, Bernardes M (2003) On the variability of the chaetognath *Sagitta friderici* Ritter-Zahony at Cananéia Lagoon Estuarine system, São Paulo, Brazil. *Hydrobiologia* 510:91–102
- Liu H, Li K, Huang H et al (2013) Seasonal community structure of mesozooplankton in the Daya Bay, South China Sea. *J Ocean U China* 12:452–458
- Lopes RM (1994) Zooplankton distribution in the Guaraú River Estuary (South–Eastern Brazil). *Estuar Coast Shelf Sci* 39:287–302
- Lopes RM, Vale R, Brandini FP (1998) Composição, abundância e distribuição espacial do zooplâncton no complexo estuarino de Paranaguá durante o inverno de 1993 e o verão de 1994. *Rev Bras Oceanogr* 46:195–211
- Loureiro Fernandes L, Sterza JM, Neves KO (2005) Seasonal chaetognath abundance and distribution in a tropical estuary (Southeastern, Brazil). *Braz J Oceanogr* 53:47–53
- Mackie GO, Pugh PR, Purcell JE (1987) Siphonophore biology. *Adv Mar Biol* 24:97–262
- Macpherson E (2002) Large-scale species-richness gradients in the Atlantic Ocean. *Proc Biol Sci* 269:1715–1720
- Magalhães EMM, PO M–J, Silva JJ et al (1996) Chaetognatha planctônicos do complexo estuarino lagunar Mundaú/Manguaba, AL. *Boletim de Estudos de Ciências do Mar* 9:63–87
- Mahiques MM, Figueira RCL, Salaroli AB et al (2013) 150 years of anthropogenic metal input in a biosphere reserve: the case study of the Cananéia–Iguape coastal system, Southeastern Brazil. *Environ Earth Sci* 68:1073–1087
- Marazzo A, Nogueira CSR (1996) Composition, spatial and temporal variations of Chaetognatha in Guanabara Bay, Brazil. *J Plankton Res* 18:2367–2376
- Marcolin CR (2008) Estrutura da comunidade zooplanctônica estuarina em relação ao impacto da atividade de carcinicultura no litoral norte da Bahia, Brasil. Masters' dissertation, Universidade Federal da Bahia
- Marcolin CR, Conceição BL, Nogueira MM et al (2010) Mesozooplankton and ichthyoplankton composition in two tropical estuaries of Bahia, Brazil. *Check List* 6(2):210–216
- Marques F, Angélico MM, Costa JL (2017) Ecological aspects and potential impacts of the non-native hydromedusa *Blackfordia virginica* in a temperate estuary. *Estuar Coast Shelf Sci* 197:69–79
- Martinez TIM, Costa BSP, Miyashita LK et al (2015) Diversity of gelatinous zooplankton (Cnidaria, Ctenophora, Chaetognatha and Tunicata) from the Cananéia–Iguape Estuarine System (São Paulo, Brazil). *Proceedings of the XVI Colacmar and XVI Senalmar, Santa Marta, Colombia*, p 35
- McLelland JA (1980) Notes on the northern Gulf of Mexico occurrence of *Sagitta friderici* Ritter-Zahony (Chaetognatha). *Gulf Res Rep* 6:343–348
- McLelland JA (1989) An illustrated key to the Chaetognatha of the Northern Gulf of Mexico with notes on their distribution. *Gulf Res Rep* 8:145–172
- Menard F, Fromentin JM, Goy J et al (1997) Temporal fluctuations of doliolid abundance in the bay of Villefranche-sur-Mer (Northwestern Mediterranean Sea) from 1967 to 1990. *Oceanol Acta* 20:733–742
- Mendes F, Figueiredo GM, Valentin JL (2012) Reproduction and structure of the population of the Chaetognath *Parasagitta friderici* in Guanabara Bay (Brazil) based on short term sampling. *An Acad Brasil Ciênc* 84:103–111

- Mesquita SDSA, Costa RM, Pereira LCC (2006) Composição, ocorrência e distribuição das hidromedusas no estuário do rio Caeté, litoral do estado do Pará. *Bol Mus Para Emílio Goeldi Ciênc Nat* 1:113–119
- Mianzan HW (1999) Ctenophora. In: Boltovskoy D (ed) South Atlantic zooplankton, vol 1. Backhuys Publishers, Leiden, pp 51–573
- Mianzan HW, Cornelius PFS (1999) Cubomedusae and Scyphomedusae. In: Boltovskoy D (ed) South Atlantic zooplankton, vol 1. Backhuys Publishers, Leiden, pp 513–559
- Mills CE (1995) Medusae, siphonophores, and ctenophores as planktivorous predators in changing global ecosystems. *ICES J Mar Sci* 52:575–581
- Mills C, Rees JT (2000) New observations and corrections concerning the trio of invasive hydromedusae *Maeotias marginata* (= *M. inexpectata*), *Blackfordia virginica*, and *Moreisia* sp. in the San Francisco Estuary. *Sci Mar* 64:151–155
- Miyashita LK, Lopes RM (2011) Larvacean (Chordata, Tunicata) abundance and inferred secondary production off southeastern Brazil. *Estuar Coast Shelf Sci* 92:367–375
- Miyashita LK, Brandini FP, JE M–F et al (2012) Comparison of zooplankton community structure between impacted and non-impacted areas of Paranaguá Bay Estuarine Complex, South Brazil. *J Nat Hist* 46:1557–1571
- Montú MA (1980) Zooplâncton do estuário da Lagoa dos Patos I – Estrutura e variações temporais e espaciais da comunidade. *Atlantica* 4:53–72
- Montú MA, Cordeiro TA (1988) Zooplankton del complejo estuarial de la Bahía de Paranaguá. I. Composición, dinámica de las especies, ritmos reproductivos y acción de los factores ambientales sobre la comunidad. *Nerítica* 3:61–83
- Moore SJ (1987) Redescription of the leptomedusan *Blackfordia virginica*. *J Mar Biol Assoc UK* 67:287–291
- Morandini AC (2003) Estrutura populacional de *Chrysaora lactea* e *Lychnorhiza lucerna* (Cnidaria, Scyphozoa) em amostras de plâncton, com a redescritção das espécies. PhD thesis, Universidade de São Paulo
- Moreira GS (1978) A preliminary laboratory study on the salinity and temperature tolerances of some medusae from the São Paulo coast, Brazil. *Bol Inst Oceanogr* 27:45–55
- Mulkana MS, McIlwain TD (1973) The seasonal occurrence and abundance of Chaetognatha in Mississippi Sound. *Gulf Res Rep* 4:264–261
- Nagata RM, Haddad MA, Nogueira Jr M (2009) The nuisance of jellyfish to shrimp trawls in central part of Southern Brazilian Bight, from the perspective of artisanal fishermen. *Panm J Aquat Sci* 4:312–325
- Nagata RM, Santos L, Stampar SN et al (2013) *Phyllorhiza punctata* in Brazilian coast: population oscillations or recurrent invasions? Proceedings of the fourth international Jellyfish blooms symposium, Hiroshima, p 128
- Nagata RM, Nogueira-Junior M, Brandini FP (2014a) Spatial and temporal variation of planktonic cnidarians density in subtropical waters of the Southern Brazilian Bight. *J Mar Biol Assoc UK* 94:1387–1400
- Nagata RM, Nogueira-Junior M, Haddad MA (2014b) Faunistic survey of Hydromedusae (Cnidaria, Medusozoa) from the coast of Paraná State, Southern Brazil. *Zootaxa* 3768:291–326
- Nair VR, Sankarankutty C (1988) Chaetognaths of the Potengi estuary (Natal, Northeast Brazil). *Atlantica* 10:5–20
- Nakamura Y (1998) Blooms of tunicates *Oikopleura* spp. and *Doliolletta gegenbauri* in the Seto Inland Sea, Japan, during summer. *Hydrobiologia* 385:183–192
- Nascimento LS (2016) Hidrozoários planctônicos do complexo estuarino de Paranaguá–Brasil. Masters’ dissertation, Universidade Federal do Paraná
- Navas-Pereira D (1973) Relatório sobre a segunda pesquisa oceanográfica e pesqueira do Atlântico Sul entre Torres e Maldonado (Lat. 29 S–35 S). Análise qualitativa e quantitativa do zooplâncton. *Publ Espuar Inst Oceanogr Sci Paulo* 3:29–92
- Navas-Pereira D (1980) Hydromedusae of the Bay of Sepetiba (Rio de Janeiro, Brazil). *Rev Bras Biol* 40:817–824
- Neumann-Leitão S, Matsumura-Tundisi T (1998) Dynamics of a perturbed estuarine zooplanktonic community: Port of Suape, PE, Brazil. *Verh Internat Verein Limnol* 26:1981–1988

- Nogueira Júnior M (2012) Gelatinous zooplankton fauna (Cnidaria, Ctenophora and Thaliacea) from Baía da Babitonga (southern Brazil). *Zootaxa* 3398:1–21
- Nogueira Júnior M, Brandini FP (2018) Community structure and spatial–temporal dynamics of the zooplankton in the South Brazilian Bight – a review. In: Hoffmeyer MS, Sabatini ME, Brandini FP, Calliari D, Santinelli N (eds) *Plankton ecology of the Southwestern Atlantic – from the subtropical to the subantarctic realm*, Springer, chapter 8, this volume
- Nogueira Júnior M, Haddad MA (2006) Macromedusae (Cnidaria) from the Paraná Coast, Southern Brazil. *J Coast Res SI* 39:1161–1164
- Nogueira Júnior M, Haddad MA (2008) The diet of Cubomedusae (Cnidaria, Cubozoa) in southern Brazil. *Braz J Oceanogr* 56(3):157–164
- Nogueira Júnior M, Oliveira JS (2006) *Moerisia inkermanica* Paltschikowa–Ostroumova (Hydrozoa, Moerisiidae) e *Blackfordia virginica* Mayer (Hydrozoa, Blackfordiidae) na Baía de Antonina, Paraná, Brasil. *Panam J Aquat Sci* 1:35–42
- Nogueira Júnior M, Souza-Conceição JMS (2010) Seasonal distribution and size class composition of the Scyphomedusae *Chrysaora lactea* (Semaestomeae) and *Lychnorhiza lucerna* (Rhizostomeae) in a subtropical estuary in Southern Brazil. *Proceedings of the third international Jellyfish blooms symposium, Mar del Plata*, p 82
- Nogueira Júnior M, Nagata RM, Haddad MA (2010) Seasonal variation of macromedusae (Cnidaria) at North Bay, Florianópolis, southern Brazil. *Fortschr Zool* 27:377–386
- Nogueira Júnior M, Brandini FP, Codina JC (2014) Distribution of planktonic cnidarians in response to South Atlantic central water intrusion in the South Brazilian Bight. *Cont Shelf Res* 89:93–102
- Nogueira Júnior M, Brandini FP, Codina J (2015a) Diel vertical dynamics of gelatinous zooplankton (Cnidaria, Ctenophora and Thaliacea) in a subtropical stratified ecosystem (South Brazilian Bight). *PLoS One* 10:0144161–0144128
- Nogueira Júnior M, Pukanski LEDM, Conceição JMS (2015b) Mesh size effects on assessments of planktonic hydrozoan abundance and assemblage structure. *J Mar Syst* 144:117–126
- Nogueira Júnior M, Silva Nascimento L (2018) The ecology and developmental changes of meristic characters of the medusa *Malagazzia carolinae* (Hydrozoa: Leptothecata) from subtropical Southwestern Atlantic estuaries. *Zoologischer Anzeiger* 274:34–45
- Oliveira MP (2007) Ctenóforos da costa brasileira: considerações taxonômicas e biológicas. PhD thesis, Universidade de São Paulo
- Oliveira OM, Mianzan H, Migotto AE et al (2007) Chave de identificação dos Ctenophora da costa brasileira. *Biol Neotrop* 7:341–350
- Oliveira OM, Miranda TP, Araujo EM et al (2016) Census of Cnidaria (Medusozoa) and Ctenophora from south American marine waters. *Zootaxa* 4194:1–256
- Paffenhöfer GA, Lee TN (1987) Development and persistence of patches of Thaliacea. In: Payne, A.I.L., Gulland, J.A. and Brink, K.H. (Eds.). *The Benguela and comparable ecosystems*. *Afr J Mar Sci* 5:305–318
- Paffenhöfer GA, Sherman BK, Lee TN (1987) Abundance, distribution and patch formation of zooplankton. *Prog Oceanogr* 9:403–436
- Paffenhöfer GA, Atkinson LP, Lee TN et al (1995) Distribution and abundance of thaliaceans and copepods off the southeastern U.S.A. during winter. *Cont Shelf Res* 15:255–280
- Pekala GA (1980) Nota preliminar sobre a composição do zooplâncton do estuário do Rio Paraíba do Norte, PB, Brasil. *Bol Inst Oceanogr* 29:291–296
- Pereira JB (2011) Composição, distribuição, biomassa e produção secundária do zooplâncton do sistema estuarino de Santos, São Paulo, Brasil. PhD thesis, Universidade de São Paulo
- Pierce EL (1951) The Chaetognatha of the west coast of Florida. *Biol Bull* 100:206–228
- Pierrot-Bults AC, Nair VR (1991) Distribution patterns in Chaetognatha. In: Bone Q, Kapp H, Pierrot-Bults AC (eds) *The biology of Chaetognaths*. Oxford University, Oxford, pp 86–116
- Porto Neto FF, Neumann-Leitão S, Gusmão LMO, Nascimento Vieira DA, Silva AP, Silva TA (1999) Variação sazonal e nictemeral do zooplâncton no Canal de Santa Cruz, Itamaracá, PE, Brasil. *Trab Oceanog Univ Fed PE* 27:43–58

- Potter IC, Chuwen BM, Hoeksema SD et al (2010) The concept of an estuary: a definition that incorporates systems which can become closed to the ocean and hypersaline. *Estuar Coast Shelf Sci* 87:497–500
- Primo AL, Marques SC, Falcão J (2012) Environmental forcing on jellyfish communities in a small temperate estuary. *Mar Environ Res* 79:152–159
- Pugh PR (1999) Siphonophorae. In: Boltovsky D (ed) *South Atlantic zooplankton*. Backhuys Publishers, Leide, pp 467–511
- Pukanski LEDM (2011) Dinâmica populacional das hidromedusas *Liriope tetraphylla* (Trachymedusae) e *Blackfordia virginica* (Leptothecata) na Baía da Babitonga. Masters' dissertation, Universidade Federal do Paraná
- Purcell JE (2005) Climate effects on formation of jellyfish and ctenophore blooms: a review. *J Mar Biol Assoc UK* 85:461–476
- Purushothaman J, Hansda S, Dey J et al (2017) An annotated checklist of thaliaceans (Chordata: tunicates). *Mar Biodivers*:1–28
- Reeve MR (1970) The biology of Chaetognatha I. Quantitative aspects of growth and egg production in *Sagitta hispida*. In: Steele JH (ed) *Marine food chains*. University of California Press, Berkeley, pp 1–550
- Resgalla C (2001) Estudo de impacto ambiental sobre a comunidade do zooplâncton na enseada do Saco dos Limões, Baía Sul da ilha de Santa Catarina, Brasil. *Atlântica* 23:5–16
- Resgalla C (2010) Parâmetros populacionais de *Sagitta friderici* Ritter–Záhony (Chaetognatha) na zona de arrebentação da praia do Cassino, sul do Brasil. *Atlântica* 32:141–149
- Rippingale RJ, Kelly SJ (1995) Reproduction and survival of *Phyllorhiza punctata* (Cnidaria: Rhizostomeae) in a seasonally fluctuating salinity regime in Western Australia. *Mar Freshw Res* 46:1145–1151
- Rocha RM, Bonecker SLC, Carvalho PF (2017) Appendicularia in: Catálogo Taxonômico da Fauna do Brasil. <http://fauna.jbrj.gov.br/fauna/faunadobrasil/156717> Accessed on 21 Sept 2017
- Russell FS (1953) The Medusae of the British Isles. Anthomedusae, Leptomedusae, Limnomedusae, Trachymedusae, and Narcomedusae. Cambridge University Press, Cambridge, p 529
- Salvador B, Bersano JGF (2017) Zooplankton variability in the subtropical estuarine system of Paranaguá Bay, Brazil, in 2012 and 2013. *Estuar Coast Shelf Sci*. <https://doi.org/10.1016/j.ecss.2017.09.019>
- Sankarankutty C, Medeiros GF, Santos NQ (1979) On diurnal variations of zooplankton in a tidal estuary. *J Mar Biol Assoc India* 21(1):187–190
- Sankarankutty C, Medeiros GF, Oliveira JE (1995) Diurnal and seasonal fluctuations of estuarine zooplankton of Potengi estuary, Natal, Northeast of Brazil. *J Mar Biol Assoc India* 37:201–211
- Sankarankutty C, Mendonça KMA, Ferreira AC et al (1997) On zooplankton of a mangrove ecosystem close to Macau, Rio Grande do Norte, Brazil. *Trab Oceanog Univ Fed PE* 25:47–59
- Sankarankutty C, Medeiros GF, Silva ACC et al (1996) On an unusual concentration of *Sagitta tenuis* conant in the estuary of Potengi, Natal, Brazil. *J Mar Biol Assoc India* 38:153–155
- Sato R, Ishibashi Y, Ishimaru T, Dagg MJ (2008) Productivity and grazing impact of Oikopleura dioica (Tunicata, Appendicularia) in Tokyo Bay. *J Plankton Res* 30:299–309
- Sato NE, Hernández D, Viñas MD (2011) Hábitos alimentarios de *Sagitta friderici* Ritter–Zahony em las aguas costeras de la Provincia de Buenos Aires, Argentina. *Bol Invest Mar Cost* 40:59–74
- Schuchert P (2011) *Dipurena* McCrady, 1859. In: Schuchert, P. (2017). World Hydrozoa database. Accessed through: World Register of Marine Species at <http://marinespecies.org/aphia.php/aphia.php?p=taxdetails&id=117069>. Accessed on 6 Oct 2017
- Silva TA, Neumann-Leitão S, Schwamborn R et al (2003) Diel and seasonal changes in the macrozooplankton community of a tropical estuary in Northeastern Brazil. *Rev Bras Zootec* 20:439–446
- Silva AP, Neumann-Leitão S, Schwamborn R et al (2004) Meso-zooplankton of an impacted Bay in North Eastern Brazil. *Braz Arch Biol Technol* 47:485–493



- Silveira FL, Cornelius PFS (2000) New observations on medusae (Cnidaria, Scyphozoa, Rhizostomae) from the northeast and South Brazil. *Acta Biol Leopold* 22:9–18
- Singarajah KV (1978) Hydrographic conditions, composition and distribution of plankton in relation to potential resources of Parafba River estuary. *Revta Nordest Biol* 1:125–144
- Souza CS, Luz JAG, Mafalda-Júnior P (2014) Relationship between spatial distribution of chaetognaths and hydrographic conditions around seamounts and islands of the tropical southwestern Atlantic. *An Acad Brasil Ciênc* 86:1151–1165
- Spinelli ML, Martos P, Esnal GB (2009) Appendicularian assemblages and their space–time variability off the la Plata River, SW Atlantic Ocean. *Estuar Coast Shelf Sci* 85:97–106
- Srinivasan M (1971) Biology of chaetognaths of the estuarine waters of India. *J Mar Biol Assoc India* 13:173–181
- Srinivasan M (1980) Life cycle and seasonal fluctuation of Chaetognatha in Ennore estuary, Madras. *Bull Zoo Surv India* 3:55–61
- Sterza JM, Loureiro Fernandes L (2006) Zooplankton community of the Vitória Bay Estuarine system (Southeastern Brazil). Characterization during a three–year study. *Braz J Oceanogr* 54:95–105
- Tavares DQ (1967) Occurrence of doliolids and salps during 1958, 1959, and 1960 off the São Paulo coast. *Bolm Inst oceanogr* 16:87–97
- Teixeira C, Tundisi J, Kutner MB (1965) Plankton studies in a mangrove environment II. The standing stock and some ecological factors. *Bol Inst Oceanogr* 14:13–41
- Teixeira-Amaral P, WJA A, de Ortiz DO (2017) The mesozooplankton of the Patos Lagoon Estuary, Brazil: trends in community structure and secondary production. *Mar Biol Res* 13:48–61
- Thuesen EV (2009) *Parasagitta* Tokioka, 1965. Accessed through: World Register of Marine Species at <http://www.marinespecies.org/aphia.php?p=taxdetails&id=105408> Accessed on 19 Sept 2017
- Tomita M, Shiga N, Ikeda T (2003) Seasonal occurrence and vertical distribution of appendicularians in Toyama Bay, southern Japan Sea. *J Plankton Res* 25:579–589
- Tse P, Souissi S, Hwang JS et al (2008) Spatial and seasonal variations in chaetognath assemblages in two subtropical marine inlets with different hydrographical characteristics. *Zool Stud* 47:258–267
- Tundisi TM (1970) On the seasonal occurrence of appendicularians in waters off the coast of São Paulo State. *Bol Inst Oceanogr* 19:131–144
- Vannucci M (1954) Hydrozoa e Scyphozoa existentes no Instituto Oceanográfico. II *Bol Inst Oceanogr* 5:95–149
- Vannucci M (1956) Biological notes and description of a new species of *Dipurena* (Hydrozoa, Corynidae). *J Zool* 127:479–487
- Vannucci M (1957) On Brazilian Hydromedusae and their distribution in relation to different water masses. *Bol Inst Oceanogr* 8:23–109
- Vannucci M (1963) On the ecology of Brazilian medusae at 25° lat. S. *Bol Inst Oceanogr* 13:143–184
- Vega-Pérez LA, Liang TH (1992) Feeding of a pelagic chaetognath, *Sagitta friderici* Ritter-Záhony off Ubatuba region (São Paulo, Brazil). *Bol Inst Oceanogr* 40:93–100
- Whitfield A, Elliot M (2011) Ecosystem and biotic classifications of estuaries and coasts. In: Wolanski E, Mcluskys DS (ed). *Estuar Coast Shelf Sci* 1:99–124
- Wintzer AP, Meek MH, Moyle PB (2011) Ecological insights into the polyp stage of non-native hydrozoans in the San Francisco Estuary. *Aquatic Ecol* 45:151–161
- Yilmaz IN (2015) Collapse of zooplankton stocks during *Liriope tetraphylla* (Hydromedusa) blooms and dense mucilaginous aggregations in a thermohaline stratified basin. *Mar Ecol* 36:595–610
- Zamponi MO, Genzano G (1994) Seasonal distribution of hydromedusae from Samborombon Bay (Buenos Aires, Argentina). *Plankton. Newsletter* 19:51–56