



Diversity of gelatinous zooplankton (Cnidaria, Ctenophora, Chaetognatha and Tunicata) from a subtropical estuarine system, southeast Brazil

Miodeli Nogueira Júnior¹ · Bárbara Santos Pulze da Costa² · Tulia Aguilar Martinez² · Frederico Pereira Brandini² · Leonardo Kenji Miyashita²

Received: 10 May 2017 / Revised: 14 May 2018 / Accepted: 2 July 2018 / Published online: 17 July 2018

© Senckenberg Gesellschaft für Naturforschung 2018

Abstract

We surveyed the gelatinous zooplankton (Cnidaria, Ctenophora, Chaetognatha, Tunicata) fauna from the Cananeia-Iguape Coastal System (CICS; São Paulo, Brazil; ~25°S). This area includes a natural reserve formed by the Atlantic Rain Forest and mangroves, having a high biological productivity and being recognized as a wildlife sanctuary. We analyzed 164 plankton samples collected between January 2012 and January 2013, along with visual records of living and stranded large (>2 cm) gelatinous zooplankton. More than 29,000 organisms were studied, which combined with literature totaled 16 orders, 40 families and 56 species: two cubomedusae, five scyphomedusae, two siphonophores, 34 hydromedusae, two ctenophores, five chaetognaths, three appendicularians and three thaliaceans. Twenty-seven species are new records for the CICS, six species for the state of São Paulo, and *Tiaricodon* sp. is newly recorded for the Brazilian coast and is described in details. Most of the species from CICS (37 spp.; 66%) are meroplanktonic, whereas the most abundant taxa are holoplanktonic (>95% of all gelatinous). Meroplanktonic taxa tended to be more species rich in brackish-waters (salinity 20–30) with most species occurring in one or two seasons, particularly during summer and/or autumn, while holoplanktonic species tended to occur throughout the year, and to be more species-rich in more saline waters (>30). These observations indicate different strategies of estuarine occupation driven by life cycle. Our results underscore the high diversity of meroplanktonic gelatinous organisms from subtropical estuaries and emphasize the need for comprehensive sampling surveys in such ecosystems, which are mostly understudied worldwide.

Keywords Biodiversity · Estuaries · South Atlantic · Gelatinous zooplankton

Introduction

The knowledge concerning species composition is one of the most basic areas of biological research, providing valuable background information for many other fields, including but not limited to ecology, biogeography and conservation biology. In addition,

such knowledge is fundamental for properly understanding local and global patterns of biodiversity distribution, mapping biodiversity hot-spots and for detecting ecosystem changes, such as invasions and extinctions, whether anthropogenically driven or not (Tewksbury et al. 2014; Gravili et al. 2015). Therefore, comprehensive field sampling and monitoring programs are necessary to keep species lists updated and track possible changes. This is especially important for taxonomic groups composed of tiny or inconspicuous species, which would easily pass unnoticed without specific sampling techniques and the trained eyes of experts. This is the case of the gelatinous zooplankton (Cnidaria, Ctenophora, Chaetognatha, Tunicata). Except for some particular gelatinous taxa (e.g. ctenophores, scyphomedusae, pyrosomes) that may reach large sizes and be colorful, but which also have relatively low diversity, most species measure a few millimeters and are transparent (Boltovskoy 1981, 1999), and thus inconspicuous and often neglected. The

Communicated by S. Piraino

✉ Miodeli Nogueira Júnior
miodeli@gmail.com

¹ Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, Cidade Universitária, João Pessoa, PB 58051-900, Brazil

² Instituto Oceanográfico, Universidade de São Paulo, Praça do Oceanográfico 191, Cidade Universitária, São Paulo, SP 05508-120, Brazil

body fragility and associated difficulties of sampling, fixating and preserving specimens, typical features of gelatinous organisms, pose further difficulties.

Estuarine ecosystems typically have high biological productivity and harbor important fishing resources, beyond plentiful human activities, having, therefore, a central ecological, economic and cultural importance. Gelatinous zooplankton are mostly marine organisms, although there are a few freshwater medusae, and thus the general diversity of estuarine gelatinous zooplankton was usually thought to be impoverished (e.g. Vannucci et al. 1970; Calder 1971; Santhakumari et al. 1999), but the diversity of meroplanktonic hydromedusae may be particularly high in some warm water estuaries (Xu and Huang 1983; Nogueira Júnior 2012). The southwestern Atlantic gelatinous zooplankton fauna is insufficiently and unevenly known (Nogueira Júnior et al. 2018), and comprehensive taxonomic reports from estuarine sites are particularly scant, hampering recognition of both local and regional biodiversity patterns, as well as detection of invasions and/or local extinctions.

The Cananeia-Iguape Coastal System (CICS) is an important Brazilian estuarine system with a high priority for conservation (MMA 2007); it has an essential socioeconomic role sustaining thousands of fishermen (Mendonça and Miranda 2008; Chiba de Castro et al. 2012) and local tourism (Filla et al. 2012; Barcellini et al. 2013). Despite its ecological and economic importance - and the presence of laboratory facilities of the Oceanographic Institute of the São Paulo University since the early 1950's - there is no comprehensive survey of gelatinous fauna from the CICS. Only a few species were recorded mostly from studies targeting particular taxa (Vannucci 1956; Teixeira et al. 1965; Liang et al. 2003; Morandini 2003; Bardi and Marques 2009), and therefore the local gelatinous zooplankton diversity patterns are poorly known. This is not a particularity of the CICS but is similar to most estuarine ecosystems from the southwestern Atlantic (Nogueira Júnior et al. 2018). Aiming to provide as comprehensively as possible an overview of gelatinous zooplankton diversity patterns from the CICS, in the present study we provide a report on species composition from extensive samplings with different gears and visual observations. Additionally, we describe the general diversity trends regarding their seasonality and variations through the salinity gradient, typically the main factor controlling diversity, distribution and structure of warm estuarine communities (Whitfield et al. 2012; Miyashita and Calliari 2016).

Material and methods

Study site

The CICS is located on the south coast of the state of São Paulo, southeast Brazil (Fig. 1). This estuarine system is

surrounded by a coastal plain area, salt marshes, mangroves and the Atlantic rainforest. The climate is subtropical humid (Alvares et al. 2013), with annual mean precipitation and air temperature of 230 mm and 23.8 °C, respectively (Miyao et al. 1986; Silva 1989). The estuary is classified as partially mixed and weakly stratified (Type 2a) and turbulent diffusion is responsible for most of the upstream salt flux (Miranda et al. 1995). Circulation along the estuary is driven by semidiel tidal currents, with amplitude of 0.83 and 0.13 m during spring and neap tides, respectively (Miyao and Harari 1989). Ribeira de Iguape River and several small rivers are the main sources of freshwater discharge. Water temperature of the CICS varies mostly following the seasonal climatic regime, while salinity varies on a daily and seasonal basis as a result of tidal and rainfall regimes respectively, as common for estuaries (Day et al. 2013).

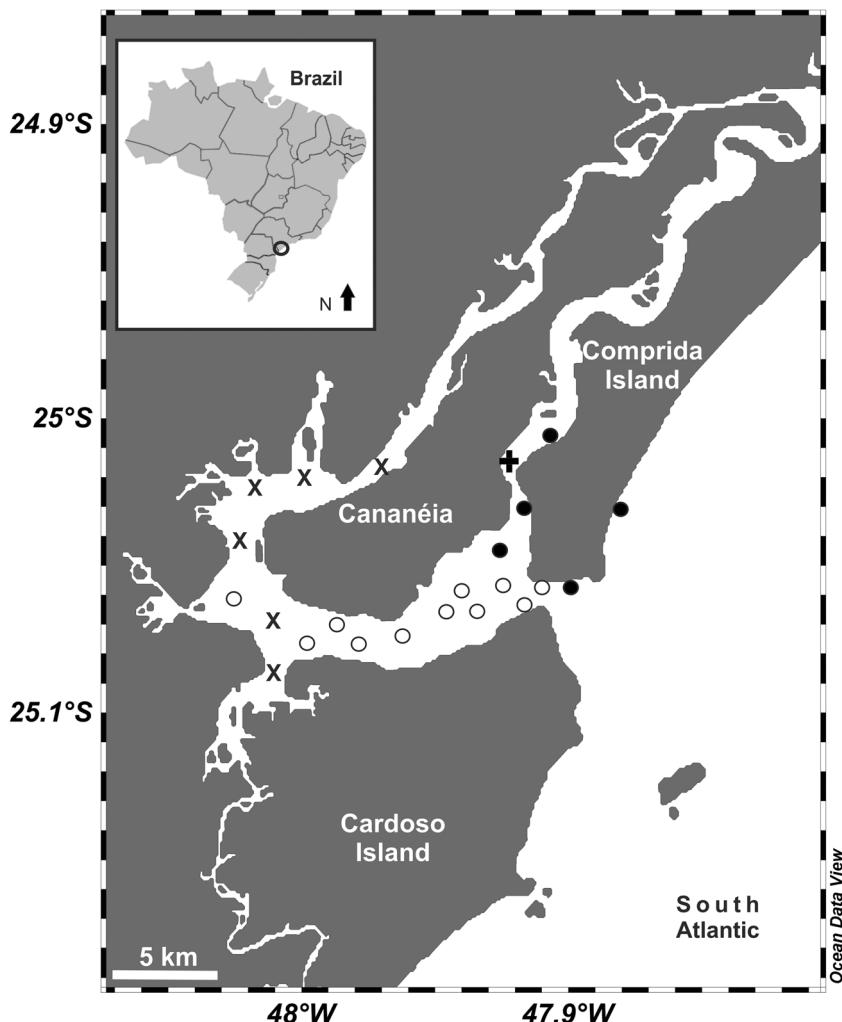
The CICS has a high primary productivity, being recognized as a wildlife sanctuary in need of conservation (MMA 2007) with great socioeconomic importance for local fisheries (Mendonça and Miranda 2008; Chiba de Castro et al. 2012) and tourism (Filla et al. 2012; Barcellini et al. 2013). Yet, the CICS has been subjected to several anthropogenic impacts, such as eutrophication (Barrera-Alba et al. 2007), heavy metal contamination (Mahiques et al. 2013), and inappropriate coastal land use (Mahiques et al. 2014).

Data collection

Gelatinous zooplankton was collected in three sampling programs within the CICS (Fig. 1; Table 1), in a total of 164 zooplankton samples:

- i) Between January 2012 and January 2013, five stations (Fig. 1) were sampled every second month during daytime (see Miyashita and Calliari 2016 for more details on sampling procedures and hydrographic conditions). On some occasions, some stations could not be sampled because of technical problems or severe weather conditions. On each station three hyperbenthic samples and one zooplankton sample were collected, with an epibenthic sledge (500-µm mesh size; mouth area of 0.06 m²) and a conical plankton net (90-µm mesh size; mouth area of 0.13 m²), respectively, in a total of 81 samples with the former and 26 with the latter net.
- ii) On 12 March 2012, eleven stations were sampled (Fig. 1) with a cylindrical-conical net with mouth area of 0.78 m² and 300-µm mesh size.
- iii) On 11 and 12 April 2012, a single station (Fig. 1) was sampled every 2 h between 09:00 and 17:00. At each sampling time, three hauls were made with a conical plankton net with mouth area of 0.196 m² and 160-µm mesh size, for a total of 30 samples. Additionally, one haul was made with a conical plankton net with mouth

Fig. 1 Map of the Cananeia-Iguape Coastal System, São Paulo, Brazil, showing the stations sampled every second month between January 2012 and January 2013 (black circles), on March 12, 2012 (open circles), on April 11–12, 2012 (cross), and on April 13, 2012 (X). Generated using Ocean Data 4 software (Schlitzer 2017)



area of 0.07 m² and 60-μm mesh size, totaling 10 samples. On 13 April 2012, six additional stations were sampled (Fig. 1) with a conical plankton net with mouth area of 0.196 m² and 160-μm mesh size.

On sampling programs “i” and “iii” subsuperficial salinity and temperature were measured with a multi probe Oakton-

600 series and Horiba U-10, respectively, and are summarized in Table 1. After collection, the samples were fixed in 4% buffered formaldehyde solution with local filtered seawater. All the samples from the sampling program “iii” and the January, March, May and July samples from the sampling program “i” were visually inspected for large, macroscopic, gelatinous zooplankton (chiefly ctenophores) right after the retrieval of the nets, and those present were separated and

Table 1 Sketch of the different sampling programs performed for gelatinous zooplankton from the Cananeia-Iguape Coastal System, between January 2012 and January 2013 along with hydrographic conditions. T = temperature (°C); S = salinity; nd = no data available

Sampling program	Period	Sampling frequency	Number of stations	Nets	Mesh size (μm)	Number of samples	T	S
i	Jan 2012-Jan 2013	Every second month	5	Conical plankton net; epibenthic sledge	90, 500	107	20.0–32.6	11.3–36.2
ii	March, 12, 2012	Once	11	Cylindrical-conical plankton net	300	11	nd	nd
iii	April, 11–13, 2012	Every 2 h during daylight	7	Conical plankton net	160, 60	46	23.5–29.5	11.4–35.6

identified on board. In the other samples, observations before formalin fixation were not made and therefore ctenophores could not be properly analyzed.

Samples were analyzed under a stereomicroscope and the gelatinous organisms (cnidarians, chaetognaths, thaliaceans and appendicularians) were sorted and identified (mostly following the appropriate chapters from Boltovskoy 1981, 1999). For cnidarians and thaliaceans, whole samples were analyzed. Appendicularians and chaetognaths were counted from 1/4–1/32 aliquots encompassing at least 300 individuals of each taxa and the rest of the samples were analyzed only qualitatively for rare species. Additional opportunistic records of large (>2 cm) species were made from visual observations of jellyfishes at the surface or stranded in the margins of the estuary between April 2012 and March 2013.

In addition, information was also obtained from previous published (Vannucci 1954, 1956, 1957; Teixeira et al. 1965; Liang et al. 2003) and unpublished (Morandini 2003; Bardi 2011; Nagata et al. 2013) studies concerning the CICS gelatinous zooplankton fauna. A list with all species was compiled and is presented. Classification schemes follow the World Register of Marine Species (<http://www.marinespecies.org/index.php>; last consulted on January 30, 2017). Numbers of analyzed individuals (colonies for siphonophores) and temperature and salinity ranges in which each species was found are also presented, along with information on their seasonal occurrence. If a species was captured both in the current study and in the literature, the data presented was based on the present study.

Months were grouped into seasons; summer: January through March; autumn: April through June; winter: July through September; and spring: October through December. The similarity percentage routine (SIMPER) was used to quantify the contribution of the species to the differences between seasons and salinity ranges (Clarke and Warwick 2001). Data was transformed by log (x+1) before running the SIMPER routine.

Voucher specimens of most sampled species were deposited in the collections of the Museu de Zoologia da Universidade de São Paulo (MZUSP) or Coleção de Invertebrados Marinhos Paulo Young da Universidade Federal da Paraíba (CIPY-UFPB).

Results

Species composition

From all samples analyzed and the visual observations we found 48 species, not including actinula larvae, a few young hydromedusae that were impossible to identify and some damaged dolioids and hydromedusae (Table 2). From literature, eight additional species can be included in the CICS

gelatinous zooplankton checklist: the hydromedusa *Coryne eximia* and *Lizzia blondina*, the scyphomedusae *Aurelia* sp., *Phyllorhiza punctata* and *Stomolophus meleagris*, the cubomedusae *Tamoya haplonema*, and the chaetognaths *Ferosagitta hispida* and *Krohnita pacifica*, totaling 56 species, 49 genera, 40 families and 16 orders (Table 2). Descriptions and photographs are provided below for *Tiaricodon* sp., newly recorded from Brazilian coast, and *Cnidostoma fallax*, whose gonads had not been previously described.

Family Hydractiniidae

Cnidostoma fallax Vanhöffen, 1911 (Fig. 2)

Description: From 0.27 to 0.95 mm high, and from 0.3 to 1 mm wide. Four well developed bulbs, each with an adaxial ocellus and a single tentacle. Manubrium typically tubular (oval in one individual) and measuring half of the subumbrellar cavity in length (ranging from 1/3 up to the umbrellar margin). Medusoid buds on upper manubrium walls with no defined radial or height position. Mouth rim with four perradial clusters of stalked cnidophores. In a single medusa, smooth sac-like gonads extended along the central 2/3 of the inter-radial walls of the manubrium, below the asexual buds (Fig. 2).

Family Halimedusidae

Tiaricodon sp. (Fig. 3)

Description: globular umbrella, slightly higher than wide; mesoglea transparent, thin laterally and thick at the apex, where it represents nearly 1/3 of the total height. Stomach cross-shaped with per-radial lobes advancing on the proximal ~1/4 of the radial canals; peduncle absent or indistinct; mouth small with four small, almost indistinct lips; manubrium reaching somewhat more than half of the sub-umbrellar cavity height (3 mm high medusae; Fig. 3b) or near the bell margin (3.3 mm medusae; Fig. 3a). Gonads on per-radial walls of the manubrium extending along stomach lobes, folded in the larger medusa (Fig. 3a). Four per-radial imperfectly moniliform tentacles, each with a well-developed bulb with a small abaxial process and a large red-yellow ocellus (Fig. 3b, d). Nematocysts from tentacles composed mainly by desmonemes (8.9–11.8 × 5–7.5 μm), with smaller numbers of microbasic euryteles (12.0–14.4 × 10.0–12.0 μm).

Abundance and diversity patterns

The hydromedusae were the most diverse (34 species), representing ~60% of all gelatinous zooplankton species from the CICS. Particularly, the meroplanktonic orders Anthothecata (16 species; 28.6%) and Leptothecata (13 species; 23.2%) were the most diverse, whereas all holoplanktonic taxa (19 spp.) represent <35% of all gelatinous species (Table 2). In contrast, holoplanktonic forms were considerably more numerous, particularly the appendicularians with densities substantially higher than the other gelatinous taxa through the year (Fig. 4), representing >95% of all gelatinous sampled here. *Oikopleura*

Table 2 Taxonomic classification of gelatinous zooplankton from the Cananeia-Iguape Coastal System, São Paulo, Brazil, along with number of individuals studied (colonies for siphonophores) in plankton hauls (P) and at visual observations (V), environmental settings range (T = temperature in °C, S = salinity) and the seasons each species was sampled (Su = summer; A = autumn; W = winter; Sp = spring). Data Source: 1 = present

study; 2 = Bardi (2011); 3 = Bardi and Marques (2009); 4 = Morandini (2003); 5 = Liang et al. (2003); 6 = Tronolone et al. (2002); 7 = Teixeira et al. (1965); 8 = Vannucci (1957); 9 = Vannucci (1956); 10 = Vannucci (1954); 11 = Nogueira Júnior and Silva Nascimento (2018). * New record for São Paulo state; ** New record for Brazilian coast (after Oliveira et al. 2016)

Taxa	Number studied			Environmental settings	Season	Data source
	P	V	T			
Phylum Cnidaria						
Class Cubozoa						
Order Carybdeida						
Family Tamoyidae						
<i>Tamoya haplonema</i> (Müller, 1859)		2			Su, W	4
Order Chirodropida						
Family Chiropsalmidae						
<i>Chiropsalmus quadrumanus</i> (Müller, 1859)	0		3		A	1
Class Hydrozoa						
Actinula larvae	42		0 25.5–26.3	23.5–27.5	Su, A, Sp	1
Young unidentified medusae	12		0 22.0–27.2	17.8–24.1	Su, A, W, Sp	1
Hydromedusae spp. (damaged)	62		0 20.3–27.5	20.0–33.5	Su, A, W	1
Subclass Hydroidolina						
Order Anthoathecata						
Suborder Aplanulata						
Family Corymorphidae						
<i>Corymorpha forbesii</i> (Mayer, 1894)	17		0 20.0–27.2	24.1–35.9	Su, A, Sp	1, 2, 7
<i>Corymorpha gracilis</i> (Brooks, 1883)	6		0 20.0–25.4	17.8–33.5	A	1
Family Tubulariidae						
<i>Ectopleura dumortieri</i> (van Beneden, 1844)	53		0 22.5–26.3	18.4–31.5	Su, Au, Sp	1, 2, 8
Suborder Capitata						
Family Corynidae						
<i>Coryne eximia</i> Allman, 1859		5		10–25 (ref 2)	Su, W	2, 8
<i>Stauridiosarsia reesi</i> (Vannucci, 1956)	3		0 23.3–26.0	22.8–24.7	Su	1, 9
Family Halimedusidae						
<i>Tiaricodon</i> sp.**	7		0 26.2–30.5	20.5–35.9	Su, A	1
Family Moerisiidae						
<i>Moerisia inkermanica</i> Paltschikowa-Ostroumowa, 1925	2		0 26.4	11.3	Su	1, 2
Suborder Filifera						
Family Bougainvillidae						
<i>Bougainvilia carolinensis</i> (McCady, 1859)	9		0 22.0–29.5	13.0–24.7	Su, A	1, 2
<i>Bougainvilia muscus</i> (Allman, 1863)	112		0 23.0–28.2	17.8–28.5	Su, A, Sp	1
Family Hydractiniidae						
<i>Cnidostoma fallax</i> Vanhöffen, 1911*	252		0 20.3–32.6	13.0–33.5	Su, A, Sp	1
<i>Podocoryna loyola</i> Haddad, Bettim and Miglietta, 2014*	1039		0 20.3–32.6	13.0–27.3	Su, A, W, Sp	1
Family Oceaniidae						
<i>Turritopsis nutricula</i> McCrady, 1857	15		0 25.4–27.2	17.8–36.2	Su, A	1
Family Pandidae						
<i>Amphinema dinema</i> (Perón and Lesueur, 1810)	2		0 22.5	23.5	Su	1
Family Proboscidactylidae						
<i>Proboscidactyla ornata</i> (McCrady, 1857)	295		0 22.0–32.6	18.4–33.5	Su, A, W	1, 2
Family Rathkeidae						
<i>Lizzia blondina</i> Forbes, 1848		55		10.0–25.0	Su, W	2
<i>Podocorynoides minima</i> (Trinci, 1903)	9		0 22.5–25.8	13.0–27.3	Su, A	1, 2, 8
Order Leptothecata						
Family Blackfordiidae						
<i>Blackfordia virginica</i> Mayer, 1910	338		0 28.2–29.5	13.5–31.5	Su, A, W	1, 2, 3
Family Campanulariidae						
? <i>Clytia gracilis</i> (Sars, 1850) as <i>C. cylindrica</i>						
<i>Clytia</i> sp.1	260		0 20.0–32.6	11.3–36.2	Su, A, W, Sp	7, 8
<i>Clytia</i> sp.2	89		0 22.0–29.5	13.0–33.5	Su, A, W	1
<i>Obelia</i> spp.	810		0 20.0–32.6	13.0–36.2	Su, A, W, Sp	1, 2
Family Cirrhovenidae						
<i>Cirrhovenia tetraneura</i> Kramp, 1959	4		0 20.4–25.8	24.1–31.5	Su, A	1
Family Eirenidae						
<i>Eirene</i> sp.*	10		0 22.5–27.2	21.8–24.7	Su, A	1
<i>Eutima mira</i> McCrady, 1859*	6		0 23.4–26.0	14.5–31.6	A	1
<i>Helgicirrha</i> sp.*	17		0 22.5–32.6	13.5–27.5	A	1

Table 2 (continued)

Taxa	Number studied		Environmental settings		Season	Data source
	P	V	T	S		
Family Laodiceidae						
<i>Laodicea minuscula</i> Vannucci, 1957	2	0	22.5–27.2	21.8–23.0	Su	1, 8
Family Lovenellidae						
<i>Eucheilota duodecimalis</i> Agassiz, 1862	68	0	23.0–28.2	17.8–31.5	Su, A, Sp	1, 2
<i>Eucheilota maculata</i> Hartlaub, 1894	663	0	20.0–28.2	11.3–33.5	Su, A, Sp	1
<i>Eucheilota paradoxica</i> Mayer, 1900	19	0	24.0–28.2	22.8–29.2	Su, A, Sp	1, 2
Family Malagazzidiidae						
<i>Malagazzia carolinae</i> (Mayer, 1900)	16	0	22.5–26.2	21.2–29.5	Su, A, Sp	1, 11
Order Siphonophorae						
Suborder Calycophora						
Family Diphyidae						
<i>Muggiae kochii</i> (Will, 1844)	158	0	20.0–32.6	27.3–36.2	Su, A	1
Suborder Physonectae						
Family Agalmatidae						
<i>Nanomia bijuga</i> (Delle Chiaje, 1844)	72	0	21.0–29.5	20.8–31.5	A, Sp	1
Subclass Trachylinae						
Order Limnomedusae						
Family Olindiidae						
<i>Olindias sambaquiensis</i> Müller, 1861	2	0	21.0	34.9	Su	1
Order Narcomedusae						
Family Cuninidae						
<i>Cunina octonaria</i> McCrady, 1859	4	0	22.4–26.4	19.4–28.5	Su, A	1, 2
Family Solmarisidae						
<i>Solmaris</i> sp.	4	0	23.4–26.3	24.1–36.2	Su	1
Order Trachymedusae						
Family Geryoniidae						
<i>Liriope tetraphylla</i> (Chamysso and Eyesenhardt, 1821)	2202	0	20.0–32.6	11.3–36.2	Su, A, W, Sp	1, 2, 7, 8
Family Rhopalonematidae						
<i>Aglaura hemistoma</i> Périon and Lesueur, 1810	1	0	27.2	33.5	A	1
Class Scyphozoa						
Subclass Discomedusae						
Order Rhizostomea						
Family Lychnorhizidae						
<i>Lychnorhiza lucerna</i> Haeckel, 1880	2 (ephyrae)	28	22.0–25.8	24.2–35.9	Su, A, W, Sp (ephyrae: Su)	1, 4
Family Mastigiidae						
<i>Phyllorhiza punctata</i> Lendenfeld, 1884	222 (ref 4), 28 (ref 6)		20–24 (ref 6)		Su, A	4, 6
Family Stomolophidae						
<i>Stomolophus meleagris</i> Agassiz, 1862	1 (ref 4), and in large quantities (ref 10)				Su	4, 10
Order Semaeostomea						
Family Pelagiidae						
<i>Chrysaora lactea</i> Eschscholtz, 1829	9 ephyrae; 1 medusa	42	23.0–26.4	23.4–36.0	Su, A, W, Sp (ephyrae: Su, A, W)	1, 4, 10
Family Ulmaridae						
<i>Aurelia</i> sp.	7				A	4
Phylum Ctenophora						
Class Nuda						
Order Beroida						
Family Beroidae						
<i>Beroe ovata</i> Bruguière, 1789	39	19	20.0–29.5	11.3–36.0	Su, A, W, Sp	1
Class Tentaculata						
Order Lobata						
Family Bolinopsidae						
<i>Mnemiopsis leidyi</i> Agassiz, 1865	27	42	20.0–32.6	11.3–36.2	Su, A, W, Sp	1
Phylum Chaetognatha						
Class Sagittoidea						
Order Aphragmophora						
Family Krohnittidae						
<i>Krohnitta pacifica</i> (Aida, 1897)	sporadic and in very few numbers					5
Family Sagittidae						

Table 2 (continued)

Taxa	Number studied		Environmental settings		Season	Data source
	P	V	T	S		
<i>Ferosagitta hispida</i> (Conant, 1895)			sporadic and in very few numbers			5
<i>Flaccisagitta enflata</i> (Grassi, 1881)	380	0	21.0–32.6	27.3–36.2	Su, A, W, Sp	1, 7
<i>Parasagitta friderici</i> (Ritter-Záhny, 1911)	5327	0	20.0–32.6	11.3–36.2	Su, A, W, Sp	1, 6, 7
<i>Parasagitta tenuis</i> (Conant, 1896)	888	0	20.0–32.6	24.0–36.2	Su, A, W, Sp	1
Phylum Chordata						
Subphylum Tunicata						
Class Appendicularia						
Order Copelata						
Family Fritillariidae						
<i>Appendicularia sicula</i> Fol, 1874	3	0	25.8	24.9	Sp	1
Family Oikopleuridae						
<i>Oikopleura dioica</i> Fol, 1872	9216	0	20.0–32.6	13.0–36.2	Su, A, W, Sp	1, 7
<i>Oikopleura longicauda</i> (Vogt, 1854)	75	0	25.4–25.8	24.7–24.9	Sp	1, 7
Class Thaliacea						
Order Doliodida						
Suborder Doliolidina						
Family Doliolidae						
<i>Dolioletta gegenbauri</i> (Uljanin, 1884)	3	0	23.4–29.5	33.5–36.2	Su, A	1
<i>Doliolum nationalis</i> Borgert, 1893	47	0	23.3–29.5	27.5–36.2	Su, A	1
Doliolida spp. (damaged)	3	0	26.4–29.5	29.5–36.2	Su	1
Order Salpida						
Family Salpidae						
<i>Thalia democratica</i> (Forskål, 1775)	8254	0	20.0–29.5	20.8–36.2	Su, A, Sp	1

dioica was the most numerous species overall, representing >95% of the appendicularians, with *Parasagitta friderici* dominating among chaetognaths and mostly *Liriope tetraphylla*, followed by *Podocoryna loyola*, *Obelia* spp. and *Eucheilota maculata* dominating among cnidarians (Table 2). The salp *Thalia democratica* was quite numerous on some occasions, however it was found in only ~19% of the samples.

Densities tended to be higher during spring for all higher taxa, except for chaetognaths whose densities were smaller during winter and remained relatively similar in the other seasons (Fig. 4a–d). Due to its considerably higher abundances, *O. dioica* was the species mostly contributing to the similarity between all seasons according to the SIMPER analysis, followed by *P. friderici* (Table 3). Other species such as *L. tetraphylla*, *P. loyola*, *Obelia* spp., *Bougainvillia* spp. and *T. democratica* had relatively high contributions in at least one of the seasons (Table 3).

Higher number of species was found in summer and autumn, when 46 and 44 species were recorded respectively (Fig. 5). In the other seasons, the number of species was considerably lower, reaching down to 18 in winter (Fig. 5). Most species observed in summer and autumn were meroplanktonic medusae (Fig. 5), mostly restricted to one or two seasons (Table 2). Conversely, the holoplanktonic forms represented most of the gelatinous diversity during winter and spring (Fig. 5), and their species richness remained relatively constant throughout the year given that most of these species occurred in all four seasons (Table 2).

For all gelatinous higher taxa, densities were smaller in lower salinities particularly those <20, peaking in salinities >30 for cnidarians, >25 for thaliaceans, >20 for chaetognaths and between 20 and 25 for appendicularians (Fig. 6a–d). According to the SIMPER, the high abundant and common *O. dioica* and *P. friderici* were the most important species through the salinity-range (Table 3). Other important species include *L. tetraphylla* mostly in salinities >20, *P. loyola* and *C. fallax* mostly in salinities <25, *Obelia* spp., *Flaccisagitta enflata* and *T. democratica* in salinities >30 (Table 3).

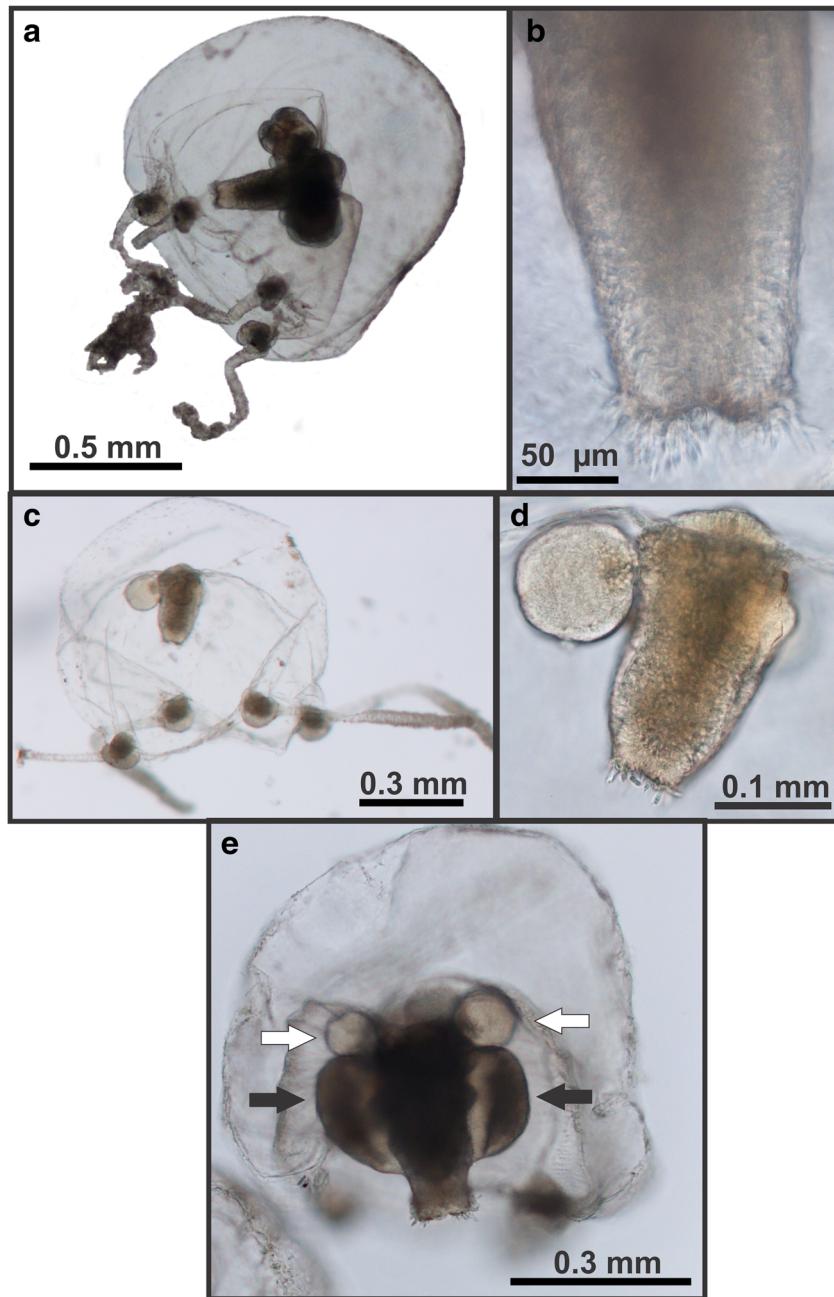
Waters with salinity between 20 and 29.9 harbored most of the species: at salinities between 20 and 24.9 most species have been found (40 spp.), decreasing considerably at salinities <20 and with only 19 species recorded at salinities <15 (Fig. 7). Overall, the number of meroplanktonic hydromedusae was higher throughout most of the salinity range sampled, reflecting its general higher species richness. In any case, their species richness tended to decrease at salinity ≥ 25 , whereas the diversity of holoplanktonic forms (both cnidarians and non-cnidarians) tended to increase at higher salinities (Fig. 7).

Discussion

Taxonomic and distributional remarks

Among the 48 species studied here, 27 (56%) are new records for the CICS, six species (12.5%) are new records for the state

Fig. 2 *Cnidostoma fallax* Vanhöfen, 1911: **a** Lateral view of medusae with medusoid buds, and **b** detail of its mouth with stalked cnidophores. **c** Lateral view of a medusa with early-developing buds, and **d** detail of its manubrium buds and mouth cnidophores. **e** Lateral view of a medusa (MZUSP 1756) with asexual buds (open arrows) and gonads (closed arrows)

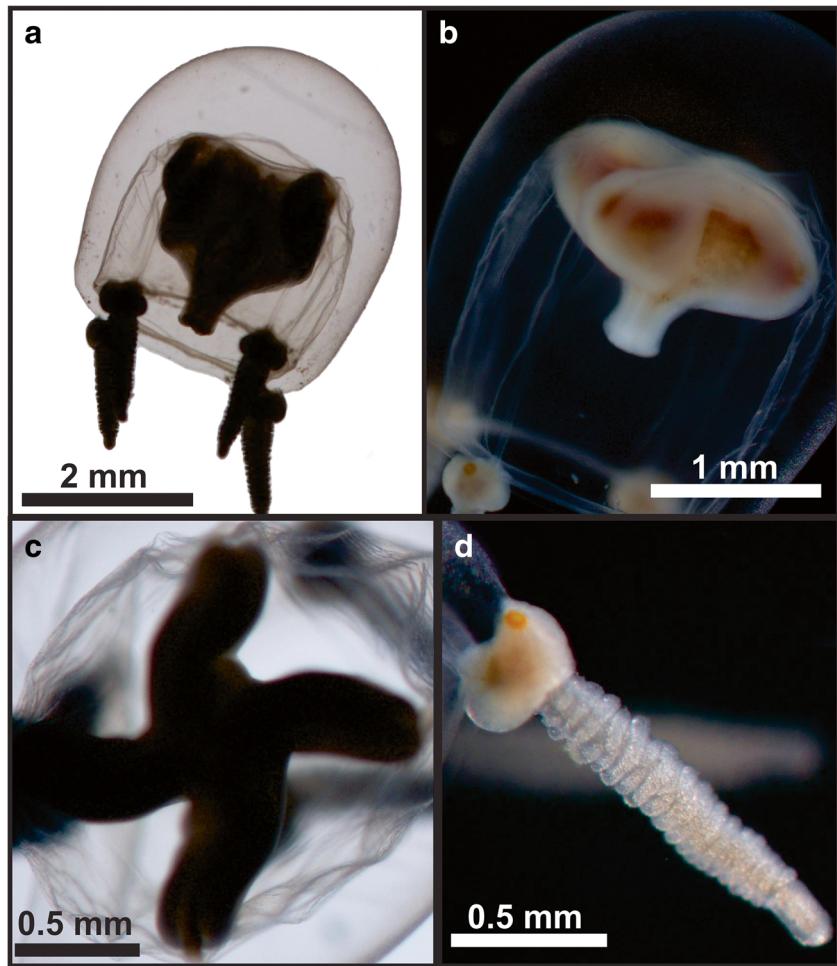


of São Paulo, and *Tiaricodon* sp. is a new record for the Brazilian coast. Most of these new records found here fill gaps on their known distribution, but their presence is not surprising since they have been previously recorded both from northwards and/or southwards Brazilian estuaries (Oliveira et al. 2016). The exception is *Tiaricodon* sp. This record extends >3000 km northwards the previously known distribution of the genus in the South Atlantic (~45–55° S; Rodriguez 2012). *Tiaricodon* is a typical cold-water genus, with records from Patagonia, Peru, Chile, Weddell Sea and New Zealand (Vannucci and Tundisi 1962; Schuchert 1996; Rodriguez 2012). Thus, its presence in warm-waters with temperatures

26.2–28.2 °C found here is intriguing. This species may not have established populations in the area but was rather transported northwards by subantarctic waters derived from the Malvinas Current, similarly to observed for cold-water foraminiferans and ostracods occurring in Sepetiba Bay (23° S) further north (Stevenson et al. 1998).

A single species of *Tiaricodon* has been described (Schuchert 2015), but the specimens studied here do not exactly match the descriptions of *Tiaricodon coeruleus*. The medusae analyzed here were considerably smaller, <3.5 mm high, in comparison with the up to 24 mm recorded in the literature for *T. coeruleus* (Kramp 1961; Schuchert 1996;

Fig. 3 *Tiaricodon* sp.: Lateral view of the medusa MZUSP 1759 (a) and MZUSP 1760 (b); aboral view of the manubrium (c) and detail of the tentacular bulb with tentacle, abaxial process and ocellus (d)



Rodriguez 2012; but Vannucci and Tundisi 1962 reported medusae between 0.5 and 10 mm), and yet all the seven specimens studied here bore gonads, apparently well-developed. Also, the manubrium of the medusae sampled here is

considerably shorter than in *T. coeruleus* (Schuchert 1996: Fig. 54; Rodriguez 2012: 67). The present specimens do possess an abaxial process in the tentacle bulbs (Fig. 2d), but in *T. coeruleus* the abaxial process is considerably more

Fig. 4 Average seasonal abundance (ind. m^{-3}) variation of the main gelatinous zooplankton higher taxa in the Cananeia-Iguape Coastal System. Error bars show the standard deviation

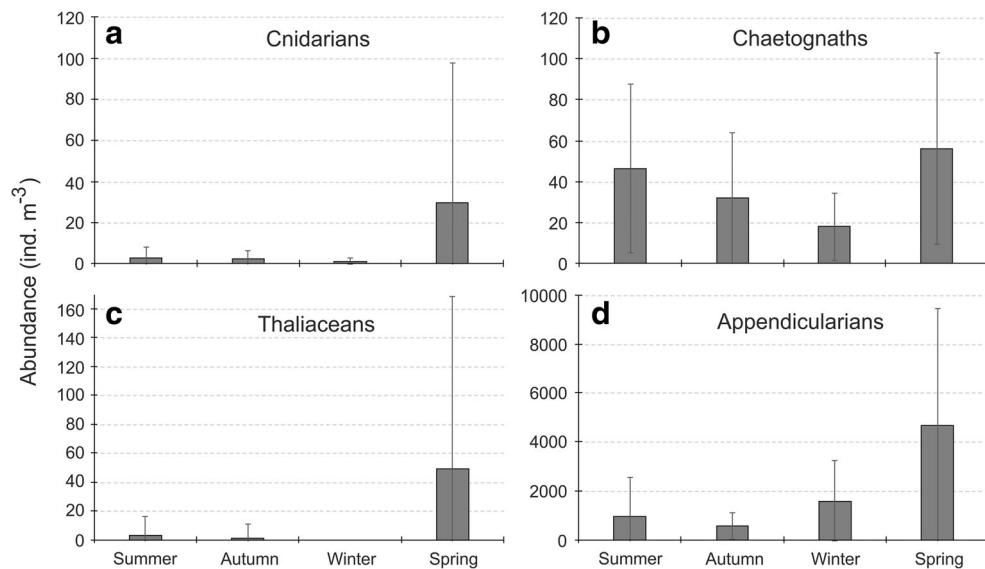


Table 3 Results of the SIMPER analysis comparing different seasons and salinity range. In parenthesis is shown the average similarity (%) of each season or salinity range and the contribution (%) of the main species

Taxa/contribution	Seasons				Salinity				
	Summer (57.8)	Autumn (90.2)	Winter (75.2)	Spring (71.3)	< 15 (80.5)	15–20 (56.7)	20–25 (64.6)	25–30 (88.3)	> 30 (71.6)
<i>Oikopleura dioica</i>	34.4	45.8	34.3	40.4	39.5	30.1	37.2	39.9	24.3
<i>Parasagitta friderici</i>	16.1	8.4	21.5	8.6	17.4	14.1	11.3	12.2	13.9
<i>Liriope tetraphylla</i>	6.7	7.9	11.9	11.5	4.2	11.9	13.2	12.9	13.9
<i>Podocoryna loyola</i>	13.6	6.8	3.9	10.3	14.5	16.5	11.4	5.6	
<i>Obelia</i> spp.		9.3	13.7	3.4	11.6	9.7	7.9	8.1	9.7
<i>Cnidostoma fallax</i>	7.7	1.1		3.7	4.2	6.9	6.7	3.9	3.2
<i>Bougainvillia muscus</i>	8.5	4.5		2.1		1.5	2.2	1.3	
<i>Bougainvillia carolinensis</i>	8.5	1.3			1.5	0.4	0.7	2.1	1.9
<i>Parasagitta tenuis</i>	1.8	3.5	8.9	2.5	3.9	5.6	2.1	3.5	
<i>Flaccisagitta enflata</i>	1.0			1.3				2.6	7.5
<i>Clytia</i> spp.		7.5	3.4	3.5	3.2	3.3	2.2	2.2	2.3
<i>Thalia democratica</i>	1.0			7.9			3.5	4.7	7.4

pronounced (Schuchert 1996: Fig. 4e). The medusae reported here may represent an undescribed species, and a detailed morphological, life cycle and/or molecular analysis should be conducted in order to clarify their specific identity.

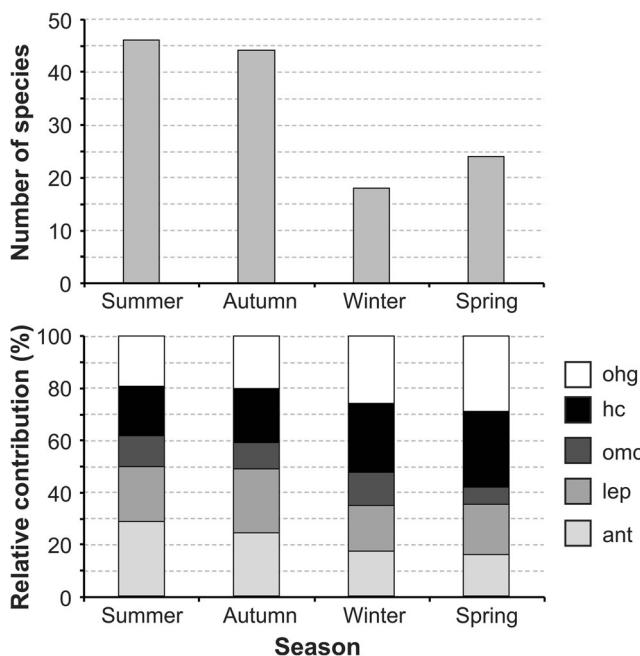
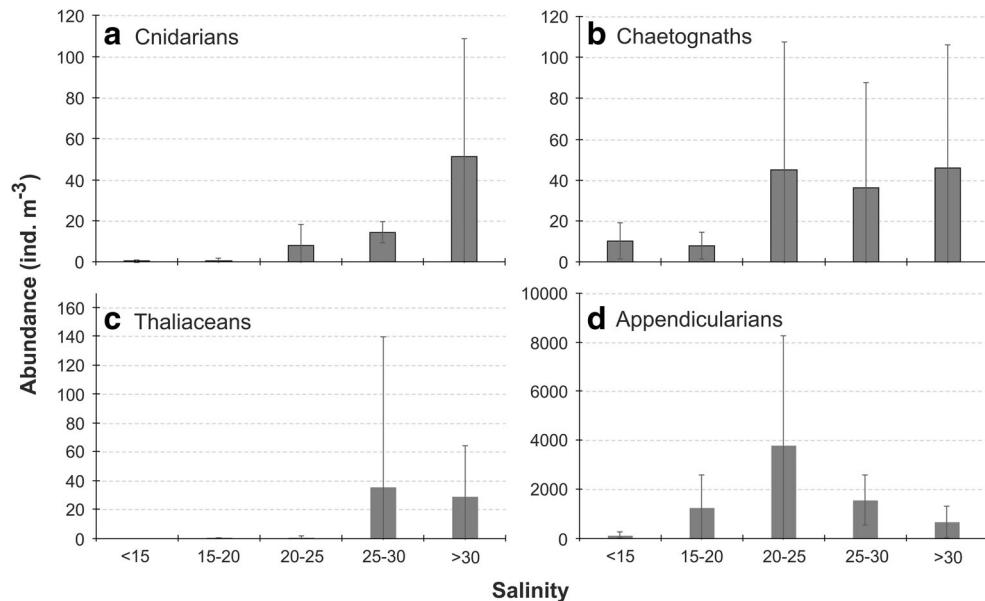


Fig. 5 Seasonal distribution of total number of gelatinous zooplankton species (upper panel) and separated by main taxa (lower panel). Data from all nets of the sampling program i, in addition to literature records (see Table 2). ant = Anthoathecata (meroplanktonic); lep = Leptothecata (meroplanktonic); omc = other meroplanktonic cnidarians (including Cubomedusae, Limnomedusae and Scyphomedusae); hc = holoplanktonic cnidarians (including Siphonophora, Narcomedusae and Trachymedusae); ohg = other holoplanktonic gelatinous (including Ctenophora, Chaetognatha and Tunicata)

Many hydromedusae change considerably through ontogeny, and the gonadal position and morphology is an important taxonomic character (e.g. Kramp 1961; Bouillon et al. 2006). Thus, the finding of a mature individual contributes to a better morphological characterization of *C. fallax*. This peculiar medusa has been assigned to different families (Kramp 1961; Bouillon 1999; Bouillon et al. 2006). Its current placement in the Hydractiniidae is uncertain since it does not have oral tentacles (Fig. 2), a main character of hydractiniid medusae (Kramp 1961; Bouillon 1999; Bouillon et al. 2006). The gonads in the inter-radial walls of the manubrium is in accordance to the observed in other species of the family Hydractiniidae, although it also can be found in many other anthomedusae families, including the Oceaniidae and Cytaeididae, i.e. other families this species has been assigned to (Kramp 1961; Bouillon et al. 2006).

Clytia gracilis (as *C. cylindrica*; Vannucci 1957; Teixeira et al. 1965) was included in Table 2, but disregarded in the total number of species since it represents a species complex and specific identifications of *Clytia* based on medusa morphology are quite difficult (Lindner and Migotto 2002; Lindner et al. 2011) and have often proved to be of low accuracy. Moreover, is probable that the *C. gracilis*-like medusa reported from the CICS (Vannucci 1957; Teixeira et al. 1965) is already represented by the morphotypes we have identified. Based on characters such as general shape and position of the gonads, number of tentacles and statocysts and shape of tentacular bulbs, two forms could be distinguished in the present study. The most common and abundant of them, called here *Clytia* sp.1, closely resemble *C. lomae* (Torrey, 1909) (Bouillon 1999: 430, Fig. 3.125; Rodriguez 2012: 115). In the southwestern Atlantic this species has been recorded

Fig. 6 Average abundance (ind. m^{-3}) of the main gelatinous zooplankton higher taxa in different salinity ranges in the Cananeia-Iguape Coastal System. Error bars show the standard deviation



in Argentina (Rodriguez 2012; Dutto et al. 2017) and NE Brazil (Gusmão et al. 2015). Considering the taxonomic problems regarding morphological identification of *Clytia* medusae exposed above, and that the polyps of *C. lomae* have not been described so far, we preferred to not attribute a formal specific name for these individuals since they probably are the medusa stage of one of the many *Clytia* hydroid-species recorded inside (Bardi 2011) and/or nearby the CICS (Oliveira et al. 2016). The medusae here called *Clytia* sp.2 is quite similar to *Clytia linearis*, with round to oval gonads located

on the mid portion of the radial canals (Lindner and Migotto 2002: Fig. 3b–e), and whose polyps have been found inside the CICS (Bardi 2011).

The record of *Hydractinia carica* Bergh, 1887 medusae from CICS (Bardi 2011) is not accurate since gonophores of *H. carica* are of the cryptomedusoid type, which are not released as free-medusae (Schuchert 2008). Bardi (2011) did not provide descriptions or figures of the studied material nor designated voucher specimens, not allowing critical re-analyses. Regardless, we suspect that the medusae she found were *Dysmorphosa minuta* Mayer 1900, as also suggested earlier (Oliveira et al. 2016). This species has traditionally been included in the genus *Hydractinia* or *Podocoryna* (Kramp 1961; Schuchert 1996, 2008; Bouillon 1999), but is currently considered a junior synonym of *Lizzia blondina* (Schuchert 2007, 2008, 2015).

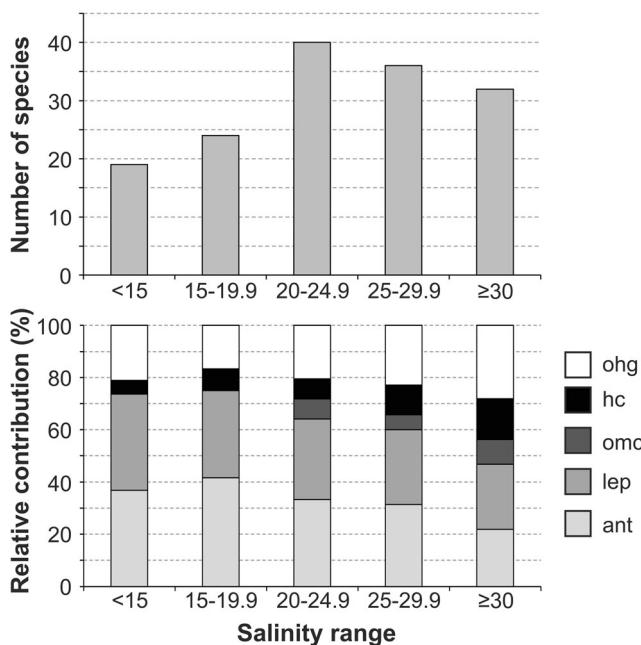


Fig. 7 Total number of gelatinous zooplankton species (upper panel) and the relative contribution (%) (lower panel) of the main taxa in different salinity ranges. Legends as Fig. 5

Abundance, diversity patterns and ecological observations

The gelatinous zooplankton fauna from the CICS with a total of 56 recorded species can be considered diverse for a relatively small estuary. Given the high sampling effort, including different seasons, gears and spatial-temporal coverage, and the high number of specimens studied, we consider that the present study, in addition to the few previous records, is a thorough representation of the CICS gelatinous fauna. Yet the total number of species probably is still slightly underestimated considering the inability to accurately distinguish between species of some genus (e.g. *Clytia* and *Obelia*, see above) and to identify younger and/or larval stages (e.g. actinula larvae), and the possibility of finding additional species in further studies.

The high diversity found here is mostly associated to the meroplanktonic life cycle strategy, particularly represented by the hydrozoans from the orders Anthoathecata and Leptothecata. In accordance, these commonly are the most species-rich gelatinous zooplankton taxa from tropical, subtropical and temperate estuaries worldwide (Vannucci et al. 1970; Calder 1971; Santhakumari et al. 1997; Guo et al. 2012; Dutto et al. 2017). Nevertheless, the actual number of meroplanktonic hydromedusae species from the CICS (30 spp.) is high and similar to the few other well-evaluated subtropical Brazilian estuaries (~25–27° S), which harbor 30–35 species (Nogueira Júnior et al. 2018; Silva Nascimento et al. *in press*). This is higher than most other tropical, subtropical and temperate brackish-water ecosystems worldwide, which typically harbor 8–22 species (Vannucci et al. 1970; Zamponi and Genzano 1994; Segura-Puertas and Damas-Romero 1997; Santhakumari et al. 1999; Du et al. 2011; Pestorcić et al. 2012; Dutto et al. 2017). Yet, some other warm-water estuaries elsewhere also harbor high meroplanktonic hydromedusae species richness, such as Bombay Harbor (19° N) with 30 species (Santhakumari et al. 1997), and Juilong River (25° N) with 38 species (Xu and Huang 1983).

The low diversity of holoplanktonic gelatinous species is in agreement with the commonly found in estuarine waters worldwide (Brunetti et al. 1990; Segura-Puertas and Damas-Romero 1997; Du et al. 2011; Liu et al. 2013). Most holoplanktonic gelatinous higher taxa are typically oceanic and not particularly diversified, with commonly only a few species inhabiting brackish-waters worldwide (Boltovskoy 1981, 1999; Bone 1998; Spinelli et al. 2009; Du et al. 2011). This may be particularly true for the South Brazilian Bight estuaries such as the CICS, since the wide (>150 km) continental shelf may difficult the colonization of estuarine ecosystems by most of these oceanic taxa. Yet, these few holoplanktonic species largely dominated (>97%) gelatinous abundances, particularly *O. dioica*, which was the most important species on all seasons and across the whole salinity range sampled (Table 3). Appendicularians commonly have high production rates in warm waters (Miyashita and Lopes 2011) such as the CICS, with very high individual and populational growth rates. Although appendicularians are more typical and diverse from shelf and oceanic waters (e.g. Esnal 1999), *O. dioica* is a typical coastal/estuarine species, commonly being the dominant appendicularian on most southwestern Atlantic estuaries (Spinelli et al. 2009; Nogueira Júnior et al. 2018) and elsewhere through its distribution (e.g. Brunetti et al. 1990).

Other abundant holoplanktonic gelatinous species found here, such as the chaetognaths *P. friderici* and *P. tenuis*, also are quite common and abundant in most coastal and estuarine ecosystems from the southwestern Atlantic (Montú and Cordeiro 1988; Liang et al. 2003), and among the few typical coastal and estuarine chaetognaths worldwide (McLellan-

1980; Pierrot-Bults and Nair 1991). *Thalia democratica* reached high abundances, however the low percentage of positive samples suggests it does not have permanent populations within the CICS, being probably transported from shelf waters where there are known abundant permanent populations (Tavares 1967; Nogueira Júnior et al. 2015a). Salps have high capacity of asexual reproduction, rapidly reaching high abundances (Esnal and Daponte 1999). This seems to be the case here, in which 86% of the individuals sampled were aggregate zooids (asexually formed by the solitary zooids).

The dominant gelatinous meroplankton were *Obelia* spp., *Podocoryna loyola* and *Eucheilota maculata* (Table 2). The former typically is common and abundant in many coastal and brackish-water ecosystems from Brazil (Nagata et al. 2014a; Nogueira Júnior et al. 2015b, 2018) and elsewhere (e.g. Vannucci et al. 1970; Pestorcić et al. 2012; Rodriguez 2012). *Podocoryna loyola* has been recently described and its known distribution is restricted to few subtropical Brazilian estuaries, where both polyps and medusae are abundantly found (Haddad et al. 2014; Bettim and Haddad 2017; Nogueira Júnior et al. 2018), including the CICS. There is no previous record of high *E. maculata* abundance from the southwestern Atlantic, with all reports based on a few individuals (e.g. Nagata et al. 2014b), but *E. maculata* and the closely related *Eucheilota ventricularis* may be abundant in temperate brackish-water ecosystems, such as the Schelde (Vansteenberghe et al. 2015) and La Plata (Rodriguez 2012) estuaries, respectively.

There was a marked seasonal variation of the gelatinous zooplankton both in abundance and number of species, with higher abundance during spring and higher number of species occurring during summer and autumn. This spring abundance peak found here is similar to the reported for total zooplankton biomass from the CICS and also for different crustacean taxa (Ara 2002, 2004; Miyashita and Calliari 2016), although chaetognaths may also peak during summer/autumn (Liang et al. 2003), as observed here (Fig. 4). Indeed, hydromedusae, chaetognaths and appendicularians tend to peak most commonly during spring and/or early summer in the southwestern Atlantic subtropical estuaries (Nogueira Júnior et al. 2018), such as in the CICS. This have commonly been attributed to the termohaline conditions of the spring period, with temperatures already increasing after the winter along with the salinity not so low as in summer when rainfall is higher (Miyashita and Calliari 2016).

Most holoplanktonic species occurred through the year, with a few exceptions as the hydromedusae *Aglaura hemistoma* and *Solmaris* sp., the appendicularians *Appendicularia sicula* and *Oikopleura longicauda* and both doliolids (Table 2). These species were rarely sampled and probably were advected from the adjacent shelf where they are known to commonly occur (Tavares 1967; Miyashita and Lopes 2011; Nagata et al. 2014a; Nogueira Júnior et al. 2014),

probably not sustaining permanent populations inside the estuary. Contrastingly, the presence of meroplanktonic species is largely dependent on the reproductive activity of their polyps and thus they were temporally restricted, generally to summer and/or autumn, increasing considerably the number of species recorded at these seasons. Among the many factors that may trigger medusae production and release by the polyps, temperature, food availability and salinity commonly are the most important (e.g. Boero et al. 2008). During the present study, water temperature ranged from 20.0 °C in winter to 32.6 °C in late summer (Miyashita and Calliari 2016; their Table 1). This temperature increase, peaking in late summer/early autumn, often accompanied by an increase in zooplankton abundance (Liang et al. 2003; Ara 2004), may have influenced the higher species-richness during these seasons. Within meroplanktonic taxa, only *Obelia* spp., *Clytia* sp.1, *P. loyola*, *Chrysaora lactea* and *Lychnorhiza lucerna* occurred in the four seasons (Table 2). The two former taxa may encompass more than a single species, which may have distinct seasonal patterns. *Podocoryna loyola* polyps are known to produce gonozooids year-round (Bettim and Haddad 2017), although medusae peak during summer (Nogueira Júnior et al. 2015b), while the two-latter species are large sized (>10 cm) with medusae of all sizes commonly occurring through most of the year (Morandini 2003; Nogueira Júnior and Haddad 2017).

Differential salinity tolerance has a paramount role in defining the occupation of a given taxa within estuaries (Potter et al. 2010; Whitfield and Elliot 2011; Miyashita and Calliari 2016). Again, the different life cycle strategies resulted in different tendencies of occupation of the estuary, likewise the observed by Vannucci et al. (1970). Most of the meroplanktonic species sampled here commonly can withstand a wide salinity range, but some such as *Bougainvillia carolinensis*, *Blackfordia virginica*, *Coryne eximia*, *Eirene* sp., *Helgicirrha* sp., *Laodicea minuscula*, *Lizzia blondina*, *Malagazzia carolinae*, *Moerisia inkermanica*, *Podocorynoides minima* and *Staurodiosarsia reesi* are more restricted to brackish-water environments (Moreira 1978; Nogueira Júnior et al. 2018), occurring mostly in salinities <25 (Table 2). Conversely, holoplanktonic gelatinous taxa are mostly oceanic (Boltovskoy 1981, 1999) and only few species were found in low salinity (<15) waters: the hydromedusae *L. tetraphylla*, both ctenophores, the chaetognath *P. friderici*, and the appendicularian *O. dioica* (Table 2). All these holoplanktonic species are typical from coastal and estuarine waters (Vannucci 1957, 1963; Liang et al. 2003; Miyashita et al. 2012; Oliveira et al. 2016), being among the few species of these taxa that may thrive at low salinities worldwide (Moreira 1978; McLelland 1980; Pierrot-Bults and Nair 1991; Spinelli et al. 2009). At salinities >25, holoplanktonic species typical of shelf waters (e.g., Vannucci 1957, Tavares 1967; Miyashita and Lopes 2011) that apparently do not maintain permanent population inside

the estuary start to appear, such as the hydromedusae *Aglaura hemistoma*, the siphonophore *Muggiaeae kochii*, and the appendicularian *Oikopleura longicauda*, which are commonly abundant in the adjacent shelf waters (Vannucci 1957, 1963; Miyashita and Lopes 2011; Nagata et al. 2014a; Nogueira Júnior and Brandini 2018).

Conclusions

The gelatinous zooplankton fauna from the CICS was found to be composed of 56 species, which probably is a slight underestimation due to both taxonomic constraints and the possibility of finding additional species. This assemblage is a typical warm water estuarine fauna with high diversity. The specific composition and number of species is analogous to the few other Brazilian estuaries comprehensively evaluated. We emphasize the high diversity of estuarine gelatinous zooplankton from warm-waters and underscore the need of comprehensive field surveys in tropical/subtropical estuaries, which potentially harbor high diversity, but historically are understudied worldwide.

The high diversity found here is mostly represented by meroplanktonic life cycle, particularly the meroplanktonic hydromedusae from the orders Anthoathecata and Leptothecata. Differently, abundances were highly dominated by a few holoplanktonic species, particularly the appendicularian *Oikopleura dioica*. The occupation of the estuary also differed contrastingly mostly according to the life cycle strategy. Meroplanktonic species tended to be more temporally restricted, mostly occurring in seasonal peaks particularly during summer and/or autumn, while holoplanktonic species mostly occurred throughout the year. Most of the euryhaline or typical brackish-water species are meroplanktonic, tolerating high salinity variations and more diluted waters, and thus inhabiting through the estuary, while the oceanic nature of the holoplanktonic gelatinous taxa restrain most of the species from less saline situations of the estuary. Thus, the life cycle strategy is an important driver of the temporal and spatial occupation of gelatinous estuarine assemblages.

Acknowledgements We thank the staff of the station Dr. João de Paiva Carvalho (IO-USP), the undergrad students of the Class 10 of the Oceanography program (São Paulo University) and Márcio Ohkawara for their invaluable help during samplings. Sílvia A. Gonzales kindly provided the samples from March 12, 2012. Drs. Monica Petti and Maria L. Flaquer and all the staff of the Biological Collection Prof. E.F. Nonato for allowing us to use their facilities.

Funding MNJ (grant 2011/09880-8), BSPC and FPB (project 2011/21290-1) were supported by the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), and LKM by the National Council for Scientific and Technological Development (CNPq, grants 142203/2010-6, 142050/2012-1 and 245466/2012-6).

Compliance with ethical standards

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

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements, if applicable.

References

- Alvares CA, Stape JL, Sentelhas PC, de Moraes G, Leonardo J, Sparovek G (2013) Köppen's climate classification map for Brazil. *Meteorol Z* 22:711–728
- Ara K (2002) Temporal variability and production of *Temora turbinata* (Copepoda: Calanoida) in the Cananéia Lagoon estuarine system, São Paulo, Brazil. *Sci Mar* 66:399–406
- Ara K (2004) Temporal variability and production of the planktonic copepod community in the Cananéia Lagoon Estuarine System, São Paulo, Brazil. *Zool Stud* 43:179–186
- Barcellini VC, Motta FS, Martins AM, Moro PS (2013) Recreational anglers and fishing guides from an estuarine protected area in southeastern Brazil: socioeconomic characteristics and views on fisheries management. *Ocean Coast Manag* 76:23–29
- Bardi J (2011) Comunidades de hidrozoários (Cnidaria) estuarinos do sudeste e sul do Brasil. PhD Thesis, São Paulo University
- 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
- Barrera-Alba JJ, Gianesella SMF, Saldanha-Correa FMP, Moser GAO (2007) Influence of an artificial channel in a well-preserved subtropical estuary. *J Coast Res* 50:1137–1141
- Bettim AL, Haddad MA (2017) Seasonal recruitment of the hydroid *Podocoryna loyola* (Hydractiniidae) in the Paranaguá Bay, South of Brazil. *Mar Biol Res* 13:560–572
- 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 (1981) Atlas del zooplancton del Atlántico Sudoccidental y métodos de trabajo con el zooplancton marino. INIDEP, Mar del Plata
- Boltovskoy D (1999) South Atlantic zooplankton. Backhuys Publishers, Leiden
- Bone Q (1998) The biology of pelagic tunicates. Oxford University Press, New York
- Bouillon J (1999) Hydromedusae. In: Boltovskoy D (ed) South Atlantic zooplankton. Backhuys Publishers, Leiden, pp 424–512
- Bouillon J, Gravili C, Gili JM, Boero F (2006) An introduction to hydrozoa. *Mem M Natl Hist Nat* 194:1–591
- Brunetti R, Baiocchi L, Bressan M (1990) Seasonal distribution of *Oikopleura* (Larvacea) in the lagoon of Venice. *Boll Zool* 57:89–94
- Calder DR (1971) Hydroids and hydromedusae of Southern Chesapeake Bay. Virginia Institute of Marine Science, Special Papers in Marine Science 1:1–125
- Chiba de Castro WA, Assunção AWA, Takao LK, Rocha GS, Janke H, Valsko J, Ebert LA, Figueroa ME, Cunha S (2012) Caracterização da produção pesqueira ao longo do tempo, no município de Cananéia, litoral sul de São Paulo. *Bol Inst Pesca* 38:265–273
- Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation, 2nd edn. PRIMER E, Plymouth
- Day JW Jr, Crump BC, Kemp WM, Yañez-Arancibia A (2013) Estuarine ecology. John Wiley and Sons, Hoboken
- 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)
- Dutto MS, Genzano GN, Schiarioti A, Lecanda J, Hoffmeyer MS, Pratolongo PD (2017) Medusae and ctenophores from the Bahía Blanca Estuary and neighboring inner shelf (Southwest Atlantic Ocean, Argentina). *Mar Biodivers Rec* 10:14
- Esnal GB (1999) Appendicularia. In: Boltovskoy D (ed) South Atlantic zooplankton. Backhuys Publishers, Leiden, pp 1375–1399
- Esnal GB, Daponte MC (1999) Salpida. In: Boltovskoy D (ed) South Atlantic zooplankton. Backhuys Publishers, Leiden, pp 1423–1444
- Filla GF, Oliveira CIB, Gonçalves JM, Monteiro-Filho ELA (2012) The economic evaluation of estuarine dolphin (*Sotalia guianensis*) watching tourism in the Cananéia region, South-Eastern Brazil. *Int J Green Econ* 6:95–116
- Gravili C, Bevilacqua S, Terlizzi A, Boero F (2015) Missing species among Mediterranean non-Siphonophoran Hydrozoa. *Biodivers Conserv* 24:1329–1357
- Guo DH, Lo G, He J (2012) Ecological studies on the medusae in the mid-eastern Pearl River estuary during the springs of 2007–2011. *Oceanologia et Limnologia Sinica* 43:584–588 (in Chinese with English abstract)
- Gusmão LM, Diaz XFG, Melo M, Schwamborn R, Neumann-Leitão S (2015) Jellyfish diversity and distribution patterns in the tropical southwestern Atlantic. *Mar Ecol* 36:93–103
- 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
- Kramp PL (1961) Synopsis of the Medusae of the World. *J Mar Biol Assoc UK* 40:1–469
- Liang TH, Ara K, Miranda LB, Bérgamo AL, Bernardes M (2003) On the variability of the chaetognath *Sagitta friderici* Ritter-Záhony at Cananéia Lagoon Estuarine system, São Paulo, Brazil. *Hydrobiologia* 510:91–102
- Lindner A, Migotto AE (2002) The life cycle of *Clytia linearis* and *Clytia noliformis*: metagenic campanulariids (Cnidaria: Hydrozoa) with contrasting polyp and medusa stages. *J Mar Biol Assoc UK* 82: 541–553
- Lindner A, Govindarajan AF, Migotto AE (2011) Cryptic species, life cycles, and the phylogeny of *Clytia* (Cnidaria: Hydrozoa: Campanulariidae). *Zootaxa* 2980:23–36
- Liu H, Li K, Huang H et al (2013) Seasonal community structure of mesozooplankton in the Daya Bay, South China Sea. *J Ocean Univ China* 12:452–458
- Mahiques MM, Figueira RCL, Salaroli AB, Alves DPV, Gonçalves C (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
- Mahiques MM, Figueira RCL, Alves DPV, Italiani DM, Martins CC, Dias JMA (2014) Coastline changes and sedimentation related with the opening of an artificial channel: the Valo Grande Delta, SE Brazil. *An Acad Bras Cienc* 86:1597–1607
- McLellan JA (1980) Notes on the northern Gulf of Mexico occurrence of *Sagitta friderici* Ritter-Záhony (Chaetognatha). *Gulf Caribb Res* 6:343–348
- Mendonça JT, Miranda LV (2008) Estatística pesqueira do litoral sul do estado de São Paulo: subsídios para gestão compartilhada. *Pan-Am J Aquat Sci* 3:152–173

- Miranda LB, Mesquita AR, França CAS (1995) Estudo da circulação e dos processos de mistura no extremo sul do mar de Cananéia: condições de dezembro de 1991. *Bol Inst Oceanogr* 43:153–164
- Miyao SY, Harari J (1989) Estudo preliminar da maré e das correntes de maré da região estuarina de Cananéia (25°S – 48°W). *Bol Inst Oceanogr* 37:107–123
- Miyao SY, Nishihara L, Sarti CC (1986) Características físicas e químicas do sistema estuarino-lagunar de Cananéia-Iguape. *Bol Inst Oceanogr* 34:23–36
- Miyashita LK, Calliari D (2016) Distribution and salinity tolerance of marine mysids from a subtropical estuary, Brazil. *Mar Biol Res* 12:133–145
- 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, Martinelli-Filho JE, Fernandes LF, Lopes RM (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
- MMA (2007) Áreas Prioritárias para a Conservação, Uso Sustentável e Repartição de Benefícios da Biodiversidade Brasileira: Atualização, Portaria N°. 09, 23 janeiro 2007. Diário Oficial da União, Brasília
- Montú MA, Cordeiro TA (1988) Zooplancton 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
- Morandini AC (2003) Estrutura populacional de *Chrysaora lactea* e *Lychnorhiza lucerna* (Cnidaria, Scyphozoa) em amostras de plâncton, com a redescricão das espécies. PhD Thesis, São Paulo University
- Moreira GS (1978) A preliminary laboratory study on the salinity and temperature tolerances of some medusae from São Paulo coast, Brazil. *Bol Inst Oceanogr* 27:45–55
- Nagata RM, Santos L, Stampar SN, Nogueira Júnior M, Morandini AC (2013) *Phyllorhiza punctata* in Brazilian coast: population oscillations or recurrent invasions? In: Proceedings of the Fourth International Jellyfish Blooms Symposium, Hiroshima, p 128
- Nagata RM, Nogueira Júnior M, Brandini FP, Haddad MA (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 Júnior M, Haddad MA (2014b) Faunistic survey of Hydromedusae (Cnidaria, Medusozoa) from the coast of Paraná State, Southern Brazil. *Zootaxa* 3768:291–326
- Navas-Pereira D (1980) Hydromedusae of the Bay of Sepetiba (Rio de Janeiro, Brazil). *Rev Bras Biol* 40:817–824
- 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 spatiotemporal dynamics of the zooplankton in the South Brazilian Bight: a review. In: Hoffmeyer M, Sabatini M, Brandini FP, Calliari D, Santinelli N (eds) Plankton Ecology of the Southwestern Atlantic. Springer, Cham, pp 149–170
- Nogueira Júnior M, Haddad MA (2017) Seasonal distribution, abundance and biomass of large medusae in subtropical coastal Brazil. In: Mariottini GL (ed) Jellyfish: ecology, distribution patterns and human interactions. Nova Publishers, New York, pp 3–25
- 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. *Zool Anz* 274:34–45. <https://doi.org/10.1017/S0025315418000486>
- 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 JCU (2015a) Diel vertical dynamics of gelatinous zooplankton (Cnidaria, Ctenophora and Thaliacea) in a subtropical stratified ecosystem (South Brazilian Bight). *PLoS One* 10:e0144161. <https://doi.org/10.1371/journal.pone.0144161>
- Nogueira Júnior M, Pukanski LEM, Souza-conceição JM (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, Maciel PV, Tilbert S, Oliveira LD (2018) Diversity, species composition and assemblage dynamics of estuarine gelatinous and semi-gelatinous zooplankton from Brazil. 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, Cham, pp 375–412
- Oliveira OMP, Araújo EM, Ayón P et al (2016) Census of Cnidaria (Medusozoa) and Ctenophora from South American marine waters. *Zootaxa* 4191:1–256
- Pestorac B, Krpo-Ćetković J, Gangai B, Lučić D (2012) Pelagic cnidarians in the Boka Kotorska Bay, Montenegro (South Adriatic). *Acta Adriat* 53:291–392
- 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
- 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
- Rodríguez C (2012) Hidromedusas del Atlántico sudoccidental: biodiversidad y patrones de distribución. PhD Thesis, Mar del Plata University
- Santhakumari V, Ramaiah N, Nair V (1997) Ecology pf hydromedusae from Bombay Harbour – Thana and Bassein Creek estuarine complex. *Indian J Mar Sci* 26:162–168
- Santhakumari V, Tiwari LR, Nair VR (1999) Species composition, abundance and distribution of hydromedusae from Dharamtar estuarine system, adjoining Bambay harbor. *Indian J Mar Sci* 28:158–162
- Schlitzer R (2017) Ocean data view. <https://odv.awi.de>. Accessed 16 November 2017
- Schuchert P (1996) The marine fauna of New Zealand: athecate hydrooids and their medusae (Cnidaria: Hydrozoa). *N Z Oceanogr Inst Mem* 106:1–159
- Schuchert P (2007) The European hydrooids and their medusae (Hydrozoa, Cnidaria): Filifera Part 2. *Rev Suisse Zool* 114:195–396
- Schuchert P (2008) The European hydrooids and their medusae (Hydrozoa, Cnidaria): Filifera Part 3. *Rev Suisse Zool* 115:221–302
- Schuchert P (2015) World Hydrozoa database. <http://www.marinespecies.org/hydrozoa>. Accessed 25 April 2016
- Segura-Puertas L, Damas-Romero M (1997) Variación estacional de la comunidad de medusas (Cnidaria) el la Laguna Bojórquez, Cancún, México. *Hidrobiológica* 7:59–64
- Silva JF (1989) Dados climatológicos de Cananéia e Ubatuba (Estado de São Paulo). *Bol Clim Inst Oceanogr* 6:1–21
- Silva Nascimento L, Nogueira Júnior M, Viana EM, Bersano JGF (in press) Biodiversity of planktonic hydrozoans from a subtropical estuary: evidences of assemblage structure change. *J Mar Biol Assoc UK*
- 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
- Stevenson MR, Dias-Brito D, Stech JL, Kampel M (1998) How do cold water biota arrive in a tropical bay near Rio de Janeiro, Brazil? *Cont Shelf Res* 18:1595–1612
- Tavares DQ (1967) Occurrence of doliolids and salps during 1958, 1959 and 1960 off the São Paulo coast. *Bol 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
- Tewksbury JJ, Anderson JGT, Bakker JD et al (2014) Natural history's place in science and society. BioScience 64:300–310
- Tronolone VB, Morandini AC, Migotto AE (2002) On the scyphozoan ephyrae in the southeastern Brazil. Biota Neotrop 2:1–18
- Vannucci M (1954) Hydrozoa e Scyphozoa existentes no instituto oceanográfico II. Bol Inst Oceanogr 5:95–148
- Vannucci M (1956) Biological notes and description of a new species of *Dipurena* (Hydrozoa, Corynidae). Proc Zool Soc Lond 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
- Vannucci M, Tundisi J (1962) Las medusas existentes en los Museos de La Plata y de Buenos Aires. Comunicaciones del Museo Argentino de Ciencias Naturales Bernardino Rivadavia 3:203–215
- Vannucci M, Santhakumari V, dos Santos EP (1970) The ecology of hydromedusae from the Cochin area. Mar Biol 7:49–58
- Vansteenbrugge L, Regenmortel TV, Troch M, Vincx M, Hostens K (2015) Gelatinous zooplankton in the Belgian part of the North Sea and the adjacent Schelde estuary: spatio-temporal distribution patterns and population dynamics. J Sea Res 97:28–39
- Whitfield AK, Elliot M (2011) Ecosystem and biotic classifications of estuaries and coasts. In: Wolanski E, Mcclusky DS (eds) Treatise on estuarine and coastal science, vol 1. Academic Press, Waltham, pp 99–124
- Whitfield AK, Elliott M, Bassett A, Blaber SJM, West RJ (2012) Paradigms in estuarine ecology e a review of the Remane diagram with a suggested revised model for estuaries. Estuar Coast Shelf Sci 97:78–90
- Xu Z, Huang J (1983) Ecological studies on the medusae of Juilong River of Fujian, China. J Xiamen Univ (Nat Sci) 22:364–374 (in Chinese with English abstract)
- Zamponi MO, Genzano G (1994) Seasonal distribution of hydromedusae from Samborombom Bay (Argentina). Plankton News 19:51–56