

**UNIVERSIDADE FEDERAL DO PARANÁ**

**LORENA SILVA DO NASCIMENTO**

**HIDROZOÁRIOS PLANCTÔNICOS DO COMPLEXO ESTUARINO  
DE PARANAGUÁ – BRASIL**



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LORENA SILVA DO NASCIMENTO

**HIDROZOÁRIOS PLANCTÔNICOS DO COMPLEXO ESTUARINO DE  
PARANAGUÁ – BRASIL**

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Orientadora: Dra. Erica A. G. Vidal  
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DE PARANAGUÁ – BRASIL"*

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Lorena Silva do Nascimento

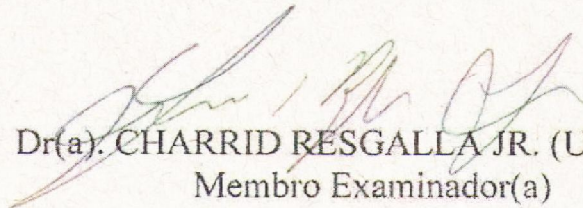
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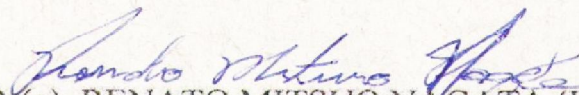
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# HIDROZOÁRIOS PLANCTÔNICOS DO COMPLEXO ESTUARINO DE PARANAGUÁ – BRASIL

Lorena Silva do Nascimento

## Resumo

Este estudo é o primeiro levantamento faunístico de hidrozoários planctônicos (hidromedusas e sifonóforos) do Complexo Estuarino de Paranaguá (CEP; Paraná, 25° S). Amostragens foram realizadas em 37 estações nos diferentes setores do estuário (Baía de Paranaguá, Laranjeiras e Pinheiros, e desembocaduras norte e sul) em dois anos de amostragens sazonais (verão e inverno de 2012 e 2013). Foram identificadas 37 espécies; 34 hidromedusas e 3 sifonóforos. Oito espécies são novos registros para o estado do Paraná, entre elas *Cnidostoma fallax*. Evidências indicam que *C. fallax* é uma espécie potencialmente invasora no CEP e em outros estuários próximos, como: 1) Comportamento oportunista; 2) Recente registro na costa do Brasil; 3) Ocorrência em regiões próximas a portos ao redor do mundo; 4) Recente ocorrência em alguns estuários brasileiros com grandes portos e intenso fluxo de embarcação. *Cnidostoma fallax* ainda foi a responsável pelo maior pico de abundância registrado neste estudo:  $> 2300 \text{ ind.m}^{-3}$  no verão de 2012, com maiores abundâncias principalmente nas porções mais internas e rasas do estuário devido à incidência de ventos de leste e menores taxas de precipitação. Outro pico de abundância dominado por *C.fallax*, *Clytia* spp., *Obelia* spp. e *L. tetraphylla* ocorreu no verão de 2013:  $\sim 1100 \text{ ind.m}^{-3}$ . O verão é a estação do ano com maior produtividade no CEP e, provavelmente, a alta disponibilidade de alimento aliada às maiores temperaturas favoreceram estes picos de abundância. As maiores riquezas ocorreram nas porções mais externas, principalmente devido à ocorrência esporádica (FO  $< 5\%$ ) de sifonóforos (*Muggiaea kochii*, *Nanomia bijuga* e *Abylopsis tetragona*) e hidromedusas comumente encontradas na plataforma interna, como *Proboscycodactyla ornata* e *Ectopleura dumortieri* (FO  $< 15\%$ ). Os resultados aqui apresentados contribuem para o conhecimento da distribuição bio-geográfica de cnidários planctônicos ao longo da costa brasileira, bem como, reforçam a importância do CEP para a conservação da biodiversidade.

**Palavras-chave:** hidromedusas, sifonóforos, biodiversidade, espécies invasoras, variação temporal e espacial

## Abstract

The present study is the first comprehensive surveys on planktonic hydrozoans fauna (hydromedusae and Siphonophorae) for the Paranaguá Estuarine System (PES) (Southern Brazil, 25° S), a World Heritage Listed Brazilian estuary. Collections were based in stations arranged throughout the estuary over four sampling campaigns during summer and winter in 2012 and 2013. A total of 148 samples were analyzed. More than 45,000 organisms were counted, totaled 37 species, including literature records: 34 hydromedusae and 3 siphonophores. Eight are new records for Paraná coast. The most abundant and frequent species were *Cnidostoma fallax* (relative abundance (RA) – 52.5 % and frequency of occurrence (FO) - 58.8 %), *Clytia* spp. (RA - 18 % and FO - 83.8 %), *Obelia* spp. (RA – 13.6 % and FO – 80.4 %) and *Liriope tetraphylla* (RA – 6.5 % and FO – 71.6 %). Some evidences indicate that *C. fallax* was recently introduced in PES and nearby estuaries, as: 1) Its opportunistic behavior; 2) The fact that it was only recently been found on Brazilian coast; 3) Its occurrence in coastal regions near ports around the world; and 4) Its recent occurrence in some Brazilian estuaries with big ports and/or heavy flow vessel. Furthermore, this is the first record of *C. fallax* dominance (> 19,000 specimens captured) which warns about potential negative impacts over the pelagic community. Planktonic hydrozoas were more abundant in the summer, with a abundance peak in 2012 (> 2300 ind.m<sup>-3</sup>) and 2013 (>1100 ind.m<sup>-3</sup>). High temperatures associated with high food availability in the summer campaigns may have favored the abundance of these species in the PES. Highest richness were recorded in outer portions, mainly due to the sporadic occurrence (FO <5%) of siphonophores (*Muggiaea kochii*, *Nanomia bijuga* and *Abylopsis tetragona*), along with the occurrence of other hydromedusae commonly found on the adjacent shelf, as *Proboscycactila ornata*, *Ectopleura dumortieri* and actinula larvae (FO <15%). The results presented herein are a useful baseline for subsequent assessments and contribute to the knowledge of the biogeographical distribution of planktonic cnidarians along Brazilian coast, as well as, strengthens the importance of the PES as a key role for regional biodiversity conservation.

**Keywords:** hydromedusae, siphonophores, invasive jellyfish, seasonal and spatial distribution, biodiversity.

## SUMÁRIO

<b>SUMÁRIO</b> .....	8
<b>PREFÁCIO</b> .....	10
<b>CAPÍTULO I</b> .....	16
<i>PLANKTONIC HYDROZOANS FAUNA (HYDROMEDUSAE AND SIPHONOPHORA) FROM PARANAGUÁ ESTUARINE SYSTEM, SOUTHERN BRAZIL</i> .....	16
ABSTRACT .....	17
1. <b>INTRODUCTION</b> .....	17
2. <b>MATERIALS AND METHODS</b> .....	19
a. STUDY AREA .....	19
b. DATA COLLECTION .....	20
3. <b>RESULTS</b> .....	21
a. SPECIES COMPOSITION .....	21
b. SPECIES DESCRIPTIONS .....	26
4. <b>DISCUSSION</b> .....	37
<b>CAPÍTULO II</b> .....	45
<i>SEASONAL AND SPATIAL DYNAMICS OF PLANKTONIC HYDROZOANS IN A SUBTROPICAL ESTUARY: EFFECTS OF ENVIRONMENTAL VARIABLES AND FOOD AVAILABILITY</i> .....	45
ABSTRACT .....	46
1. <b>INTRODUCTION</b> .....	46
2. <b>MATERIAL AND METHODS</b> .....	49
2.1 STUDY SITE .....	49
2.2 FIELD WORK .....	50
2.3 LABORATORY AND DATA ANALYSIS .....	51
3. <b>RESULTS</b> .....	53
3.1 METEOROLOGICAL AND ENVIRONMENTAL CHARACTERIZATION.....	53
3.2 POTENTIAL FOOD STRUCTURAL AND TEMPORAL DISTRIBUTION .....	54
3.3 PLANKTONIC HYDROZOANS COMPOSITION AND STRUCTURAL AND TEMPORAL DISTRIBUTION .....	59

3.4	RELATIONSHIP OF PLANKTONIC HYDROZOANS WITH ENVIRONMENTAL VARIABLES AND FOOD AVAILABILITY .....	68
4.	<b>DISCUSSION</b> .....	72
	<b>CONSIDERAÇÕES FINAIS E CONCLUSÕES</b> .....	83
	<b>REFERÊNCIAS</b> .....	87
	<b>ANEXO - DADOS BRUTOS</b> .....	100

## PREFÁCIO

Uma das características diagnósticas comuns a todos cnidários é a presença de cnida, uma organela geralmente utilizada para alimentação e defesa (Bouillon 1999; Daly *et al.* 2007). Os invertebrados pertencentes a este filo possuem anatomias diversas, de acordo com sua estratégia evolutiva e ciclo de vida, variando desde organismos rígidos fixos ao substrato a seres frágeis gelatinosos (Daly *et al.* 2007). Este filo se divide em dois clados: Anthozozoa com representantes exclusivamente bênticos, ocorrendo em curtos períodos no plâncton através da larva planula; e Medusozoa, que podem possuir alterações de geração (metagênese), com uma forma polipóide bêntica geralmente associada à reprodução assexuada, e a forma de medusa planctônica associada à reprodução sexuada (Salvini-Plawen 1978; Bridge *et al.* 1995). Contudo, entre os cnidários, muitos grupos e espécies possuem diferentes estratégias de ciclo de vida, havendo animais holoplanctônicos (como narcomedusas, traquimedusas e sifonóforos), pólipos que não liberam medusas (Bouillon *et al.* 2004, Bouillon *et al.* 2006), e ainda larvas cerinulas de pólipos com longo tempo de vida no plâncton - centenas de dias - as quais podem ser transportados por cerca de 2.000 - 4.000 km ao longo da costa (Stampar *et al.* 2015).

Entre os Medusozoa, a classe Hydrozoa é a mais diversa, com 3.671 espécies reconhecidas como válidas (Schuchert 2015), e é principalmente formada por espécies marinhas (Calder 1976; Cognetti & Maltagliati 2000). Cerca de 230 espécies de hidrozoários planctônicos já foram registradas no Brasil (Migotto *et al.* 2002; Nogueira Júnior & Oliveira 2006; Stampar *et al.* 2006; Stampar & Kodja 2007; Nogueira Júnior *et al.* 2013; Haddad *et al.* 2014), das quais aproximadamente 150 espécies são hidromedusas e 80 são sifonóforos. Entre as hidromedusas, as traquimedusas e narcomedusas são holoplanctônicas, e limnomedusas, leptomedusas e anthomedusas são meroplanctônicas (Bouillon *et al.* 2006). Os pólipos desse grupo, os hidróides, são geralmente coloniais e fixos a substratos consolidados, porém há exceções planctônicas e solitárias (Bouillon 1984; Genzano *et al.* 2009; Cabral *et al.* 2015). Já os sifonóforos são colônias polimórficas holoplanctônicas, a única exceção é um pequeno grupo formado pela família Rhodaliidae que são

bênticos (Pugh 1999; Mapstone 2014). Cada colônia é formada por vários medusóides e polipóides individuais que funcionam como um organismo único, podendo atingir dezenas de metros de comprimento no caso dos fisonéctes (Pugh 1999).

Por sua diversidade e facilidade de captura em amostras de zooplâncton, os hidrozoários são os mais estudados entre os medusozoários planctônicos. Apesar disso, a dificuldade na quantificação e identificação dos hidrozoários planctônicos devido a sua fragilidade e sua ocorrência, muitas vezes intermitente, levou à ideia de que hidrozoários são pouco importantes para as comunidades pelágicas marinhas (Möller 1984, Boero & Mills 1997, Purcell 1997, Mills 2001, Hansson et al. 2005, Møller & Riisgård 2007). Recentemente, foi destinada mais atenção a estes organismos, pois há várias evidências de que grandes concentrações de gelatinosos estão aumentando em frequência e persistindo mais do que o habitual (Purcell *et al.* 2007). Além disso, muitos estudos mostram ligações entre a abundância dos cnidários planctônicos e variações climáticas nos ecossistemas marinhos em todo o mundo (e.g. Mills 2001; Purcell 2005; Xian *et al.* 2005, Richardson *et al.* 2009).

Os cnidários planctônicos em geral são considerados importantes na teia trófica pelágica, destacando-se pelos seus hábitos carnívoros. Em geral, alimentam-se dos mais variados tipos de zooplâncton, incluindo copépodes e outros crustáceos, bem como outros gelatinosos, e ovos e larvas de peixes (Purcell & Arai 2001; Bouillon *et al.* 2004). Devido às altas taxas de alimentação, estes organismos são conhecidos por controlar populações de muitos organismos bênticos, planctônicos e nectônicos, podendo inclusive comprometer o recrutamento de espécies comerciais (Mills 1995; Purcell & Arai 2001; Lynam *et al.* 2006; Purcell *et al.* 2007). Pouco se sabe sobre a taxa de predação de hidrozoários planctônicos e seu impacto no ecossistema, mas há indícios que a predação e competição que estes organismos exercem sobre alguns organismos, associada à característica de crescimento populacional explosivo dos cnidários planctônicos, podem alterar a estrutura do fluxo trófico vigente e os ciclos de energia, ciclo do carbono, do fósforo e do nitrogênio em diversos ecossistemas (Matsakis & Conover 1991; Richardson *et al.* 2009). Além disso, podem gerar uma série de impactos socioeconômicos na pesca,

aquicultura, turismo, usinas de refrigeração, entre outros (Purcell *et al.* 2007; Lucas *et al.* 2014).

A capacidade dos hidrozoários planctônicos de explorar rapidamente as condições favoráveis do ambiente é em geral a responsável pelo crescimento populacional explosivo destes organismos (Purcell 2005; Richardson *et al.* 2009). Além disso, estratégias de reprodução assexuada podem gerar ocasionalmente aumentos populacionais em algumas espécies de hidrozoários no plâncton, devido ao seu rápido crescimento e desenvolvimento em resposta às condições favoráveis (Mayer, 1910; Alldredge, 1984; Kawamura & Kubota, 2008), sendo mesmo a principal estratégia reprodutiva em algumas espécies, como é o caso da hidromedusa *Proboscyclactila ornata* (Kawamura & Kubota, 2008).

Diversas variáveis ambientais são mencionadas como influenciadoras da distribuição espacial e temporal dos hidrozoários planctônicos. Em regiões de plataforma do Brasil e do mundo se observa um gradiente continente-oceano na distribuição horizontal dos hidrozoários planctônicos, associada principalmente às variações na disponibilidade de alimento, na disponibilidade de áreas de assentamento para os pólipos e à salinidade (e.g. Gusmão *et al.* 2014; Nagata *et al.* 2014b; Nogueira Júnior *et al.* 2014). Ademais, variações sazonais e interanuais são comuns em assembléias de hidrozoários planctônicos ao redor do mundo, geradas principalmente pelas variações na disponibilidade de alimento e de temperatura e, em alguns casos, associadas às variações climáticas de larga escala e suas influências nos ventos e correntes oceânicas (e.g. Páges & Gili, 1991; Raskoff 2001; Primo *et al.* 2012; Blackett *et al.* 2014). Estas variações populacionais dos hidrozoários planctônicos no tempo e no espaço estão principalmente relacionadas às fortes associações entre as espécies e as variáveis ambientais. Algumas espécies possuem estreitas tolerâncias às variações de temperatura e salinidade, sendo boas indicadoras dos eventos hidrográficos de mesoescala e possuindo um forte acoplamento com massas d'água (Vannucci 1957; Raymont 1983). Como exemplo, recentemente, a hidromedusa *Solmaris corona* foi associada à intrusão da Água Central do Atlântico Sul na plataforma sul brasileira, ocorrendo principalmente no verão sob influência dessa massa d'água (Nogueira Júnior *et al.* 2014).

A grande importância dos hidrozoários planctônicos nas regiões sul e sudeste do Brasil é reconhecida. Nesta região, os hidrozoários foram apontados como o segundo grupo mais diverso do zooplâncton, sendo menos diversos apenas que os copépodes (Lopes *et al.* 2006). Não obstante, o conhecimento sobre a fauna de cnidários planctônicos ainda é inadequado. A maioria dos trabalhos sobre este grupo no Brasil enfoca sua distribuição faunística, sistemática e ciclo de vida (Migotto *et al.* 2002; Stampar *et al.* 2006; Stampar & Kodja 2007). Estudos ecológicos sobre estes animais ainda são incipientes no Brasil, sem dados históricos sobre sua dinâmica populacional, o que torna impossível avaliar flutuações ou mesmo detectar aumentos populacionais, como em outros países com programas de monitoramento com longas séries de amostragens. Além disso, registros recentes indicam a presença de hidrozoários planctônicos invasores na costa brasileira (e.g. Nogueira Júnior & Oliveira 2006; Haddad *et al.* 2014), o que ressalta a importância de investigações e monitoramentos deste grupo no país.

Entre os poucos estudos produzidos no Atlântico sudoeste sobre hidrozoários planctônicos, a maioria foi conduzida em regiões de plataforma, e, apenas em alguns casos, em estuários e baías (Vannucci 1951; Navas-Pereira 1980; Zamponi & Genzano 1994; Tronolone, 2001; Mesquita *et al.* 2006; Bardi 2011; Nogueira Júnior 2012; Guerrero *et al.* 2013). Há apenas um trabalho conduzido no Complexo Estuarino de Paranaguá (CEP) que teve como um dos objetos de estudo os hidrozoários planctônicos: a tese de Bardi (2011), que tece comparações sobre as comunidades de hidrozoários (pólipos e medusas) do CEP com mais três estuários na costa sul e sudeste do Brasil. Outros estudos que analisaram a comunidade zooplanctônica no CEP foram os realizados por Montú & Cordeiro (1988), Lopes *et al.* (1998) e a dissertação de Salvador (2015) que citam apenas superficialmente alguns representantes de Hydrozoa. Nenhum estudo sobre hidrozoários planctônicos realizado no CEP ou no Atlântico sudoeste alia o detalhamento espacial (37 pontos distribuídos pelo estuário) com o temporal (amostragens sazonais ao longo de dois anos) proposto no presente estudo, que permite efetivamente caracterizar a fauna encontrada na área de estudo e determinar algumas relações espécie-ambiente.

Devido aos impactos negativos que algumas espécies de hidrozoários planctônicos podem gerar no ecossistema e em algumas atividades humanas, e pela importância ecológica e econômica da área de estudo, as informações geradas por estudos como este são essenciais para o estabelecimento de práticas adequadas de gestão, a fim de buscar a conservação e preservação dos recursos do CEP. Neste contexto, o objetivo deste estudo foi fornecer uma visão abrangente da composição e diversidade de hidrozoários planctônicos de PES, focando particularmente em descrições de novas ocorrências e espécies pouco conhecidas/mal descritas, e analisar a distribuição temporal e espacial da composição e densidade dos hidrozoários planctônicos no CEP, PR, Brasil, durante o verão e inverno de 2012 e 2013, verificando a influência de variáveis ambientais sobre estas distribuições. Para tanto, foram coletadas 148 amostras de zooplâncton durante o projeto BIOMAR, financiado pela Fundação Boticário. As estações amostrais estavam dispostas por todo CEP em duas campanhas de verão (Março de 2012 e Fevereiro de 2013) e duas de inverno (Agosto de 2012 e Junho de 2013).

As hipóteses propostas no presente estudo foram: i) se as espécies marinhas de hidrozoários são mais numerosas, e se a salinidade influencia a distribuição espacial dos hidrozoários planctônicos, então esperamos encontrar um decréscimo na riqueza de hidrozoários planctônicos de jusante à montante no CEP; ii) se o aumento de temperatura aliada à disponibilidade de alimento pode favorecer a produção e liberação de medusas, então a abundância dos hidrozoários planctônicos será maior nas campanhas mais quentes; e iii) se as grandes concentrações de nutrientes na Baía de Paranaguá e na Zona de Máxima Turbidez durante o verão favorecem a agregação de copépodes e outros zooplâncton nesta região, então esperamos que o mesmo ocorra aos hidrozoários planctônicos.

Esta dissertação é formada por dois capítulos, sendo que o primeiro deles discorre sobre a composição taxonômica dos hidrozoários planctônicos no CEP que será submetido para uma revista no perfil da *Journal of the Marine Biological Association UK* ou similar; o segundo capítulo aborda a distribuição espacial e temporal dos hidrozoários planctônicos no CEP, bem como a influência das variáveis ambientais e disponibilidade de alimento nestas

distribuições e será submetido para uma revista no perfil da *Marine Environmental Reseach* ou similar.



## CAPÍTULO I

Planktonic hydrozoans (hydromedusae and Siphonophorae) from Paranaguá  
Estuarine System, southern Brazil

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**Planktonic hydrozoans fauna (hydromedusae and Siphonophora) from the Paranaguá Estuarine System, southern Brazil: an estuary dominated by a probably introduced species *Cnidostoma fallax* (Hydrozoa, Hydractiniidae)**

ABSTRACT

*The present study is the first comprehensive surveys on planktonic hydrozoans fauna (hydromedusae and Siphonophorae) for the Paranaguá Estuarine System (PES) (Southern Brazil, 25° S), a World Heritage Listed Brazilian estuary. Collections were based in stations arranged throughout the estuary over four sampling campaigns during summer and winter in 2012 and 2013. A total of 148 samples were analyzed. More than 45,000 organisms were counted, totaled 37 species, including literature records: 34 hydromedusae and 3 siphonophores. Among those, Amphinema dinema, Corymorpha forbesii, Corymorpha januarii, Stauridiosarsia reesi, Eutima mira, Laodicea minuscula, Helgicirrha sp. and Cnidostoma fallax are new records for the Paraná coast. Furthermore, this is the first record of C. fallax dominance (> 19,000 specimens captured) which warns about potential negative impacts over the pelagic community, because its probably an introduced species in PES and in nearby estuaries. Some evidences of C. fallax introduction are: 1) Its opportunistic behavior; 2) The fact that it was only recently been found on Brazilian coast; 3) Its occurrence in coastal regions near ports around the world; and 4) Its recent occurrence in some Brazilian estuaries with big ports and/or heavy flow vessel. The results presented herein are a useful baseline for subsequent assessments and contribute to the knowledge of the bio-geographical distribution of planktonic cnidarians along Brazilian coast, as well as, strengthens the importance of the PES as a key role for regional biodiversity conservation.*

**Keywords:** biodiversity, estuary, southwestern Atlantic, invasive species, alien species

INTRODUCTION

Planktonic hydrozoans have been often neglected as an important component of marine biodiversity, although recent studies have highlighted its ecological role in ecosystems and impacts on human activities (Lynam *et al.*, 2006; Purcell *et al.*, 2007). They are mostly predators (Mills, 1995), feeding on zooplankton and/or ichthyoplankton, and can exert pressure on populations of both prey and competitors and often affect some species stocks (Purcell *et al.*, 1994; Purcell & Arai, 2001; Lynam *et al.*, 2006; Purcell *et al.*, 2007). For example, *Rathkea octopunctata* had a high feeding rate in Bedford Basin in Canada, especially during spring hydromedusan blooms, when hydromedusa potential daily impact is at least 59% over mesozooplankton concentration (Matsakis & Conover,

1991). Hydromedusae abundance also impacted other zooplankton population in the Sea of Marmara, where Cladocera and other crustaceans abundance decreased significantly during *Liriope tetraphylla* blooms, indicating substantial predation (Yilmaz, 2014).

Some species may form dense aggregations, changing the structure of food webs and biogeochemical cycles (Matsakis & Conover, 1991; Richardson *et al.*, 2009), negatively affecting populations of other organisms, including those of commercial interest. Furthermore, planktonic hydrozoans were already considered harmful to aquaculture activities, killing species in aquaculture pens, and causing some stinging events in swimmers and fishermen around the world (Purcell *et al.*, 2007). For example, *Solmaris corona* was already associated to the kill of salmon farming in Scotland, generating more than 2 million of salmon killed and £ 5 million loss (Johnson, 2002).

Estuarine regions of dense populated areas usually suffer considerable human pressure, due to a variety of economic and exploratory activities. Among many anthropogenic impacts on these areas, eutrophication, hypoxia and alien invasions are common and can cause profound negative impacts on local biodiversity and planktonic hydrozoan fauna (Arai, 2001; Ishii, 2006; Purcell *et al.*, 2007). In the matter of fact, the disappearance of some hydromedusae species has been already observed in coastal regions linked to these human impacts (Benovic *et al.*, 1987; 2000; Arai, 2001; Mills, 2001). Since little is known about the planktonic hydrozoan fauna in PES, we do not know how the species would respond to local anthropogenic pressures. Thus, faunistic inventories are fundamental for marine biodiversity conservation.

Paranaguá Estuarine System (PES) is one of the largest estuarine systems of South America, ca. 550 km<sup>2</sup> of total water body (Noernberg *et al.*, 2006). It is part of the Cananéia-Iguape-Peruíbe estuarine-lagoon complex, which is considered a Federal Environmental Protected Area (ICMBIO, 2015). The PES encompasses two conservational areas - the Superagüí National Park and the Environmental Protected Area of Guaraqueçaba. Around 19% of the remaining Brazilian Atlantic rainforest are situated there, being considered as a Natural World Heritage site by UNESCO (2015). Besides its ecological importance, PES is also important for harboring two large ports; the port of Paranaguá, the largest grain exporting of South America (Marone *et al.*, 2000),

and the port of Antonina. Major environmental impacts on PES are related to ports and agricultural activities, however sewage from the main urban areas, especially Paranaguá city, represent other significant source of pollution in PES (Kolm *et al.*, 2002; Marone *et al.*, 2005; Martins *et al.*, 2010).

Given its ecological and economic importance and the human impacts in PES, extensive surveys of local biodiversity are needed. The ichthyofauna in PES was recently stoutly evaluated (Passos *et al.*, 2012), and the benthic fauna, mostly particularly polychaetes, is well known (e.g. Lana *et al.*, 1986; Netto & Lana, 1995; Lana *et al.*, 2006), however most studies were developed in Paranaguá Bay, and little is known about the fauna of the others sectors of the estuary. Biological knowledge such as species composition of an ecosystem is useful for the interpretation of disturbance events and the detection of local introductions or extinctions and for the development of an adequate conservation and preservation management policy and sustainable use of resources (Hobbs & Huenneke, 1996).

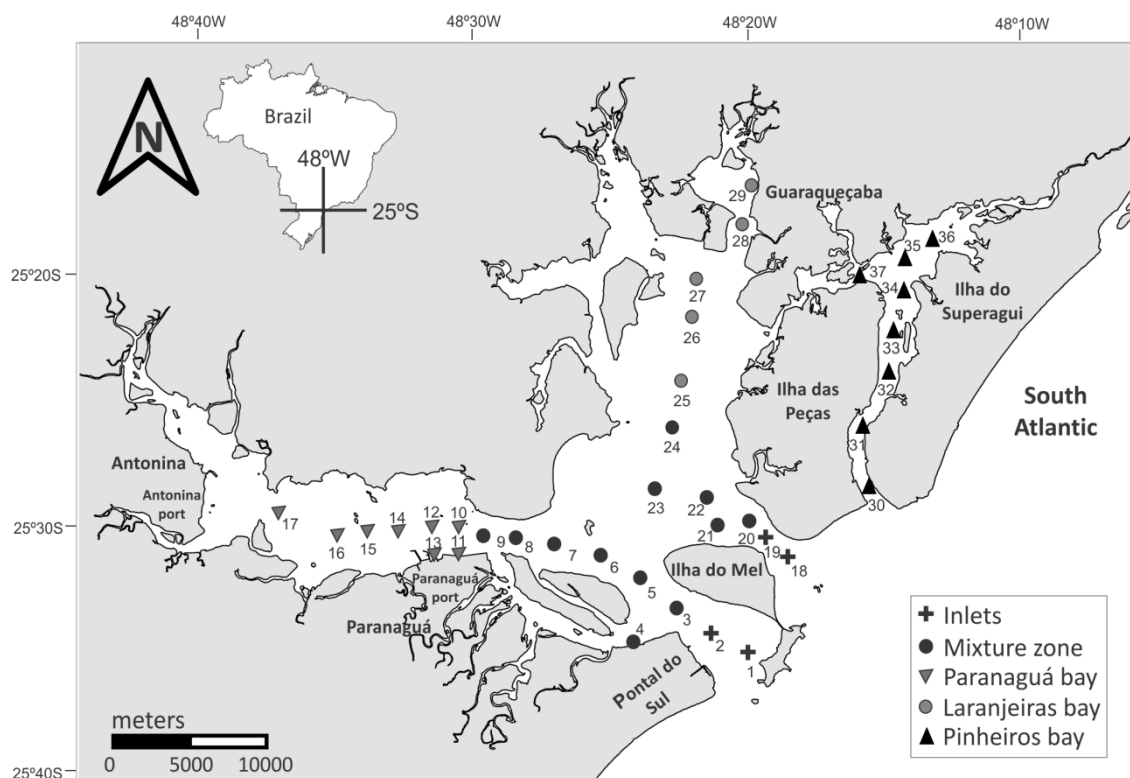
A total of 18 planktonic hydrozoan species have been recorded in PES in a few studies: two studies focused on the copepods and mention a few hydromedusae species (Montú & Cordeiro, 1988; Lopes *et al.*, 1998), another study described two cryptogenic species in the Antonina Bay (Nogueira Júnior & Oliveira, 2006), and a PhD thesis recorded 17 hydromedusae species in the Paranaguá Bay (Bardi, 2011). Thus, the present work is the first comprehensive study on planktonic hydrozoans diversity throughout PES. Aiming to provide an overview of planktonic diversity from PES, the taxonomic composition of the planktonic hydrozoan fauna from 148 plankton samples was studied and is presented here, along with literature records.

## MATERIALS AND METHODS

### **Study area**

The Paranaguá Estuarine System (Figure 1) is an estuary located on the northern limit of Paraná coast, southern Brazil. The climate of the region is tropical (transition), with an average rainfall of 2,500 mm (maximum 3,500 mm) (Lana *et al.*, 2001). The system can be divided into five sectors (Paranaguá,

Antonina, Laranjeiras and Pinheiros bays and mixture zone) based on Noernberg *et al.* (2006). In the present study, we studied only Paranaguá, Laranjeiras and Pinheiros bays and mixture zone, along two main tidal channels (inlets). The tidal cycle is semidiurnal with diurnal inequalities and average range of 2.2 m, with water residence of 3.5 days (Marone & Jamiyanaa, 1997) and average fresh water runoff up to  $200 \text{ m}^3 \text{ s}^{-1}$  in the Paranaguá Bay (Marone *et al.*, 1995). Great diversity of environments as coastal plain areas, mangroves, salt marshes and one of the largest continuous Atlantic rainforest preserved areas of South America are found around PES (Lana *et al.*, 2001; Marone *et al.*, 2005). Main human activities around the bay are port industries, agriculture, tourism, artisanal fisheries and aquaculture. Although considered pristine, there is dense urban occupation in the Southern vicinity of the bay.



**Fig. 1.** Map of Paranaguá Estuarine System, southern Brazil, showing the 37 stations sampled on March and August 2012 and February and June 2013, in each sector: inlets, mixture zone, Paranaguá, Laranjeiras and Pinheiros bays.

### Data collection

Planktonic hydrozoans were collected in four sampling campaigns: March (13 – 16th) and August (23rd and 24th) 2012, and February (21st and 22nd) and June

(18 and 19th) 2013, at 37 stations spread over the PES covering Paranaguá, Laranjeiras and Pinheiros bays, mixture zone and north and south inlets (Figure 1). Planktonic hydrozoans were collected by oblique tows (speed = 2 knots for 2 min), from the bottom to the surface, with a net model WP-2 (2 m long, 0.5 m mouth diameter, 200 $\mu$ m mesh) equipped with a calibrated flowmeter. Samples (n=148) were fixed with 4% buffered formaldehyde and sodium tetraborate for posterior analysis in laboratory.

At each station, surface temperature and salinity were measured with mercury thermometer and refractometer, respectively. In addition, vertical temperature and salinity profiles were obtained by calibrated CTDs, model Alec Compact – JFE in 2012 and CastAway-CTD in 2013. In summer 2012 sampling campaign, CTD profiles are only available for stations 18-29.

Samples were analyzed in laboratory under a stereomicroscope and all the planktonic hydrozoans were sorted and identified from whole samples. Identification followed predominantly Bouillon (1999) and Pugh (1999). A list with all species was compiled and is presented (Table 1). Classification followed Schuchert (2015). Number of analyzed individuals (colonies for siphonophores) and frequency of capture of a given species are also presented with additional records from the literature.

## RESULTS

### **Species composition**

More than 45,000 planktonic hydrozoans were analyzed, totaling 37 species belonging to 25 families and 6 orders, including literature records (Table 1). Representative examples can be found on Figures 4-23. Damaged and unidentified organisms were not a significant proportion of the collection and represented less than 1% of the total organisms recorded here. The number of species found on each sampling station varied from 17, on the Pinheiros Bay, to 7 on the Laranjeiras Bay (Figure 2). In general, the highest richness was found in the Pinheiros Bay and in external stations and the lowest diversity in the Laranjeiras Bay (Figure 2). However, considering the total amounts of species found in each sector, the highest species number was found in Paranaguá bay,

with 24 species captured in total for this sector, followed by Pinheiros bay and mixture zone, with 22 species, and further, the inlets and Laranjeiras bay, with 18 species captured in total.

The number of species found on each sampling campaign averaged 22.2, ranging from 26, in August 2012, to 20, in July 2013 (Figure 3). The accumulated number of recorded species increased substantially from the first campaign to the second, thereafter only a few additional species were found, and again rises from the third campaign to the fourth (Figure 3).

The orders Anthoathecata (18 spp.) and Leptothecata (10 spp.) were by far the dominant in terms of species richness. The most diverse families were Hydractiniidae, Bougainvillidae, Corymorphidae and Lovenellidae, all with three species. Unexpectedly, *Cnidostoma fallax* (Figure 6-7) was the most abundant species and it is probably an introduced species. Other common and abundant species were *Corymorpha gracilis* (Figure 12), *Eucheilota duodecimalis* (Figure 16), *Liriope tetraphylla* (Figure 20-21), *Clytia* spp. and *Obelia* spp. (Figure 22). Siphonophores species were sampled in only some occasions (*Muggiaea kochii* present in 2% of all samples, and *Nanomia bijuga* and *Abylopsis tetragona* in 1.35%). Other taxa which were frequently captured (>15% of samples) were *Ectopleura dumortieri*, actinula larvae and *Bougainvillia muscus* (Figure 4).

Most of the species found in PES were already recorded and described for the Paraná coast (Nagata *et al.* 2014a; b), thus attention will be directed only to the new regional records, with some comments on the morphological characteristics found and distribution of *Cnidostoma fallax*, *Amphinema dinema*, *Corymorpha forbesii*, *Corymorpha januarii*, *Stauridiosarsia reesi* (Figure 11), *Eutima mira* *Laodicea minuscula* (Figure 14), along probably a new species *Helgicirrho* sp., and three probably introduced species in the region captured in the present study: *Blackfordia virginica* (Figure 13), *Cnidostoma fallax* (Figure 6-7), and *Podocoryna loyola* (Figure 8).

From literature data, four additional species can be included in PES planktonic hydrozoans checklist: *Moerisia inkermanica*, *Dipurena* sp., *Coryne eximia* and *Geryonia proboscidalis* (Nogueira Júnior & Oliveira, 2006; Bardi, 2011; Montú & Codeiro, 1988). However, we suggest that the *Dipurena* sp. occurrence in the PES is probably uncertain, since the source which was taken this information (Bardi, 2011) cites times but not often this occurrence for the

estuary. In this case, we preferred to consider the occurrence of this species in the region, but we emphasize the doubt of this information.

Photographs of some species captured in the presente study are shown in figure 4-23. Voucher specimens will be soon deposited in the specific marine invertebrate collection of Paraíba and Paraná University, Brazil.

**Table 1.** Taxonomic classification, frequency of capture in this study and number of individuals (N°; colonies for siphonophores) of planktonic cnidarians species recorded from Paranaguá Estuarine System, Southern Brazil, in plankton hauls. Salinity (S) and temperature (T; in °C) range of each species also is shown. N = 148 trawls. Destroyed unidentified organisms (n = 173) were not included. Data source: 1 = present study; 2 = Nogueira Júnior & Oliveira (2006); 3 = Bardi (2011); 4 = Montú & Codeiro (1988); 5= Lopes et al. (1998); 6 = Haddad, Bettim & Miglieta (2014). ? = information not available in the present study or in the literature.

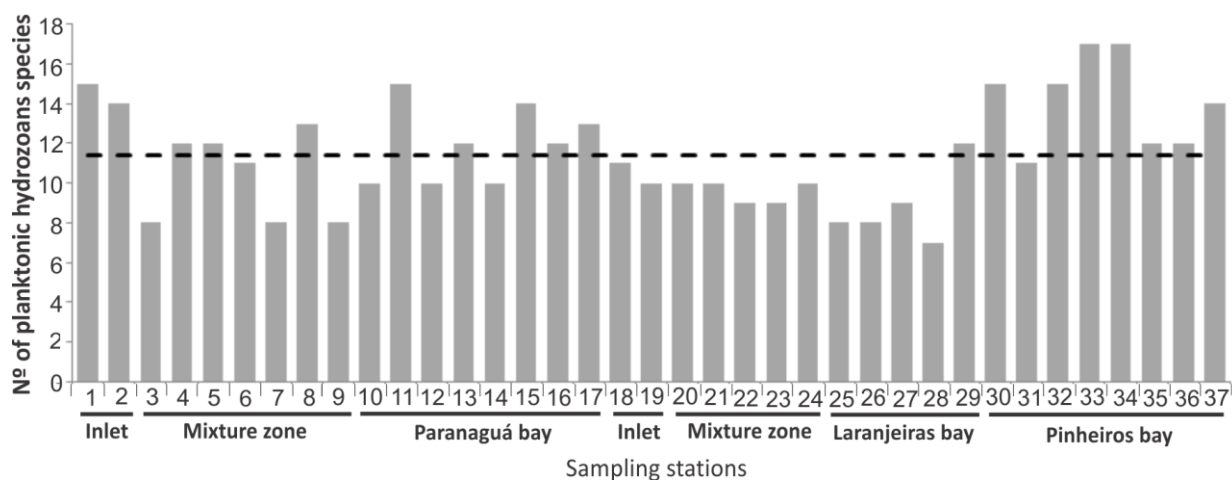
Species	Frequency of Capture (%)	N°	Environmental settings		Data source
			S	T	
<b>Phylum Cnidaria</b>					
<b>Class Hydrozoa</b>					
<b>Actinula larvae</b>	25	933	33-23	30-19	1
<b>Subclass Hydroidolina</b>					
<b>Order Anthoathecata</b>					
<b>Suborder Filifera</b>					
<b>Family Bougainvillidae</b>					
<i>Bougainvillia muscus</i> Allman, 1863	18.9	74	34-16	29-20	1
<i>Bougainvillia frondosa</i> Mayer, 1900	2	6	34-30	21-20	1
<i>Bougainvillia carolinensis</i> McCady, 1859	2.1	8	29-10	30.5-20	1, 3
<b>Family Hydractiniidae</b>					
<i>Cnidostoma fallax</i> Vanhöffen, 1911	58.8	1928 3	34-17	31-20	1
<i>Lizzia blondina</i> Forbes 1848	6	20	34-15	30-21	1, 3
<i>Podocoryna loyola</i> Haddad, Bettim & Miglieta 2014	8.1	26	34-16	29-19	1, 6
<b>Family Oceaniidae</b>					
<i>Turritopsis nutricula</i> McCrary, 1857	6.7	12	34-14	30-20	1
<b>Family Pandeidae</b>					
<i>Amphinema dinema</i> Péron & Lesueur, 1810	7.4	155	34-16	28-19	1
<b>Family Proboscidae</b>					
<i>Proboscylactila ornata</i>	11.5	134	33-16	30-15	1, 3

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<b>McCrary, 1857</b>						
<b>Family Rathkeidae</b>						
<i>Podocorynoides</i>	<i>minima</i>	5.9	56	30-10	31-19	1, 3
<b>(Trinci, 1903)</b>						
<b>Suborder Capitata</b>						
<b>Family Corymorphidae</b>						
<i>Corymorpha</i>	<i>gracilis</i>	54	1933	34-15	30-20	1, 3
<b>Brooks, 1882</b>						
<i>Corymorpha</i>	<i>forbesii</i>	3.4	27	30-21	29-20	1
<b>1894</b>						
<i>Corymorpha</i>	<i>januarii</i>	1.3	3	30-21	28-20	1
<b>Steenstrup, 1855</b>						
<b>Family Moerisiidae</b>						
<i>Moerisia</i>	<i>inkermanica</i>	?	6	20-0	30.5-24	2, 3
<b>Paltschikowa-Osroumowa, 1925</b>						
<b>Family Corynidae</b>						
<i>Dipurena</i>	sp.	4.0	3	25	?	3
<i>Stauridiosarsia</i>	<i>reesi</i>	8.9	19	33-20	31-21	1
<b>(Vannucci, 1956)</b>						
<i>Coryne</i>	<i>eximia</i>	?	3	15-10	?	3
<b>Allman, 1859</b>						
<b>Family Tubulariidae</b>						
<i>Ectopleura</i>	<i>dumortieri</i>	38.5	950	34-16	31-21	1, 3
<b>van Beneden, 1844</b>						
<b>Order Leptothecata</b>						
<b>Suborder Conica</b>						
<b>Family Blackfordiidae</b>						
<i>Blackfordia</i>	<i>virginica</i>	1.3	52	29-2	28-20	1, 2, 3
<b>Mayer, 1910</b>						
<b>Family Cirrholovenidae</b>						
<i>Cirrholovenia</i>	<i>tetranema</i>	2.7	4	31-20	31-21	1
<b>Kramp, 1959</b>						
<b>Family Eirenidae</b>						
<i>Eutima</i>	<i>mira</i>	2.7	6	28-14	30-27	1
<b>McCrary, 1857</b>						
<i>Helgicirra</i>	sp.	0.7	1	25	20	1
<b>Family Laodiceidae</b>						
<i>Laodicea</i>	<i>minuscula</i>	2	6	31-28	30-24	1
<b>Vannucci, 1957</b>						
<b>Family Lovenellidae</b>						
<i>Eucheilota</i>	<i>duodecimalis</i>	50.7	1521	34-15	31-19	1, 3
<b>A. Agassiz, 1862</b>						
<i>Eucheilota</i>	<i>paradoxa</i>	14.2	103	33-20	30-20	1, 3
<b>Mayer, 1900</b>						
<i>Eucheilota</i>	<i>maculata</i>	6.7	80	34-15	30-20	1, 3
<b>Hartlaub, 1894</b>						
<b>Suborder Proboscoida</b>						
<b>Family Campanulariidae</b>						
<i>Obelia</i>	spp.	80.4	6847	34-15	30-19	1, 3
<i>Clytia</i>	spp.	83.8	7620	34-15	31-19	1, 3
<b>Order Siphonophora</b>						

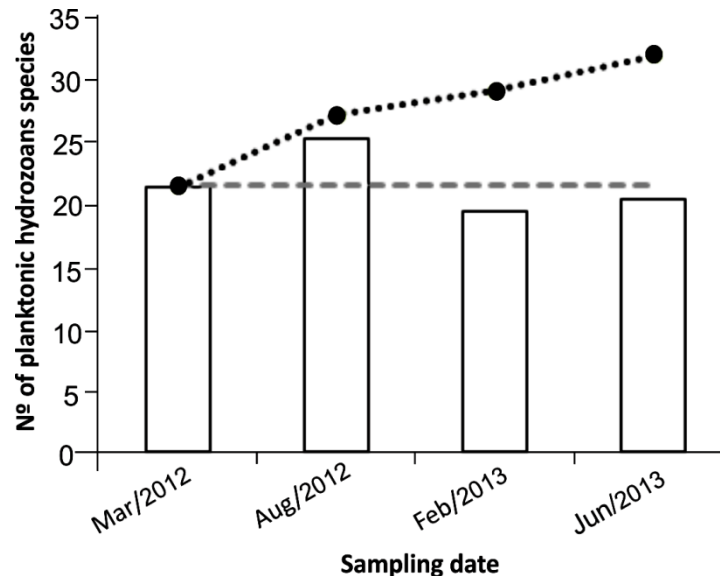
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<b>Suborder Calycophora</b>					
<b>Family Abylidae</b>					
<i>Abylopsis tetragona</i> Otto, 1823	1.3	2	33-26	29-24	1
<b>Family Diphyidae</b>					
<i>Muggiaea kochii</i> Will, 1844	2	4	34-30	24-21	1, 5
<b>Suborder Physonectae</b>					
<b>Family Agalmatidae</b>					
<i>Nanomia bijuga</i> delle Chiaje, 1841	4.7	9	33-23	31-20	1
<b>Subclass Trachylina</b>					
<b>Order Limnomedusae</b>					
<b>Family Olindiasidae</b>					
<i>Gossea brachymera</i> Bigelow, 1909	2	4	33-28	28-20	1
<b>Family Geryoniidae</b>					
<i>Geryonia proboscidalis</i> Forsskål, 1775	?	6	?	?	4
<b>Order Narcomedusae</b>					
<b>Family Cuninidae</b>					
<i>Cunina octonaria</i> McCrady, 1857	2.7	14	34-17	28-19	1
<b>Family Solmarisidae</b>					
<i>Solmaris sp.</i>	10.1	46	34-23	28-20	1
<b>Order Trachymedusae</b>					
<b>Family Geryoniidae</b>					
<i>Liriope tetraphylla</i> Chamysso & Eyesenhardt, 1821	71.6	5594	34-17	31-10	1, 3, 4, 5
<b>Family Rhopalonematidae</b>					
<i>Aglaura hemistoma</i> Péron & Lesueur, 1810	0.7	1	34	21	1



**Fig. 2.** Number of planktonic hydrozoans species from the 37 sampling stations (columns), on each sector (inlets, mixture zone, Paranaguá, Laranjeiras and

Pinheiros Bays), at Paranaguá Estuarine System, southern Brazil, in March and August 2012 and February and June 2013. The dotted line indicates the average number of species from all sampling stations (37).



**Fig. 3.** Number of planktonic hydrozoans species found on each sampling campaign (columns) at Paranaguá Estuarine System, southern Brazil, and cumulative number of recorded species (closed circles) in March and August 2012 and February and June 2013. The dotted grey line indicates the average number of species from all campaigns (4).

### Species descriptions

Class Hydrozoa → Subclass Hydroidolina → Order Anthoathecata → Suborder Filifera → Family Bougainvillidae

#### ***Cnidostoma fallax* Vanhöffen, 1911**

(Figure 6-7)

**Number of medusae examined:** March 2012 – 16260; August 2012 – 112; February 2013 – 2910; June 2013 – one.

**Morphological characteristics:** Medusae captured assigned to this species completely match the descriptions of *C. fallax* (Vanhöffen, 1911; Picard & Rahm, 1954 as *Archeoceania tournieri*; Kramp 1959a, b; Bouillon, 1999 as *Hydractinia tournieri*; Nogueira Júnior, 2012). Diagnostic characters of this species are four large tentacle bulbs each with one tentacle and adaxial ocelli, mouth with perradial clusters of stalked cnidophores and stomach with medusa buds. The gonads are undescribed to date and were also absent in the studied medusae. Most analyzed specimens had medusa buds.

**Distribution:** There are few records of this species, with three records on the Mouth of River Congo and in Ebrié Lagoon, Ivory coast (Vanhöffen, 1911; Picard & Rahm, 1954; Kramp, 1959b). In these records, *C. fallax* was captured in water with salinities ranging from 10 to 30 (Picard & Rahm, 1954). In Brazil, *C. fallax* have been registered the south and southeast coast: in the Babitonga Bay, (Nogueira Júnior, 2012), Cananéia estuary (Martinez *et al.*, 2015) and Santos Bay (M. Nogueira Júnior, unpublished data), with only some specimens captured, and in the Patos Lagoon, where it was also registered a *C. fallax* swarm in March 2012 ( $> 11000 \text{ ind.m}^{-3}$ ) (Teixeira-Amaral *et al.*, 2016). In PES, this species was recorded in a wide range of salinities (between 17 and 34), increasing its occurrence and abundance in salinities higher than 30 and corroborating its occurrence in brackish water habitat (Picard & Rahm, 1954). Some evidences indicating that *C. fallax* is probably an introduced species in the south and southeast Brazilian coast (see “Discussion”).

Class Hydrozoa → Subclass Hydroidolina → Order Anthoathecata → Suborder Filifera → Family Hydractiniidae

#### ***Podocoryna loyola* Haddad, Bettim & Miglieta 2014**

(Figure 8)

**Number of medusae examined:** March 2012 – one; August 2012 – six; February 2013 – three; June 2013 – sixteen.

**Morphological characteristics:** In this study, the 26 medusae assigned to this species were mostly mature and match completely with the description given for *P. loyola* (Haddad *et al.* 2014). Main morphological characteristics are eight tentacles, with marginal bulbs; without ocelli; manubrium square in cross section, reaching umbrella margin; mouth with four simple lips; and four interradial gonads on manubrium.

**Distribution:** PES is the type locality of *P. Loyola* from where polyps were sampled and medusae reared in laboratory (Haddad *et al.*, 2014). Both polyp and medusae were also recorded from Babitonga Bay (Nogueira Júnior, 2012 as *Hydractinia* sp.1; Cabral, 2013 as *Hydractinia* sp. nov.). and both polyp and medusae for Babitonga Bay (Nogueira Júnior, 2012 as *Hydractinia* sp.1; Cabral,

2013 as *Hydractinia* sp. nov.). *Podocoryna loyola* is probably an alien species in south Brazilian estuaries (Haddad *et al.*, 2014), but more studies are needed to confirm this hypothesis.

Class Hydrozoa → Subclass Hydroidolina → Order Anthoathecata → Suborder Filifera → Family Pandeidae

***Amphinema dinema* Perón & Lesueur 1810**

**Number of medusae examined:** March 2012 – 0; August 2012 – 154; February 2013 – one; June 2013 – 0.

**Morphological characteristics:** All medusa identified as *A. dinema* completely match the descriptions of this species (Bouillon, 1999; Schuchert, 2007). Diagnostic characters are marginal tentacles with large elongated conical basal bulbs; without ocelli; mouth with 4 prominent lips; and 8 simple adradial gonads, with large conical solid apical projection.

**Distribution:** *A. dinema* have been reported from northern and western Europe; the Mediterranean; western Africa; South Asia (Kramp, 1961; Benovic *et al.*, 2005); in the Bahía de la Ascensión, Mexico (Canché-Canché & Castellanos-Osorio, 2005); and Argentina (Genzano *et al.*, 2008). In Brazil, this species was previously captured in south and southeast coast (Vannucci, 1957; 1963; Goy, 1979; Navas-Pereira, 1981; Nogueira Júnior, 2012).

Class Hydrozoa → Subclass Hydroidolina → Order Anthoathecata → Suborder Capitata → Family Corymorphidae

***Corymorpha forbesii* Mayer 1894**

**Number of medusae examined:** March 2012 – 0; August 2012 – 154; February 2013 – one; June 2013 – twenty six.

**Morphological characteristics:** Specimens captured in this study had morphological characteristics typical of the *C. forbesii* (Schuchert, 2010). Diagnostic characters are a single tentacle, long, stout, with large terminal, cnidocyst swelling, four periradial marginal bulbs, small and rudimentary, mouth simple, short gastric peduncle and without ocelli.

**Distribution:** The medusa has been registered in Mediterranean waters (Bouillon *et al.*, 2004), archipelago of Seychelles, southeast Africa (Bouillon, 1978; Buecher *et al.*, 2005) and Bahía de la Ascensión, Mexico (Canché-

Canché & Castellanos-Osorio, 2005). In Brazil, this species was previously recorded for Sepetiba Bay (~ 22° S) (Migotto *et al.*, 2002), Babitonga Bay (~ 26° S) (Nogueira Júnior, 2012) and Rio Grande do Sul coast (~30° S) (Migotto *et al.*, 2002).

Class Hydrozoa → Subclass Hydroidolina → Order Anthoathecata → Suborder Capitata → Family Corymorphidae

***Corymorpha januari* Steenstrup, 1855**

**Number of medusae examined:** March 2012 – 0; August 2012 – 0; February 2013 – two; June 2013 – one

**Morphological characteristics:** The three organisms assigned to *C. januarii* completely match the descriptions for this species (Silveira & Migotto, 1992; Genzano *et al.* 2009). The diagnostic morphological characteristics are the apical process and axial canal, margin of umbrella perpendicular to its axis, without exumbrellar nematocysts tracks, four radial canals and one ring canal, manubrium shorter than umbrella and gonads surrounding manubrium in mature specimens.

**Distribution:** This species is endemic from Southwestern Atlantic (Genzano *et al.*, 2009), with records between Rio de Janeiro and Santa Catarina, central-southern Brazil (Migotto *et al.*, 2002, Nogueira Júnior, 2012) and between 39 and 42°S on the Argentinian continental shelf (Genzano *et al.*, 2009).

Class Hydrozoa → Subclass Hydroidolina → Order Anthoathecata → Suborder Capitata → Family Corynidae

***Stauridiosarsia reesi* Vannucci, 1956**

(Figure 11)

**Number of medusae examined:** March 2012 – ten; August 2012 – three; February 2013 – six; June 2013 – 0.

**Morphological characteristics:** The medusae assigned to this species completely match the available descriptions for *S. reesi* (Vannucci, 1956). The diagnostic morphological characteristics are four radial canals, four tentacles, four ocelli and a simple tubular stomach. Most captured specimens were adults and their manubrium was higher than the subumbrellar cavity.

**Distribution:** In Brazil, this species has been registered in São Paulo, Espírito Santo and Santa Catarina coast (Migotto *et al.*, 2002, Nogueira Júnior, 2012). In Babitonga Bay, Santa Catarina, the first record of this medusa was found in natura (Nogueira Júnior, 2012).

Class Hydrozoa → Subclass Hydroidolina → Order Leptothecata → Suborder Conica → Family Blackfordiidae

***Blackfordia virginica* Mayer 1910**

(Figure 13)

**Number of medusae examined:** March 2012 – twenty two; August 2012 – four; February 2013 – nine; June 2013 – two.

**Morphological characteristics:** The specimens captured agrees with the morphological characteristics of *B. virginica*, with dozens of hollow tentacles extending inwards from the bell margin into mesoglea, a narrow short manubrium and mouth with 4 lips, bell diameter higher than hemispherical, with rounded apex, and linear gonads extending from the corners to the manubrium to somewhat more than half-length of the 4 radial canals and surrounding them (Bouillon, 1999; Mills & Rees, 2000).

**Distribution:** *Blackfordia virginica* is typically from the Black Sea, but is considered invasive in many parts of the world (Mills & Sommer, 1995), especially in sheltered and port regions with heavy flow of vessels. There are known populations of *B. virginica* in Chesapeake and San Francisco bays (Mills & Rees, 2000), in coastal lagoons in Mexican Atlantic and Pacific Mexican coasts (Álvares-Silva, 1999), and in the Rio de la Plata estuary (Genzano *et al.*, 2006). In Brazil, this species was registered in mangrove near Recife (northern Brazil; ~ 08° S, 34° W) (Paranaguá, 1963; Freire *et al.*, 2014), in São Paulo coast (central-southern Brazil; ~25° S 48° W) (Bardi & Marques, 2009), and in Babitonga Bay, Santa Catarina (~26° S 48° W) (Nogueira Júnior, 2012). In PES, *B. virginica* was previously captured in Antonina Bay (Nogueira Júnior & Oliveira, 2006), and its occurrence extended to Paranaguá Bay (Bardi 2011; present study) and Pinheiros Bay (present study).

Class Hydrozoa → Subclass Hydroidolina → Order Leptothecata → Suborder Conica → Family Eirenidae

***Eutima mira* McCrady, 1857**

**Number of medusae examined:** March 2012 – five; August 2012 – 0; February 2013 – one; June 2013 – 0.

**Morphological characteristics:** Specimens assigned to this species were all adults and completely match the several available descriptions of *E. mira* (McCrady, 1857; Kramp, 1961; Goy, 1979; Bouillon, 1999; Bouillon *et al.*, 2006; Guo *et al.*, 2008). The diagnostic morphological characteristics of this species are the presence of only four tentacles, four gonads on the sub-umbrellar portion of the radial canals and four on the gastric peduncle.

**Distribution:** *E. mira* has been found in the China Seas, in the western Pacific, and on the coast of the US, in the western Atlantic (Kramp, 1961). In addition, there are two records of this species in the Argentine shelf (Zamponi, 1983; Zamponi & Suárez, 1991). In Brazil, *E. mira* has been captured in the northeast, near Fernando de Noronha (Vannucci, 1957; 1958), on the coast of Alagoas and Bahia (Goy, 1979), and in Babitonga Bay (Nogueira Júnior, 2012), its first record in southern Brazil. *Eutima mira* is often found in areas of mangroves areas and bays, very common at low salinities and high temperatures, as observed in the present study.

Class Hydrozoa → Subclass Hydroidolina → Order Leptothecata → Suborder Conica → Family Eirenidae

***Helgicirra* sp.**

(Figure 17)

**Number of medusae examined:** March 2012 – 0; August 2012 – one; February 2013 –0; June 2013 – two.

**Morphological characteristics:** Medusae of *Helgicirra* sp. match with the description of the genus (Kramp, 1961; Bouillon *et al.*, 2004; 2006) and probably it is the same species recorded in nearby areas (Nogueira Júnior, 2012), however these specimens apparently do not exactly fit to any described species of *Helgicirra* and the margin of all individuals was damaged hampering a more accurate description. Thus, a more detailed taxonomic analysis is needed to determine if they belong to a known or a new species.

**Distribution:** The first record of this genus in southwestern Atlantic was in Babitonga Bay (Nogueira Júnior, 2012), and this is its second record, which

may be indicative that this species is widely distributed in Brazilian subtropical estuaries.

Class Hydrozoa → Subclass Hydroidolina → Order Leptothecata → Suborder Conica → Family Laodiceidae

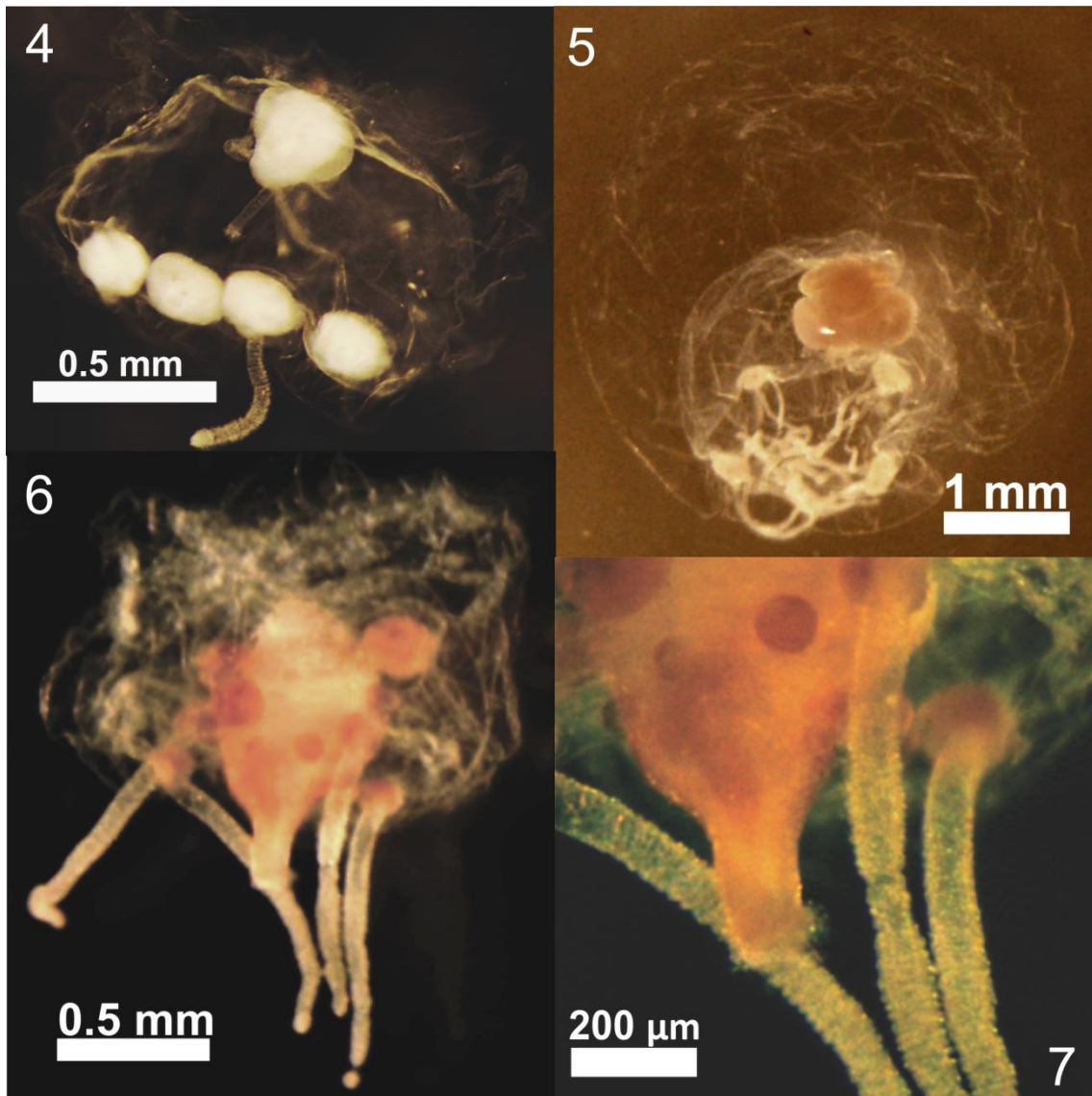
***Laodicea minuscula* Vannucci 1957**

(Figure 14)

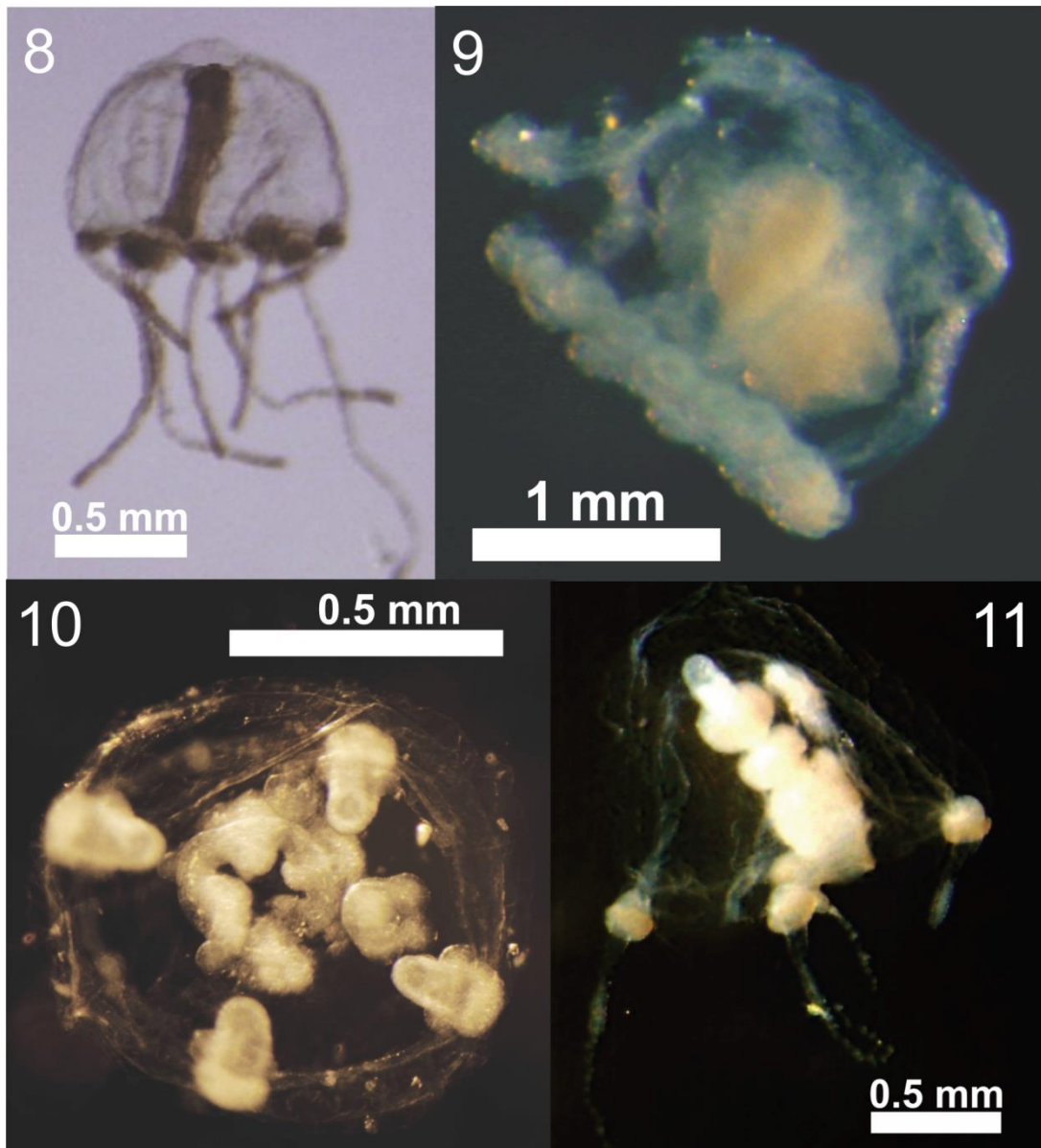
**Number of medusae examined:** March 2012 – four; August 2012 – two; February 2013 – 0; June 2013 – 0.

**Morphological characteristics:** The six individuals captured match completely with the description for *L. minuscula*, with only 4 tentacles and bulbs, ocelli not observed, manubrium small, mouth with 4 simple lips, horizontal large gonads, 8 cordyli and a few cirri (Vannucci, 1957; Bouillon, 1999).

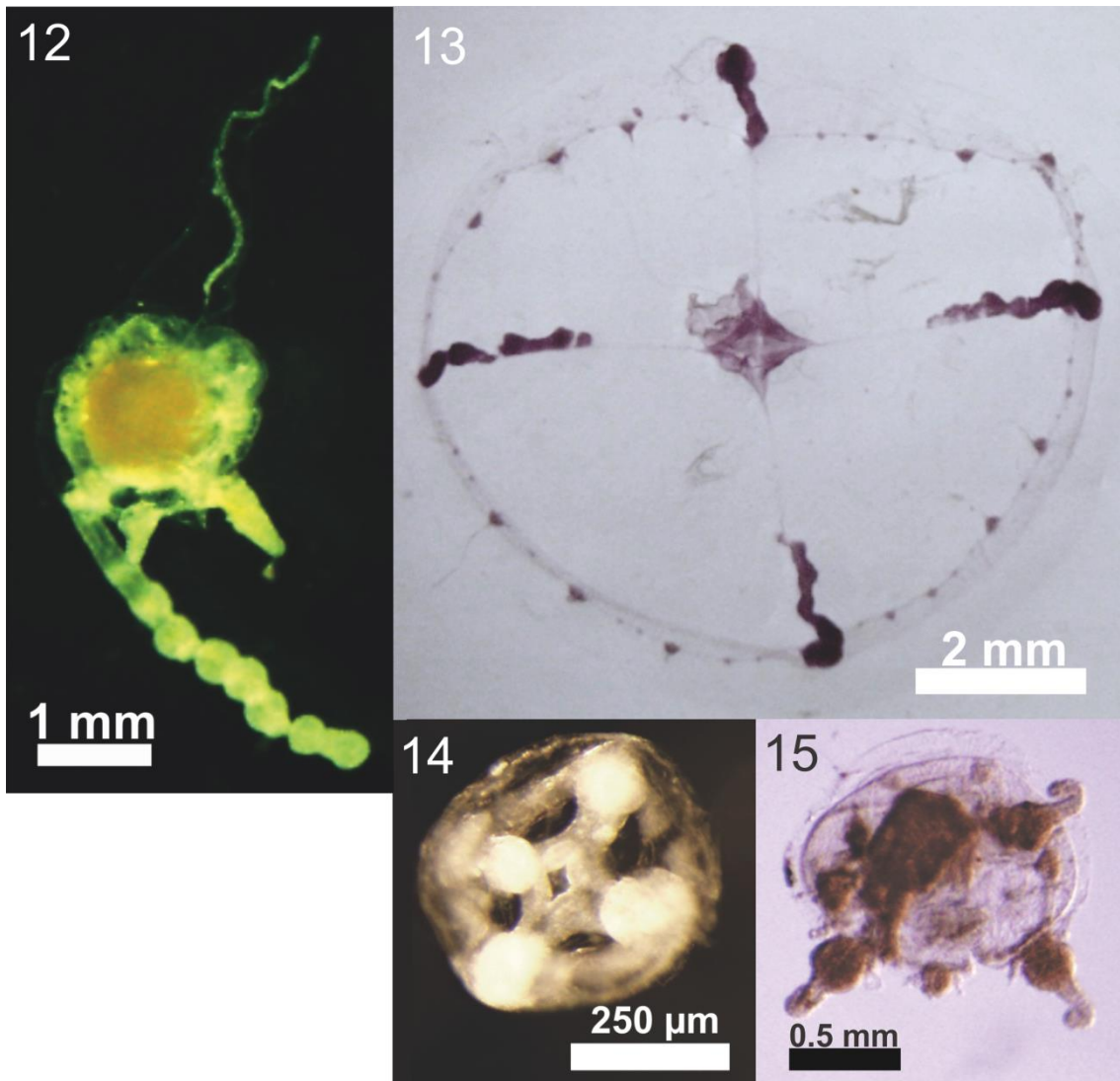
**Distribution:** *Laodicea minuscula* is considered a rare species in plankton samples (Vannucci, 1958), probably because it has a short life in the plankton or because of selectivity of the mesh used (Nogueira Júnior et al. 2015). It is endemic from Brazilian coast areas, found between 25 and 26°S, on coastal and estuarine waters from São Paulo (Vannucci, 1957, 1963; Moreira 1973), Paraná (present study) and Santa Catarina States (Nogueira Júnior, 2012).



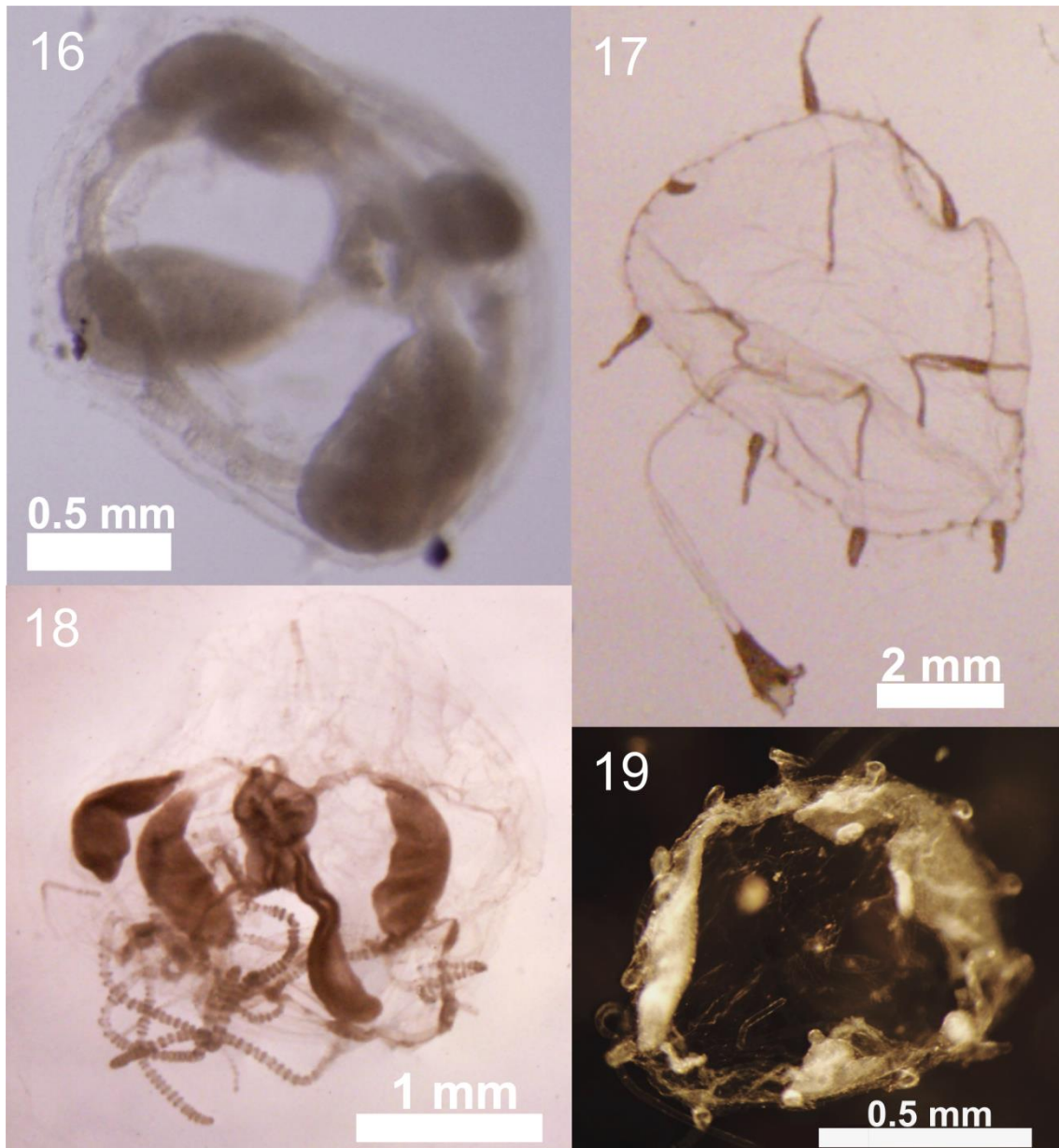
**Fig. 4-7.** *Bougainvillia muscus* (Allman, 1863): lateral view (4), *Bougainvillia carolinensis* (McCrary, 1859): lateral view (5), *Cnidostoma fallax* (Vanhöffen, 1911): lateral view (6), manubrium with medusoid buds and cnidophores on mouth rim (7).



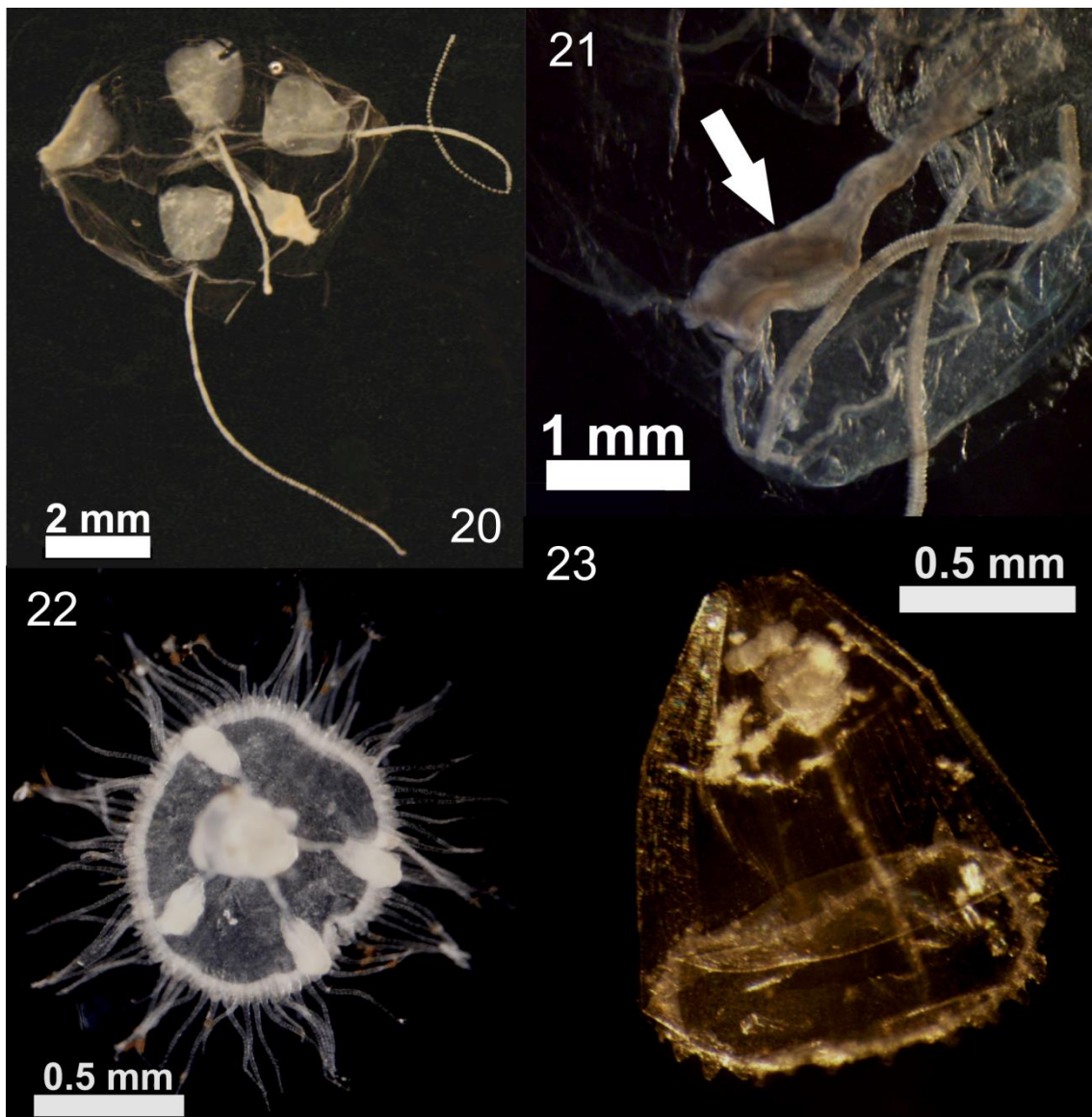
**Fig. 8-11.** *Podocoryna loyola* (Haddad, Bettim & Miglieta 2014): lateral view (**8**), *Turritopsis nutricula* (McCrary, 1857): lateral view (**9**), *Proboscycdactila ornata* (McCrary, 1857): oral view showing medusoid buds (**10**), and *Stauridiosarsia reesi* (Vannucci, 1956): lateral view with one copepod in the umbrella (**11**).



**Fig 12-15.** *Corymorpha gracilis* (Brooks, 1882): lateral view **(12)**, *Blackfordia virginica* (Mayer, 1910): aboral view **(13)**, *Laodicea minuscula* (Vannucci, 1957): oral view **(14)**, and *Eucheilota paradoxica* (Mayer, 1900): lateral view showing tentacular bulbs with lateral cirri alternating with rudimentary bulbs without tentacles, but with lateral cirri **(15)**.



**Fig. 16-19.** *Eucheilota duodecimalis* (A. Agassiz, 1862): aboral view showing gonads in the distal portion of the radial canals (**16**), *Helgicicrrha* sp.: adult medusae with a developed peduncle (**17**), *Gossea brachymera* (Bigelow, 1909): lateral view from an adult specimen with apparent gonads (**18**), *Cunina* sp.: oral view from a damaged specimen (**19**).



**Fig. 20-23.** *Liriope tetraphylla* (Chamisso & Eyesenhardt, 1821): lateral view with apparent gonads (**20**) and one copepod in its manubrium (arrow) (**21**), *Obelia* spp.: oral view (**22**), and *Aglaura hemistoma* (Péron & Lesueur, 1810): laral view (**23**).

## DISCUSSION

This is the first comprehensive survey on planktonic hydrozoans fauna from PES. Among the 37 species found, seven were recorded for the first time in Paraná state and one is probably a new species (Table 1). Most planktonic hydrozoans identified (73% of total) are known as “cosmopolitan” species, while species endemic from the western Atlantic represented 15% of total, and 8%

are endemic from the southwestern Atlantic (Kramp, 1959a; Bouillon & Boero, 2000; Genzano *et al.*, 2008; Gusmão *et al.*, 2014); besides *Podocoryna loyola* may be a “pseudoindigene” species from southern Brazilian estuaries, as it is probably an introduced species which is not known from elsewhere (Haddad *et al.*, 2014). Others probably introduction in PES are the medusae *Blackfordia virginica*, *Moerisia inkermanica* and *Cnidostoma fallax*.

All species identified in the present study have already been identified for the Brazilian coast (Migotto *et al.*, 2002; Nogueira Júnior, 2012; Haddad *et al.*, 2014), and most of them are common in the region. The most diverse families were Hydractiniidae, Bougainvillidae, Corymorphidae and Lovenellidae, all with three species and, in general, are very diverse in estuaries in southern and southeastern Brazil (Vannucci, 1951; Bardi, 2011; Nogueira Júnior, 2012). The orders Anthoathecata (18 spp.) and Leptothecata (10 spp.) were by far the dominant in terms of species richness, an expected pattern since these two orders are highly diversified (Marques *et al.*, 2003), especially in shallow coastal waters such as studied herein. Anthomedusae and leptomedusae have polyps in their life cycle and tend to be distributed mainly in coastal regions where there is greater availability of substrates for the polypoid stage (Gibbons & Richardson, 2009). As PES is a coastal shallow area, meroplanktonic species with polyp stage are best represented.

Anthomedusae found on PES represent 26% of recorded from Brazil and 16.6% from South Atlantic and leptomedusae represent 20% and 17%, respectively (Bouillon, 1999; Migotto *et al.*, 2002; Mesquita *et al.*, 2006; Stampar *et al.*, 2006; Stampar & Kodja, 2007; Morandini *et al.*, 2009, Nogueira Júnior *et al.*, 2013, Haddad *et al.*, 2014). Holoplanktonic hydrozoans were less representative in PES. The colonial forms of siphonophores (three species; 3.3% of Brazilian siphonophores; Migotto *et al.*, 2002; Nogueira Júnior *et al.*, 2014) were poorly represented in PES, as well as holoplanktonic hydromedusae of the orders Narcomedusae (3 spp.) and Trachymedusae (3 spp.) respectively 12% and 17% of those recorded from Brazil (Migotto *et al.*, 2002). Mostly holoplanktonic species found herein are common in the adjacent continental shelf (Vannucci, 1957; Nagata *et al.*, 2014a; b; Nogueira Júnior *et al.*, 2014), therefore their higher proportion in PES may be related to the higher influences of adjacent shelf, mainly in the sectors of the estuary. *Liriope*

*tetraphylla* was one of the most frequent species in PES, and it is also the most common species in the Paran shelf and across south and southeast Brazilian shelf (Nagata *et al.*, 2014a; b; Nogueira Jnior *et al.*, 2014). The occurrence of holoplanktonic species and typical planktonic hydrozoan from open shelf waters in the outer portions of the estuary contributed to the greatest diversity observed in the inlets, in the mixture zone, and in the Pinheiros Bay (Figure 2), indicating marked marine influence in the PES.

The new records from Paran (*Cnidostoma fallax*, *Amphinema dinema*, *Corymorpha forbesii*, *Corymorpha januarii*, *Stauridiosarsia reesi*, *Eutima mira*, *Helgicirrha* sp. and *Laodicea minuscula*) fill gaps in their distribution, but were expected, since these species have been found to the south and north of the PES. Five species have been reported to PES but we did not capture them in the present study (Mont & Cordeiro, 1988; Nogueira Jnior & Oliveira, 2006; Bardi, 2011): (i) *Geryonia proboscydalis*, (ii) *Aglanta* sp., (iii) *Moerisia inkermanica*, (iv) *Halitiara formosa* and (v) *Coryne eximia*. *Aglanta* sp. is typically oceanic with bathypelagic and epipelagic distribution in the South Atlantic (Bouillon, 1999) and no formally recorded from Brazilian coast except from Mont & Cordeiro (1988), and therefore we expected it may have been a misidentification, perhaps with *Aglaura hemistoma* which is similar and may be commonly found in the shallow shelf nearby (Nagata *et al.*, 2014a). *Moerisia inkermanica* is an invasive species that was found in Paranagu Bay in salinities between 0 and 11 (Nogueira Jnior & Oliveira, 2006), and probably due to the absence of sampling stations in inner-most regions of the bay with low salinities and larger continental influences, this species was not found in the present study.

Siphonophores (3 spp.) only occurred on some occasions, present in a few samples in the present study, suggesting their population are not resident in the estuary and were probably advected from adjacent marine waters where it is known to occur with higher frequencies and abundances (Nagata *et al.*, 2014b; Nogueira Jnior *et al.*, 2014). Hydromedusa was more diverse, totaling 34 species. Other studies conducted in estuarine regions in southwestern Atlantic found a smaller number of hydromedusa species (Vannucci, 1951; Navas-Pereira, 1980, Mont & Cordeiro, 1988, Zamponi & Genzano, 1994, Mesquita *et al.*, 2006, Bardi, 2011), except for Babitonga Bay, with 36 spp.

(Nogueira Júnior, 2012). However, it is difficult to compare the diversity observed herein with these other studies due to highly different sampling effort and devices employed.

Most species in PES occurred in a wide range of salinity (Table 1), being captured in most estuary sectors, which may have favored the great diversity found. The hydromedusae diversity registered in PES is higher than in shallow shelf areas off PES (22 spp.) (Nagata *et al.*, 2014a). This is likely to the number of plankton samples analyzed in the present study that is twice higher than in Nagata *et al.* (2014a), as well as the water volume filtered in trawls. Besides the greater sampling effort undertaken, the greatest diversity found herein indicates that PES harbors a high diversity of hydromedusae, contrasting with the general view that estuarine fauna is impoverished in relation to adjacent coastal waters (Calder, 1976; Santhakumari *et al.*, 1999). In fact, estuarine regions in the southwestern Atlantic are in general more diverse (e.g. Nogueira Júnior, 2012 – 36 spp.; the present study – 34 spp.) than shelf regions (e.g. Vannucci, 1957 – 27 spp.; 1963 – 17 spp.; Nagata *et al.*, 2014 – 22 spp.), but Nogueira Júnior *et al.* (2014) recorded 33 hydromedusae species in a cross-shelf transect over Santa Catarina shelf. This greater diversity found in the estuaries may be related to the occurrence of low salinity species that did not occur on the neritic zone, as *Moerisia inkermanica*, *Blackfordia virginica*, *Cnidostoma fallax*, *Podocoryna loyola*, *Helgicirrho* sp., *Corymorpha januarii*, *Laodicea minuscula* and *Eucheilota maculata*, along with the occurrence of non-resident species which can enter in the estuary in specific conditions, such as *Aglaura hemistoma*, *Muggiaea kochii* and *Abylopsis tetragona*.

Specific identification of some genera such as *Obelia* and *Clytia* is difficult due to the absence of morphological characteristics to diagnostic species (Bouillon, 1999; Lindner & Migotto, 2002; Lindner *et al.*, 2011), their medusae can only be identified with accuracy when they are obtained from polyps directly or by genetic analysis. Polyps from *O. bidentata*, *O. integra*, *O. dichotoma*, *C. gracilis*, *C. hemisphaerica*, *C. hummelincki*, *C. noliformis* and *C. lineares* were already found in PES and nearby waters (Migotto *et al.*, 2002; Neves *et al.*, 2007; Bardi, 2011; Miranda *et al.*, 2011) and probably the medusa of these species also occur in PES. Actinula larve are also difficult to identify, this is only possible with molecular analysis or cultures of these organisms to

determinate the next stage (either polyp or jellyfish). Actinula larvae are represented by the intermediate stage of planula of some hydroids, originating polyps (meroplanktonic) (Bouillon *et al.*, 2004; 2006), or by the intermediate stage of some trachymedusae and narcomedusae species, originating jellyfish (holoplanktonic). There is a record of actinula larvae in Babitonga Bay, southern Brazil, with only few individuals captured (Nogueira Júnior, 2012). However, they may be more common in shelf regions, representing about 20% of total jellyfish abundance in the South Brazilian Bight (Nogueira Júnior *et al.*, 2014), and probably the actinula larvae found herein is the same captured in southeast continental shelf of Brazil, because they have similar morphological characteristics (Nogueira Júnior *et al.*, 2014). Both records are probably formed by the intermediate stage of meroplanktonic jellyfish, as their general morphology is similar to that described for some species of *Ectopleura* (Schuchert, 2010).

The meroplanktonic hydromedusae *Blackfordia virginica* and *Moerisia inkermanica* are well-known invasive species worldwide, with several records in Brazil (Paranaguá, 1963; Nogueira & Oliveira, 2006; Chícharo *et al.*, 2009; Pukanski, 2011, Bardi, 2011; Nogueira Júnior, 2012, Freire *et al.*, 2014). *Podocoryna loyola* probably also is an introduced species in PES, polyp colonies from this meroplanktonic species was found in Paranaguá Bay in artificial substrate, but not in earlier decades (Atlvater, 2009; Cangussu *et al.*, 2010; Haddad *et al.*, 2014). Probably these invasions occurred by human impact, associated to ballast water and extensive shipping traffic. Introduced species frequently have negative effects on the biodiversity of aquatic ecosystems (Agostinho *et al.*, 2005). For example, in the Guadiana estuary of southeast Portugal and southwest Spain *Blackfordia virginica* has reduced populations of all zooplankton organisms including eggs of anchovy (Chícharo *et al.*, 2009). On Brazil, however, there are no information regarding the trophic ecology of this species to estimate its predatory impact. Thus faunistic inventories and monitoring programs are fundamental to get a sense of the occurrence of invasive species and to monitor these populations.

Another probably introduced species in PES is *Cnidostoma fallax*, which may have been favored by the environmental conditions found in the estuary. Records of this species are scarce and all from South Atlantic (Vanhöffen,

1911; Picard & Rahm, 1954; Kramp, 1959b, Nogueira Júnior, 2012). Until recently, *C. fallax* has exclusively been found from east African estuaries (e.g. Vanhoffen, 1911; Kramp, 1959). In southern Brazil, this species has only been recorded in Babitonga Bay (~26° S), with only four specimens collected (Nogueira Júnior, 2012). In the present study, *C. fallax* was the most abundant species, representing more than 50% of all medusae abundance. The numeric dominance here found warns about potential negative impacts over the pelagic community, because its occurrence may indicate that the fauna in the PES is changing which may negatively affect the ecosystem.

Evidences of *C. fallax* introduction in PES are:

1) Its has a noticeable opportunistic behavior, reaching large abundances during favorable conditions (warm temperatures and high food availability). The opportunistic characteristic is common for medusae which produce medusae buds, as *C.fallax*, which can rapidly produce a dense population by asexual reproduction in higher and specific temperatures (Carré and Carré, 1990; Kawamura and Kubota, 2008); and similar to other jellyfish considered invasive in other regions around the world (.g. Zaitsev, 1992; Graham & Bayha, 2008);

2) The fact that it was only recently been found on Brazilian coast (Nogueira Júnior 2012; the present study) despite studies available in open coastal (e.g. Vannucci 1957; 1963; Navas-Pereira, 1981; Tronolone 2007; Nagata *et al.* 2014a; b; Nogueira Júnior *et al.*, 2014) and estuarine (Navas-Pereira, 1980; Montú & Cordeiro, 1988, Bardi 2011) waters;

3) In all records of this species around the world, individual were captured in coastal regions near ports (Vanhöffen, 1911; Picard & Rahm, 1954; Kramp, 1959b; Nogueira Júnior, 2012; Martinez *et al.*, 2015; Teixeira-Amaral *et al.*, 2016) and this is probably the source of introduction of this species in PES and other Brazilian estuaries. *Cnidostoma fallax* was only captured recently in coastal regions with big ports and/or heavy flow vessel, as Babitonga Bay (Nogueira Júnior, 2012), Paranaguá Estuarine System (the present study); Cananéia estuary (Martinez *et al.*, 2015), Santos Bay (M. Nogueira Júnior, unpublished data), and another swarm of *C. fallax* was registered in the Patos Lagoon, also in March 2012 associated to a La Niña event (Teixeira-Amaral *et al.*, 2016). Port activities and flow vessel were already associated with other species invasions in PES which have well-established populations in the

estuary, as examples the medusa *Blackfordia virginica* e *Moerisia inkermanica* (Nogueira Júnior & de Oliveira, 2006), the copepod *Temora turbinata* (Lopes & Brandini, 1998; Salvador, 2015) and the microalgae *Coscinodiscus wailesii* (Procopiak *et al.* 2006).

The present study constitutes a comprehensive survey from a World Heritage Listed Brazilian estuary. Given the high sampling effort employed (148 samples analyzed and > 45,000 organisms studied), it can be considered that the planktonic hydrozoans fauna from PES is well represented in the present study. Nevertheless, only 4 sampling campaigns were conducted each with many new species being recorded and the cumulative number of recorded species did not stabilize (Figure 3), suggesting that other species could be captured as collection effort increases. Therefore, the diversity of planktonic hydrozoans in PES seems to be still slightly underestimated because of:

- (i) Only one type of collecting gear was used, reducing the representation of the fauna. The use of larger nets sample a larger water volume and could increase the possibility of sample large hydromedusae and more species;
- (ii) The inability to distinguishing species of *Clytia* and *Obelia* and actinula larvae;
- (iii) The fragility of planktonic hydrozoans which resulted in damaged unidentifiable specimens;
- (iv) The difficulty of identify properly some young medusa;
- (v) The absence of sampling stations in the sub-estuaries (salinities <14), and;
- (vi) The absence of samplings program in other seasons and in shorter intervals (daily, fortnights). Although species with short life span in plankton were captured, as *C. januarii*, *C. forbesii*, *A. dinema* and *L. minuscule*, short-term samplings strategies (days-to-weeks) could increase the possibility of sampling more short-lived meroplanktonic species.

The results presented herein are a useful baseline for subsequent assessments, because reports as the present one contributes to the knowledge of the bio-geographical distribution of planktonic hydrozoans along Brazilian coast, where the fauna is still insufficiently known. In addition, the high

biodiversity observed for planktonic hydrozoans and other aquatic organisms (e.g. Lana *et al.*, 2006; Passos *et al.*, 2012) in PES indicates that the estuary harbors a diverse aquatic fauna and is a key role for regional biodiversity conservation.

The PES biodiversity may be threatened, since the dominant species in PES is an apparently introduced species: *C. fallax*, and probably the assembly structure of planktonic cnidarians changed due to its and other species occurrences. *Cnidostoma fallax* occurred over two years sampled, with several individuals captured (> 19000), covering both juveniles and adults, male and female. These results indicated that it is an established species in the estuary, which makes the situation even more problematic, since the eradication of an established introduction is very difficult or even impossible (Critchley *et al.*, 1986; Bax *et al.*, 2001) and can usually cause detectable impacts in the local community. There is not enough knowledge about the biology of this species, but due to the abundance registered in PES, probably it should pose a threat to other jellyfish species through competition and predation. Only understanding the biology and ecology of *C. fallax* will lead to a recognition of the invasion, its impacts, and help to identify tools to control it. Then, some important themes for future studies are to study *C. fallax* diet and its predatory impact, as well as, its dispersive and reproductive potential.

## CAPÍTULO II

Seasonal and spatial dynamics of planktonic hydrozoans in a subtropical estuary: effects of environmental variables and food availability

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## Seasonal and spatial dynamics of planktonic hydrozoans in a subtropical estuary: effects of environmental variables and food availability

### Abstract

The spatial and temporal variability of planktonic hydrozoans were studied in the Paranaguá Estuarine System (PES), a subtropical estuary in southern Brazil. Four sampling campaigns (winter 2012 and 2013 and summer 2012 and 2013) were analyzed with 37 stations distributed across the estuary in each one. The most abundant and frequent species were *Cnidostoma fallax* (relative abundance (RA) – 52.5 % and frequency of occurrence (FO) - 58.8 %), *Clytia* spp. (RA - 18 % and FO - 83.8 %), *Obelia* spp. (RA – 13.6 % and FO – 80.4 %) and *Liriope tetraphylla* (RA – 6.5 % and FO – 71.6 %). Highest richness were recorded in outer portions, mainly due to the sporadic occurrence (FO <5%) of siphonophores (*Muggiaea kochii*, *Nanomia bijuga* and *Abylopsis tetragona*), along with the occurrence of other hydromedusae commonly found on the adjacent shelf, as *Proboscydactila ornata*, *Ectopleura dumortieri* and actinula larvae (FO <15%). In addition to the species preferences to environmental factors, the spatial distribution was also apparently influenced by weather conditions coupled with the estuarine circulation, generating aggregations in different sectors of the estuary. As an example, the highest abundance of planktonic hydrozoans occurred in the inner and shallow portions of the estuary due to the incidence of easterly winds and lower precipitation rate (66 mm) in the summer of 2012; and in outer portions in the summer of 2013 mainly due to higher rainfall rates (140 mm) and greater water column stratification. The planktonic hydrozoans were more abundant in summer than in winter, with two peaks of abundance recorded: > 2300 ind.m<sup>-3</sup> in 2012, dominated exclusively by *C. fallax*, and ~ 1100 ind.m<sup>-3</sup> in 2013, dominated by *C. fallax*, *Clytia* spp., *Obelia* spp. and *L. tetraphylla*. High temperatures associated with high food availability in the summer campaigns may have favored the abundance of these species in the PES. However, the seasonal pattern observed for most species in this study differs from other studies in nearby regions, suggesting that the temporal distribution of planktonic hydrozoans in tropical and subtropical regions does not have the seasonal and successional pattern as observed in some temperate regions. Apparently the regional and local factors are particularly important in tropical and subtropical estuaries.

**Keywords:** hydromedusae, siphonophores, seasonal variation, spatial variation, Paranaguá Estuarine System.

### 1. Introduction

Planktonic hydrozoans have opportunistic life histories, quickly responding to environmental changes. They can increase their feeding, growth, and reproduction in optimal conditions and in many cases they reach massive populations (Purcell, 2005). These proliferations have both ecological and economic implications, affecting fishing activities (Purcell and Arai, 2001; Lynam et al., 2006), or causing dominance changes from fish to jellyfish, affecting the

structure of the food web and thus the pathway of energy in the ecosystems (Matsakis and Conover, 1991; Richardson et al., 2009). Since jellyfish are typically voracious carnivores (Costello, 1988), the predation impact can be intensified by the sheltered nature of these environments. In bays and harbors areas, planktonic hydrozoans have the potential to affect the structure and abundance of other zooplankton species (Fulton and Wear, 1985; Purcell and Nemazie, 1992; Purcell et al., 1994).

Some studies have shown that changes in temperature, salinity, currents, and increased food availability are very likely to cause changes in the population sizes, distributions and timing of some planktonic hydrozoans species (e.g. Graham et al., 2001; Purcell, 2005; Boero et al., 2008; Blackett et al., 2014; Yilmaz et al., 2015). Seasonal and spatial variations of these multiple factors, as well as the interactions and feedbacks among them and many direct human influences, make interpretations of population dynamics in estuaries and coastal areas even more complex. Furthermore, processes and consequently the main driving factors can differ locally.

Knowledge about population dynamics and assemblage structure of planktonic hydrozoans is mostly based on long-term monitoring, mainly in temperate regions, such as North Sea (Greve et al., 2004) and North Atlantic (Gibbons and Richardson, 2009). In estuarine and sheltered environments in temperate regions, the diversity of planktonic hydrozoans is usually considered as low, and its seasonality tends to be more regular, with population peaks and reproductive activity concentrated in warmer months when biological productivity increases (e.g. Larson, 1986; Zamponi and Genzano, 1994; Ballard and Myers, 2000; Hosia and Bamstedt, 2007; Hosia and Bamstedt, 2008; Primo et al., 2012). On the other hand, in equatorial and tropical regions the diversity tends to be higher (Gusmão et al., 2014; Grossman et al., 2015), and the seasonality patterns less predictable (Nagata et al. 2014b). Moreover, there is little information on the assemblage structure seasonality in tropical estuaries (e.g. Ganapati and Nagabhushanam, 1958; Santhakumari et al., 1999; Mesquita et al., 2006), hindering the perception of general distribution patterns.

Due to the ecological and economic importance of planktonic hydrozoans, identifying the factors shaping their population and assemblage structure is fundamental to achieve an ecosystem approach of coastal and

fishery management (Lynam et al., 2005). Despite its importance, planktonic hydrozoans are usually neglected as a component of coastal zooplankton because of minor abundance compared to other groups such as copepods and its body fragility which contributes to damaging and hindering species identification (Harbison, 2009). In addition, they have complex life cycles, including several modifications to the classical metagenetic life cycle, as well as, highly intermittent occurrence and population peaks that may escape from direct observation (Boero et al., 2008).

The major obstacle detecting trends in planktonic hydrozoans populations is the scarcity of seasonal monitoring and detailed spatial coverage sufficient to describe the connections between environmental variables/processes and assemblage dynamics. Particularly estuarine sites in southwest Atlantic are largely understudied and none of the few available studies (Vannucci, 1951; Navas-Pereira, 1980; Zamponi and Genzano, 1994; Mesquita et al., 2006; Bardi 2011; Guerrero et al., 2013) unite seasonal, multi-annual and spatial approaches as presented in the present study in the Paranaguá Estuarine System (PES).

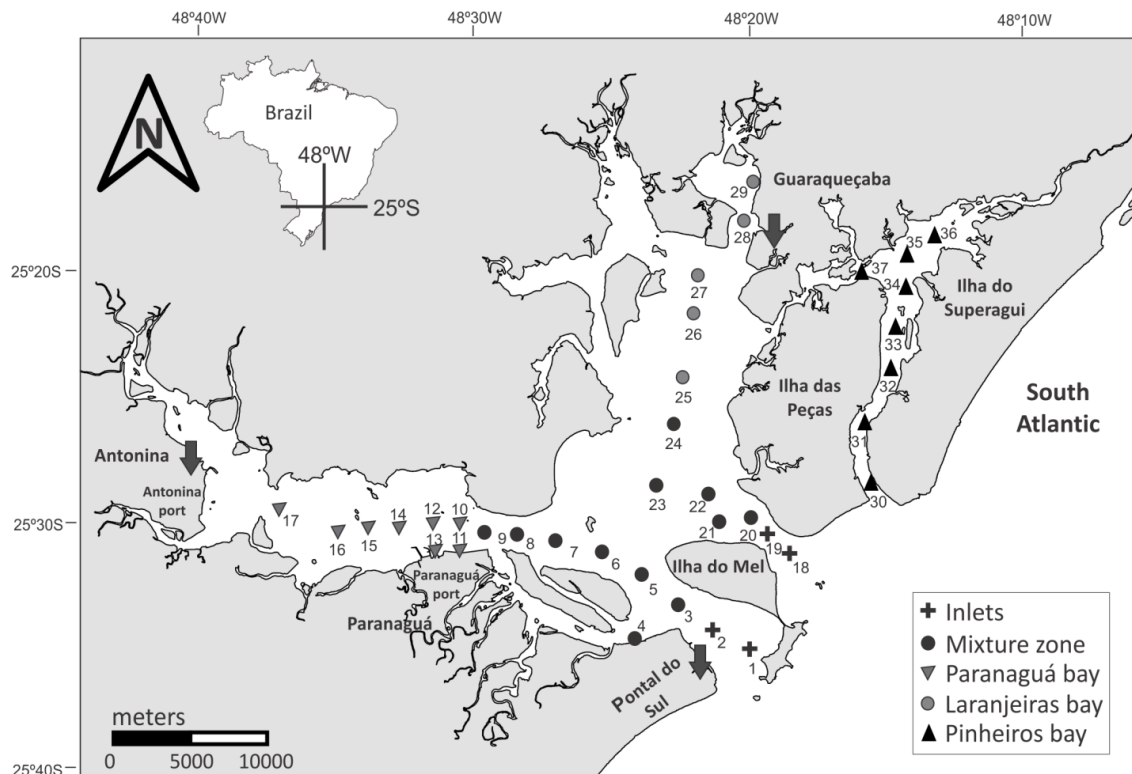
The hypothesis proposed in the present study were: i) the temperature increase coupled with the food availability can promote the production and release of jellyfish, then we expected that the planktonic hydrozoans abundance will be higher in the warmest sampling campaigns; and ii) whether the marine species of hydrozoans are more numerous, and salinity affect their spatial distribution, so we expect to find a decrease in the planktonic hydrozoans richness from downstream to upstream in the PES; and iii) if large concentrations of nutrients in the estuarine turbidity maximum zone' (ETMZ) in the Paranaguá and Antonina bays during the summer favor the aggregation of copepods and other zooplankton in this region, so we hope the same happens to planktonic hydrozoans.

Here we tested spatial and seasonal differences in the assemblage structure of planktonic hydrozoans during two years (2012-2013) in a wide spatial extent in one of the largest Brazilian estuaries. In addition, we explored the possible linkages between the assemblage, environmental variables and food availability.

## 2. Material and methods

### 2.1 Study site

Paranaguá Estuarine System (PES) is a subtropical estuary located in the southwestern Atlantic (Fig. 1), where seasonal variations are generally characterized by climatic factors (rain and wind conditions) (Lana et al., 2001). Its seasonality drives the local hydrodynamic, where contrasting circulation patterns are common (Marone et al., 2005). PES is the largest estuary in the South Brazilian Bight with an area of 551.8 km<sup>2</sup> (Noernberg et al., 2006), volume of approximately 2 x 10<sup>9</sup> m<sup>3</sup>, and mean fresh water runoff up to 200 m<sup>3</sup> s<sup>-2</sup> (Marone et al., 1995). According to its morphological and hydrological characteristics PES can be divided into five sectors (Paranaguá and Antonina, Laranjeiras and Pinheiros bays and mixture zone) (Fig 1; Noernberg et al., 2006) and a north and south channel that connect the estuary with the South Atlantic Ocean (Fig. 1). Paranaguá and Antonina bays are in EW axis, and Laranjeiras and Pinheiros bays in the NS axis. Tide is semidiurnal with diurnal inequalities with mean range of 2.2 m, and water residence of 3.5 days (Marone and Jamiyanaa, 1997).



**Fig. 1.** Study site and location of sampling stations in the Paranaguá Estuarine System, southern Brazil. Black arrows are the locations of meteorological stations where the data was extracted.

## 2.2 Field work

Samplings were carried out in austral summer and winter 2012 (March 13-16 and August 23-24, respectively) and austral summer and winter 2013 (February 21-22 and June 18-19, respectively), at 33 stations distributed in the five sectors defined by Noernberg et al. (2006) based on physical and morphological characteristics. In addition, other four stations, two in the south inlet (EW axis) and two in the north inlet (NS axis), were taken, totaling 37 stations at each sampling campaign (Fig. 1). At each station, we measured surface temperature and salinity with mercury thermometer and refractometer, respectively. Vertical temperature and salinity profiles were also obtained by calibrated CTDs (Alec Compact – JFE in 2012 and CastAway-CTD in 2013). There are CTD profiles only for stations 18 to 29 for summer 2012. Water transparency depth was obtained by Secchi disk.

Zooplankton was collected by oblique tows at constant speed (2 knots), integrating most of the water column, from near the bottom to the surface, lasting about two min. Samples were obtained with a WP-2 net (2 m long, 0.5 m mouth diameter, 200  $\mu\text{m}$  mesh) equipped with mechanic flowmeter for estimating the water volume sampled (Hydrobios in 2012 and General Oceanics Inc. in 2013). Samples ( $n=148$ ) were fixed with 4% buffered formaldehyde and sodium tetraborate for posterior analysis in laboratory.

Precipitation and air temperature data was provided by the Meteorological System of Paraná (SIMEPAR). The two automatic meteorological stations used are located in nearby Guaraqueçaba and Antonina city, in the upstream estuary (Fig. 1). Both meteorological stations provided very similar information, thus we used mean values. For data analysis, we used cumulative rainfall of fifteen days prior to each campaign. The Physical Oceanography Group (CEM/UFPR) located next to south inlet (Fig. 1), provided the wind data (speed and direction) (Fig. 1). Predominant wind direction, based on Galvani *et al.* (1999), and mean velocities were also estimated from daily resultants of the fifteen days prior to each campaign.

### 2.3 Laboratory and data analysis

The planktonic hydrozoans were sorted, identified and counted from whole samples using an Olympus SZ61 stereo microscope. The identification was carried out at the lowest taxonomic level possible, based on Vannucci (1957), Bouillon (1999), Pugh (1999), Bouillon et al. (2004), Nogueira Júnior (2012) and Nagata et al. (2014a). Other zooplanktonic groups were counted from 10 ml aliquots of the same samples, counting at least 300 organisms at least. Information about other zooplankton groups was used as potential food available for the planktonic hydrozoans. The density of organisms was standardized as individuals.m<sup>-3</sup>. Besides hydromedusae and siphonophores, other cnidarians, as cerinula larvae and ephyrae, were captured in small quantities (maximum abundance of 0.04 ind.m<sup>-3</sup> for cerinula larvae and 5.5 ind.m<sup>-3</sup> for ephyrae) but were not analyzed in the present study.

Considering salinity, we made interpolated vertical profiles from CTD measurements on horizontal transects through the EW axis (Paranaguá bay and south inlet), SN axis (Laranjeiras and Pinheiros bays and north inlet) in the Surfer 8, using the gridding method triangular with linear interpolation. We also calculated for all species, the frequency of occurrence (FO), as a percentage of samples a given species occurred from the total samples taken (n= 148), and the relative abundance (RA), as a percentage of specimens a given species accounted of the total abundance. Multivariate statistical analyses were performed with PRIMER-E software v. 6.1.15 with PERMANOVA+ v. 1.0.3 (Anderson et al., 2008), PAST v. 2.17 (Hammer et al., 2001), and Canoco v. 4.5 (terBraak and Smilauer, 1998).

The PERMANOVA was applied in order to detect structural (sectors) and temporal (seasons nested in years) differences ( $P < 0.05$  after 999 runs) in the planktonic hydrozoans assemblage structure: ~ time(seasons) x sectors. All factors were fixed and fully orthogonal. When PERMANOVA was significant, post-hoc unplanned comparisons were done using PERMANOVA pairwise ( $P < 0.05$  after 999 runs). Before the tests, the densities were root-transformed in order to include the rarer species. All procedures were performed using Bray-Curtis dissimilarity index (Legendre and Legendre, 1998). Patterns of planktonic

hydrozoans assemblages were determined and visualized using hierarchical agglomerative clustering techniques based on the Bray-Curtis similarity measures. In the agglomerative techniques each observation starts in its own cluster, and pairs of clusters are merged as one move up the hierarchy. For this analysis, we used mean values of each sector, determined a priori, in each season and year. In addition, the similarity percentage analyses (SIMPER) were used to identify the species that mostly contributed to similarities/differences on each identified group (Clarke and Ainsworth, 1993; Clarke and Warwick, 1994). We showed the contribution percentages for each species only up to the sum to ~80%.

A preliminary detrended correspondence analysis (DCA) (Hill, 1980) (run with all species data) revealed comparatively short length of gradient, which indicates that non-unimodal responses to environmental variables would be expected for most species (ter Braak and Šmilauer, 1998). Thus, assuming that most species would exhibit a linear response to the explanatory variables, we proceeded with a constrained ordination using canonical redundancy analysis (RDA) (Jongman et al., 1995, ter Braak and Šmilauer, 1998). RDA analysis was performed for summer and winter of both years (Lepš and Šmilauer, 2003). The exploratory variables matrix included copepods ( $\text{ind.m}^{-3}$ ), other zooplankton groups abundance (except planktonic hydrozoans and copepods) ( $\text{ind.m}^{-3}$ ), subsurface temperature (-2 m) ( $^{\circ}\text{C}$ ), subsurface salinity (-2 m), Temperature and Salinity Stratification Index (obtained by subtracting the mean of subsurface values from the bottom ones), water transparency depth (m), cumulative precipitation (mm), and zonal (EW) and meridional (NS) wind components. Water transparency depth and TSI were highly correlated, and the factor water transparency depth was excluded, the same occurred for meridional wind component and precipitation and meridional wind component was also excluded. These exclusions were performed in order to avoid inflation of the explanatory power of the model. The response and explanatory variables were log<sub>10</sub>-transformed and centered and the explanatory variables were also standardized. The significance of the RDA models and of the selected variables was determined by 499 Monte Carlo permutations at  $P < 0.05$  (Legendre and Legendre, 1998).

We used the method of Perry and Smith (1994) for identifying associations between environmental conditions and the distribution of planktonic hydrozoans. We applied this method to the range of temperature and salinity measured in this study and to the distributions of most abundant taxa (*Cnidostoma fallax*, *Clytia* spp., *Obelia* spp. and *Liriope tetraphylla*). First, we characterized the general frequency distribution of the environmental variables (temperature and salinity). Second, we associated the catch, in density, of particular taxa in each set with the environmental conditions at that set as a weight. And third, we determined the strength of the association between catch and the environmental variable by assessing the visual difference between the two curves (planktonic hydrozoan taxa and environmental variables).

### 3. Results

#### 3.1 Meteorological and environmental characterization

Prevailing winds were from east in the cumulative fifteen days prior the summer 2012 campaign, and in summer 2013, were from northeast (Table 1). Winter survey had predominantly winds from southeast in 2012 and from south in 2013 (Table 1). Mean wind speed was  $1.5 \text{ m}^{-1} \text{ s} (\pm 0.1)$ , with strongest winds during summer 2012 and winter 2013 (mean  $1.8 \text{ m}^{-1} \text{ s} \pm 0.12$ ). Cumulative rainfall was higher during summer samplings. In summer 2013, the highest mean cumulative rainfall reached 140 mm, and in summer 2012, 66 mm (Table 1). The driest period was in winter 2012, when the previous fortnight rainfall was nearly 0 mm at both meteorological stations (Table 1).

There is a marked structural and temporal variation in hydrological data associated with regional precipitation regime. Surface salinity reached maximum of 34 during summer 2012 and 2013 and minimum of 20 in winter 2012 and 15 in winter 2013, with major differences between summer and winter 2013 (Fig. 2a, Fig. 3). Along the estuary, salinity decreased consistently from downstream to upstream in all campaigns (Fig. 3). A clear stratification process of the water column was found in summer 2013, when occurred the highest Salinity Stratification Index (SSI), with a SSI about 10 in Paranaguá and

Laranjeiras bay and high values in all sectors ( $> 5$ ) (Fig. 3, Fig. 4a). In summer and winter 2012 and winter 2013, the SSI was lower, with an average values of  $\sim 2$  ( $\pm 0.61$ ) in all sectors (Fig. 3, Fig. 4a). Surface temperature varied seasonally, with maximum values during summer (26 to 31 °C) (Fig. 2b). During winter, surface temperature varied from a minimum of 19 °C in both years to a maximum of 25.5 °C in 2012 and 21 °C in 2013 (Fig. 2b). There were no considerable structural differences in temperature, horizontally and vertically (Fig. 4b). The Temperature Stratification Index (TSI) was usually higher in the summer than in the winter (Fig. 4b). Mean TSI was never larger than 3 °C ( $\pm 0.54$ ), with higher values in the inlets (Fig. 4b). Average water transparency depths were higher in 2013, with maximum of 4 m in summer and 3 m in the winter; lower values occurred in summer 2012, with minimum of 0.8 m (Fig. 4c). There is a clear tendency of increasing water transparency from the bays towards the inlets (Fig. 4c).

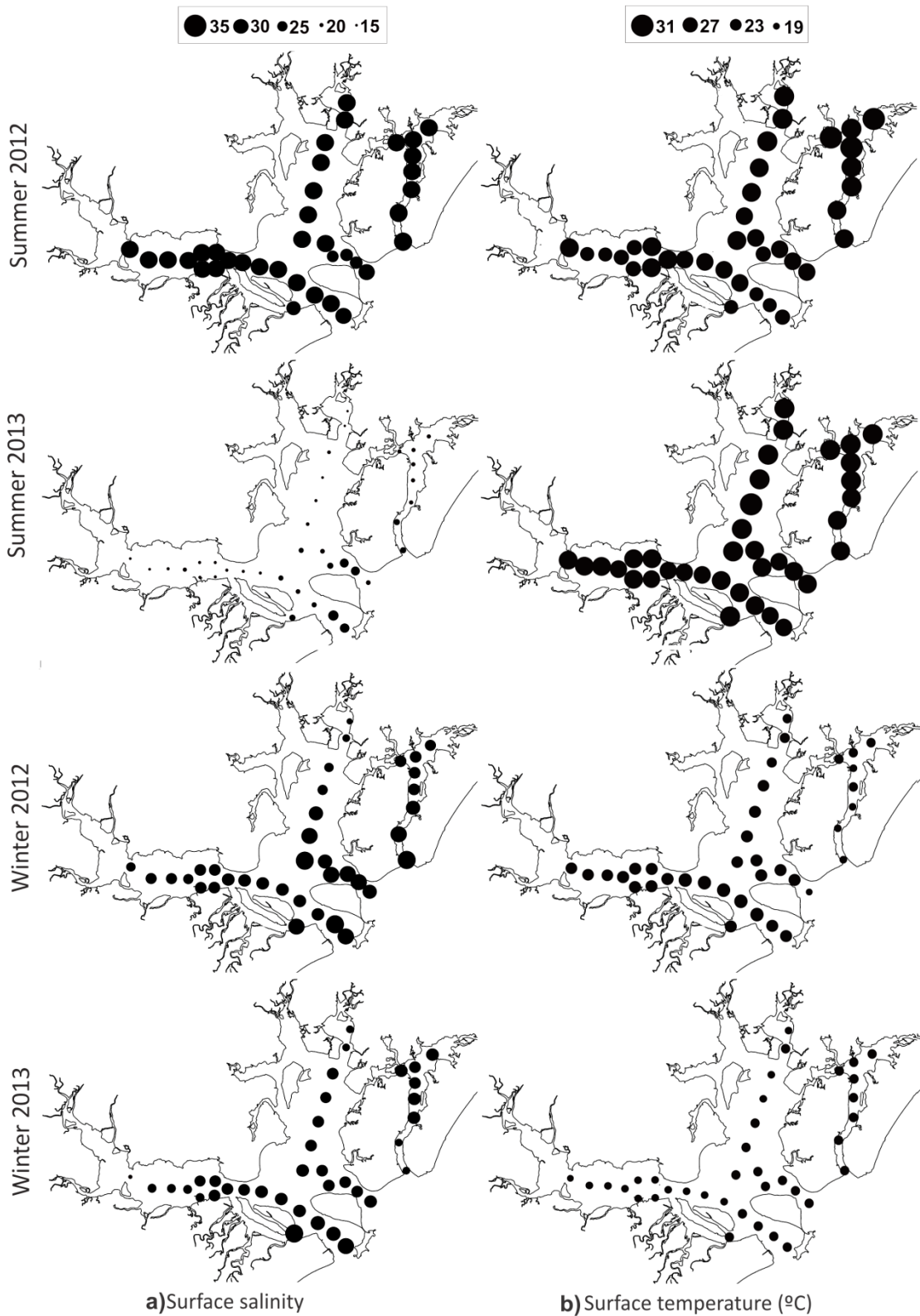
### *3.2 Potential food structural and temporal distribution*

Copepoda was the most abundant and frequent group, representing about 95% of the total zooplankton abundance. Other important groups, in descending abundance were: Appendicularia (1.7% of total zooplankton abundance), Decapoda (1.24%), Cirripedia (1.2%), Amphipoda (0.08%), Polychaeta (0.06%), Mollusca (0.04%), Chaetognatha (0.03%) and fish larvae (0.01%). During summer campaigns zooplankton species were more abundant than winter campaigns (Fig. 4d; 4e; 4f). The highest copepods abundances occurred in summer 2012, with a mean abundance of 15349 ind.m<sup>-3</sup> ( $\pm 1974.95$ ) whereas other zooplankton taxa were more abundant in summer 2013, mean of 460 ind.m<sup>-3</sup> ( $\pm 135.91$ ) (Fig. 4d). Minimum values occurred in winter campaigns, with mean of 1,436 ( $\pm 241.67$ ) and 106 ( $\pm 12.27$ ) ind.m<sup>-3</sup> for copepods and other zooplankton respectively (Fig. 4d; 4e). Regarding structural variation, copepods and other zooplankton taxa were more abundant in Paranaguá bay, with mean of 17837 ( $\pm 3703.58$ ) and 953 ( $\pm 53.44$ ) ind.m<sup>-3</sup>, respectively (Fig. 4d; 4e). Minimum mean for copepods abundance was found in Pinheiros bay (2,673 ind.m<sup>-3</sup>;  $\pm 123.15$ ) (Fig. 4d) and for other taxa, in Laranjeiras bay (145 ind.m<sup>-3</sup>;  $\pm 10.59$ ) (Fig. 4e).

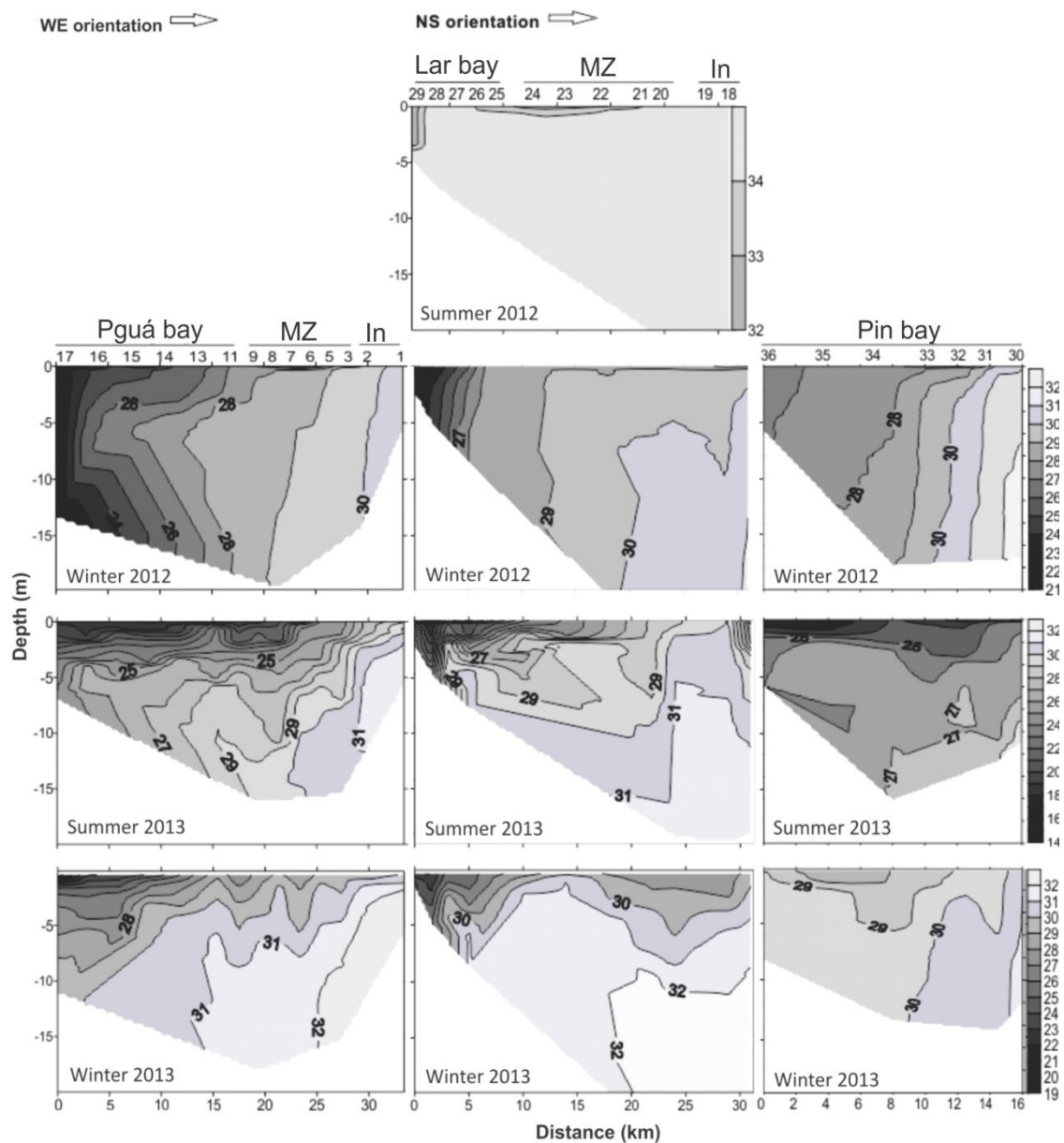
**Table 1**

Summary of the meteorological data from Paranaguá Estuarine System. (A) Prevailing wind direction (WD), wind frequencies of occurrence (FO - %), and mean wind speeds (WS - m/s) measured at Pontal do Sul meteorological station, (B) Average cumulative precipitation (mm) between Guaraqueçaba and Antonina meteorological stations. All values correspond to 15 days prior each sampling survey.

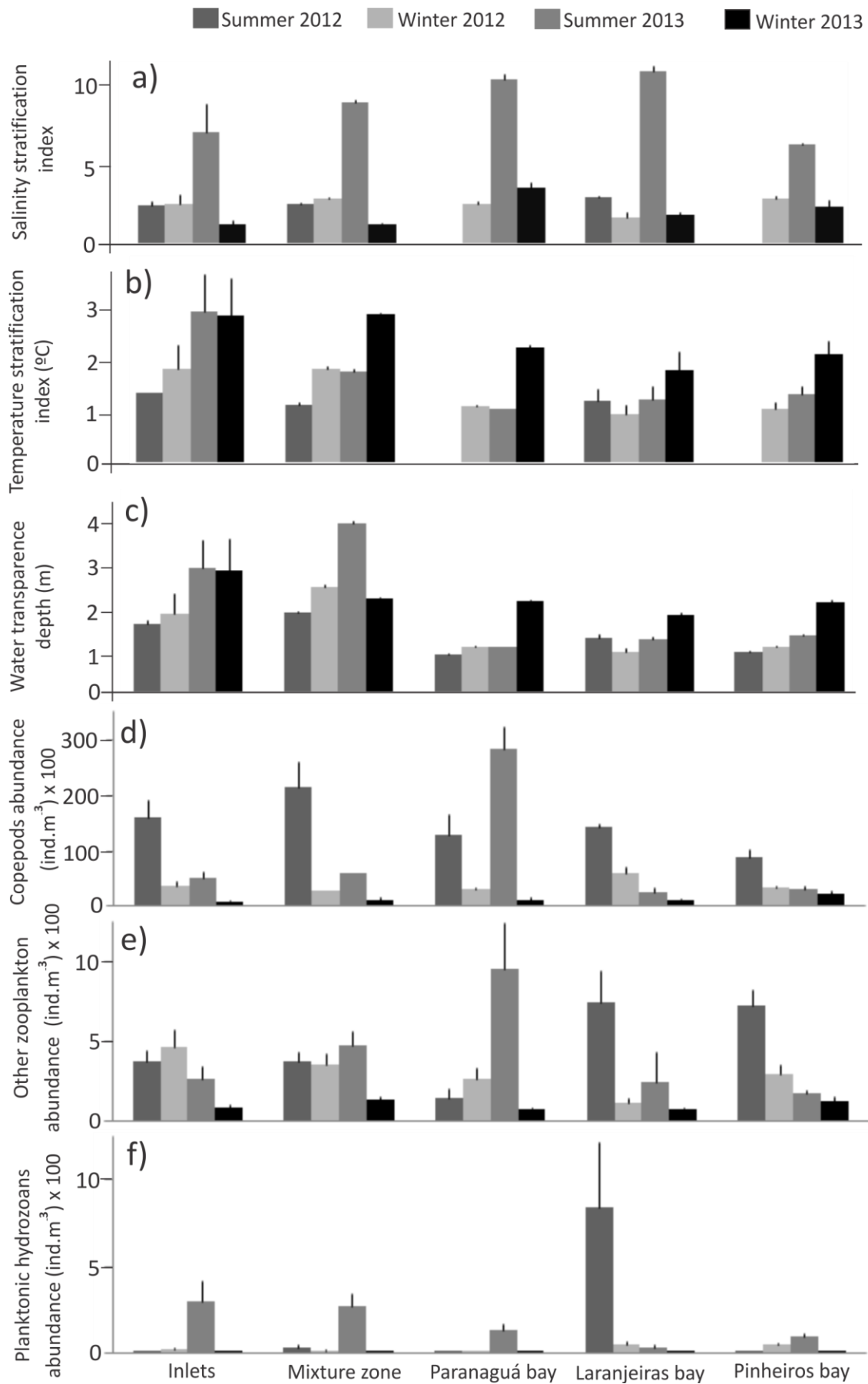
	(A)	Wind		(B)
	WD	FO (%)	WS (m/s)	Precipitation (mm)
<b>Summer 2012</b>	East	53	1.82	66.60
<b>Winter 2012</b>	Southeast	40	1.11	0.50
<b>Summer 2013</b>	Northeast	40	1.19	140.60
<b>Winter 2013</b>	South	40	1.83	39.30



**Fig. 2.** Structural and temporal distribution of surface salinity (a) and temperature (b - °C) in Paranaguá Estuarine System during summer and winter 2012 and 2013.



**Fig. 3.** Interpolated vertical salinity profiles from CTD measurements on horizontal transects through the EW axis and SN axis for each sampling period in the Paranaguá Estuarine System. No data are available for WE orientation and Pinheiros bay in summer 2012. Pguá bay = Paranaguá bay, Lar bay = Laranjeiras bay, Pin bay = Pinheiros bay, MZ = mixture zone, and In = inlets.



**Fig. 4.** a) Mean Salinity Stratification Index; b) Temperature Stratification Index ( $^{\circ}\text{C}$ ); c) Water transparency depth (m); d) Copepods abundance ( $\text{ind.m}^{-3}$ ), e) Other zooplankton abundance (except copepods and planktonic hydrozoans) ( $\text{ind.m}^{-3}$ ) and; f) Planktonic hydrozoans abundance ( $\text{ind.m}^{-3}$ ) for summer and winter 2012 and 2013 in each Paranaguá Estuarine System sector, southern Brazil. X = no available data. Vertical bars represent standard error.

### 3.3 Planktonic hydrozoans composition and structural and temporal distribution

A total of 33 taxa of planktonic hydrozoans were sampled, 24 meroplanktonic and 9 holoplanktonic (Table 2). The meroplanktonic *Cnidostoma fallax* was numerically dominant (52.5% of all planktonic hydrozoans), followed by the meroplanktonic *Clytia* spp. (18%), *Obelia* spp. (13.6%), and holoplanktonic *Liriope tetraphylla* (6.2%) (Table 2). Other holoplanktonic hydromedusae and siphonophores species had relative abundance lower or equal to 0.1% (Table 2). Thus, temporal and structural pattern of variation of planktonic hydrozoans abundance and richness were mainly explained by hydromedusae population.

Planktonic hydrozoans had higher abundances in the summer and lower in the winter (Fig. 4f; Fig. 5a; 5b). Maximum abundance occurred in summer 2013 with an average of  $171 \text{ ind.m}^{-3}$  ( $\pm 31.81$ ), and minimum values in winter 2013, with an average of  $3 \text{ ind.m}^{-3}$  ( $\pm 0.71$ ) (Fig. 4f; Fig. 5a). In general, planktonic hydrozoans abundance was evenly distributed at sampling stations and sectors, except for a peak abundance in Laranjeiras bay (average of  $606 \text{ ind.m}^{-3}$ ;  $\pm 30.59$ ) (Fig. 4f; Fig. 5a). This peak abundance corresponds to the peak abundance of hydromedusae during summer 2012, at station 28 ( $> 2,300 \text{ ind.m}^{-3}$ ), composed predominantly (99.7%) of *C. fallax* (Fig. 5a). Other hydromedusae peak abundance occurred at station 3 ( $1,094 \text{ ind.m}^{-3}$ ), in the mixture zone, in summer 2013 (Fig. 5a), composed mainly by *C. fallax* (36.4%), *Clytia* spp. (34%) and *Obelia* spp. (11.7%).

While hydromedusae were more abundant in the summer, siphonophores were more abundant in the winter (Fig. 5b). Siphonophores occurred sporadically ( $\text{FO} < 5\%$ ; Table 2), and the highest abundances occurred in the winter 2012, in the south inlet, at station 1 ( $2.7 \text{ col.m}^{-3}$ ), and in the winter 2013, in Pinheiros bay, at station 30 ( $2.2 \text{ col.m}^{-3}$ ) (Fig. 5b). Siphonophores occurred mainly at the more external stations (inlets, mixture zone and outer stations of

Pinheiros bay), except during summer and winter 2012, when *Nanomia bijuga* was captured at Paranaguá and Pinheiros bays (Fig. 5b). The number of planktonic hydrozoans taxa per sample ranged from 1 (winter 2013, station 7, mixture zone) to 15 (winter 2012, station 1, south inlet) (Figure 5c). In summer campaigns, a higher richness was usually found at the inlets and outer stations of Pinheiros bay (Figure 5c).

*Cnidostoma fallax* was particularly abundant in the Laranjeiras bay and in summer 2012, with more than 90% of contribution of total abundance in each one (Fig. 6a; 6b). *Clytia* spp. was more abundant in Pinheiros bay (about 50%), being also abundant in the inlets and mixture zone (~30% of contribution) (Fig. 6a). *Obelia* spp. was more abundant in the inlets (~30%) and mixture zone (~40%); and *L. tetraphylla* in the inlets and Pinheiros bay (~20%) (Fig. 6a). *Clytia* spp. divided the dominance with *Obelia* spp. and *Liriope tetraphylla* in winter 2012 and *C. fallax* and *Obelia* spp. in summer 2013 (~ 30%) (Fig. 6b).

The PERMANOVA indicates significant differences in planktonic hydrozoans assemblage structure in considering temporal (years (seasons);  $P < 0.001$ ) and structural ( $P < 0.01$ ) factors, as well as in its interaction ( $P < 0.01$ ) (Table 3). The pairwise comparisons of the PERMANOVA indicated that the planktonic hydrozoans assemblage structure is similar between inlets and Pinheiros bay, inlets and mixture zone, Paranaguá bay and Laranjeiras bay, Paranaguá bay and mixture zone and mixture zone and Pinheiros bay (Table 4). The PERMANOVA results suggested a structural and temporal relationship in the planktonic hydrozoans assemblage structure, and the cluster analysis identified four distinct assemblage groups at the 40% similarity level, which are mainly formed by each campaign, except for summer 2012 that was dispersed within winter 2012 and 2013 (Fig. 7).

About the cluster analysis, the Group A comprised samples collected in the summer 2013, with *Clytia* spp., *Obelia* spp. and *C. fallax* contributing 80% to the similarity of the group (Fig. 7). Group B primarily contained samples of winter 2012 and samples of inlets and mixture zone of summer 2012. *Obelia* spp., *A. dinema*, *L. tetraphylla* and *E. duodecimalis* had the highest contribution to the similarity matrix (Fig. 7). Group C was an outlier composed by summer 2012, Laranjeiras bay, which shared only ca 30% of similarity with all others and *C. fallax* was the most representative species in this sample (70%) (Figure 7).

Group D contained samples from winter 2013 and samples of Pinheiros and Paranaguá bay of summer 2012, which *L. tetraphylla*, *P. loyola*, *Obelia* spp. and *E. maculata* were the most representative species (Fig. 7).

**Table 2**

Species and their frequency of occurrence (FO), relative abundance (RA), maximum abundance (MaxA), and mean abundance (MA) for summer and winter 2012 and 2013. The taxonomy system follows Schuchert (2015). Dominant species are in bold (> 5 % total abundance).

Species	FO	RA	MaxA	MA 2012		MA 2013	
				Summ er	Winter	Summ er	Winter
Not identified	0.9	<0.1	1.2	<0.1	<0.1	<0.1	<0.1
Actinula larvae	25	0.9	32.3	0.6	0.2	2	0
<b>Order Anthoathecata</b>							
<i>Bougainvillia muscus</i> Allman, 1863	18.9	<0.1	1.6	<0.1	<0.1	<0.1	<0.1
<i>Bougainvillia frondosa</i> Mayer, 1900	2	<0.1	0.3	0	<0.1	0	0
<i>Cnidostoma fallax</i> Vanhöffen, 1911	<b>58.8</b>	<b>52.5</b>	<b>2305.2</b>	<b>119.7</b>	<b>0.3</b>	<b>51.5</b>	<b>&lt;0.01</b>
<i>Hydractinia carica</i> Bergh, 1887	6	<0.1	0.9	<0.1	<0.1	<0.1	0
<i>Podocoryna loyola</i> Haddad, Bettim & Miglieta 2014	8.1	<0.1	2.9	<0.1	<0.1	<0.1	<0.1
<i>Turritopsis nutricula</i> McCrady, 1857	6.7	<0.1	1.8	<0.1	<0.1	<0.1	<0.1
<i>Amphinema dinema</i> Péron and Lesueur, 1810	7.4	0.1	5.5	0	0.3	<0.1	0
<i>Proboscydactila ornata</i> McCrady, 1857	11.5	0.9	61.3	<0.1	<0.1	2.3	<0.1
<i>Corymorpha gracilis</i> Brooks, 1882	54	2.5	55.5	0.5	3	4.1	0.6
<i>Corymorpha forbesii</i> Mayer, 1894	3.4	<0.1	1.3	0	0	<0.1	<0.1
<i>Corymorpha januarii</i> Steenstrup, 1855	1.3	<0.1	2.2	0	0	<0.1	<0.1
<i>Stauridiosarsia reesi</i> Vannucci, 1956	8.9	<0.1	1.1	<0.1	<0.1	<0.1	0
<i>Ectopleura dumortieri</i> van Beneden, 1844	38.5	1.0	34.9	<0.1	1.3	1.8	0.3
<b>Order Leptothecata</b>							
<i>Blackfordia virginica</i> Mayer, 1910	25	<0.1	0.1	<0.1	<0.1	0.1	0.1
<i>Cirrholovenia tetranema</i> Kramp, 1959	2.7	<0.1	0.7	<0.1	0	<0.1	<0.1
<i>Eutima mira</i> McCrady, 1857	2.7	<0.1	0.6	<0.1	0	<0.1	0
<i>Helgicirrha</i> sp.	0.7	<0.1	0.1	0	0	0	<0.1
<i>Laodicea minuscula</i> Vannucci, 1957	2	<0.1	0.1	<0.1	<0.1	0	0
<i>Eucheilota duodecimalis</i> A. Agassiz, 1862	50.7	3.5	74.7	0.4	1.2	9.6	<0.1
<i>Eucheilota paradoxica</i> Mayer, 1900	14.2	<0.1	1.2	<0.1	0.2	<0.1	0
<i>Eucheilota maculata</i> Hartlaub, 1894	0.7	<0.1	2	0	0	0	0.1
<i>Obelia</i> spp.	<b>80.4</b>	<b>13.6</b>	<b>263.8</b>	<b>1.4</b>	<b>6.1</b>	<b>36.6</b>	<b>0.4</b>
<i>Clytia</i> spp.	<b>83.8</b>	<b>18</b>	<b>371.3</b>	<b>2</b>	<b>6</b>	<b>50.7</b>	<b>0.2</b>
<b>Order Siphonophora</b>							

<i>Abylopsis tetragona</i> Otto, 1823	1.3	<0.1	0.2	0	<0.1	<0.1	0
<i>Muggiaea kochi</i> Will, 1844	2	<0.1	1.3	0	<0.1	0	<0.1
<i>Nanomia bijuga</i> delle Chiaje, 1841	4.7	<0.1	2.2	<0.1	0.1	0	<0.1
Order Limnomedusae							
<i>Gossea brachymera</i> Bigelow, 1909	2	<0.1	0.2	<0.1	<0.1	0	0
Order Narcomedusae							
<i>Cunina octonaria</i> McCrady, 1857	2.7	<0.1	1.7	0	<0.1	<0.1	0
<i>Cunina</i> sp.	10.1	0.1	8.1	0	0.1	0.2	0
<i>Solmaris</i> sp.	10.1	<0.1	0.7	0.1	<0.1	0	<0.1
<i>Liriope tetraphylla</i> Chamysso & Eyesenhardt, 1821	<b>71.6</b>	<b>6.5</b>	<b>96.5</b>	<b>0.8</b>	<b>6.9</b>	<b>11.2</b>	<b>1.5</b>
<i>Aglaura hemistoma</i> Péron & Lesueur, 1810	0.7	<0.1	0.1	<0.1	0	0	0

**Table 3**

Results of the PERMANOVA applied for planktonic cnidarians community structure ~ years(seasons) x sectors. Years are 2012 and 2013, Seasons are summer and winter and Sectors are Paranaguá, Laranjeiras and Pinheiros bays, mixture zone and inlets. Number of permutations = 999.

Source	df	P value
Years (Seasons)	1	<b>0.001</b>
Sectors	4	<b>0.01</b>
Years (Seasons) X Sectors	2	<b>0.008</b>
Residual	96	
Total	103	

**Table 4**

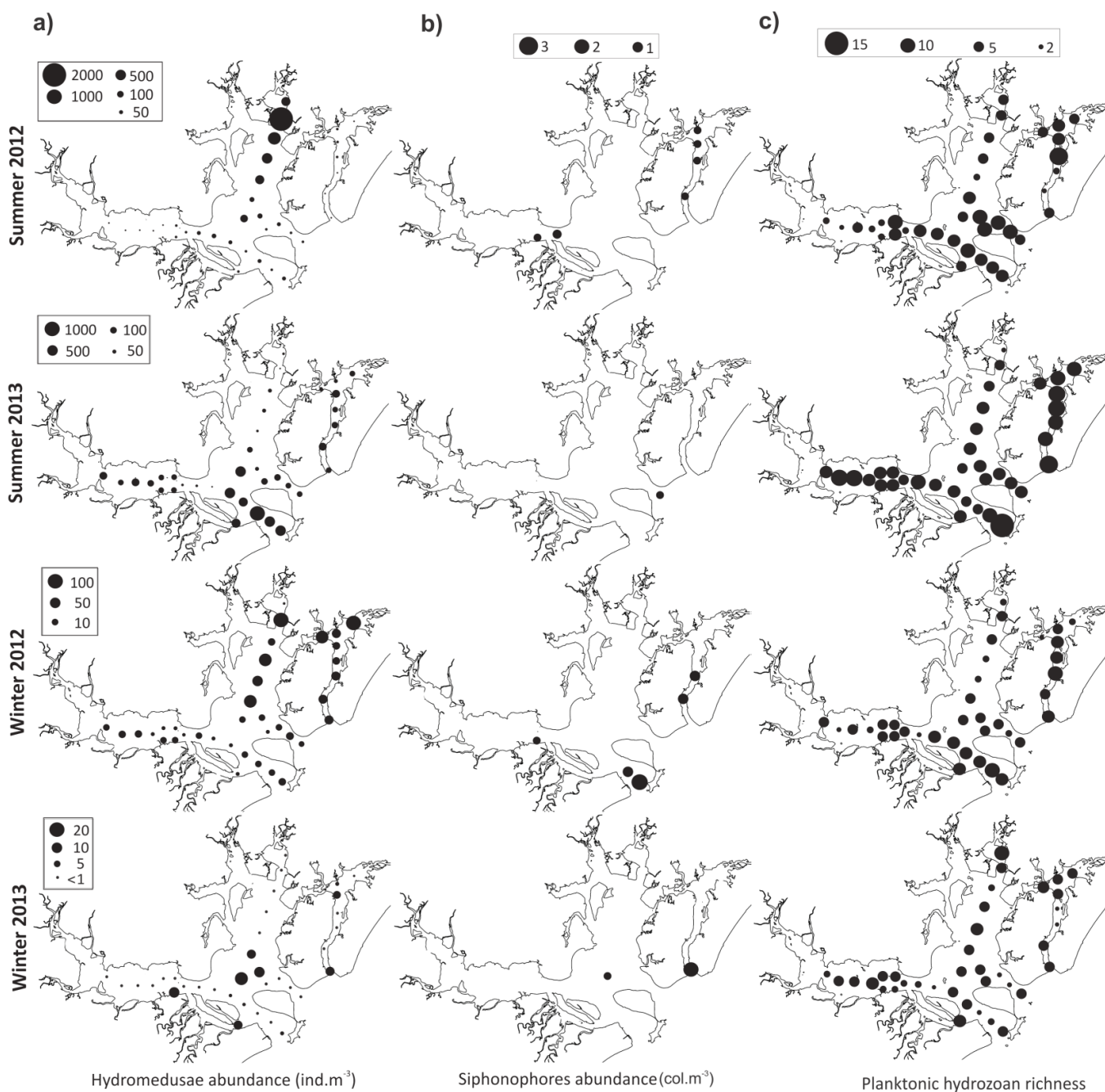
Results of pairwise PERMANOVA applied for sectors of Paranaguá Estuarine System. Number of permutations = 999. *df* = degrees of freedom; *t* = parameter calculated by the test; ns = not significant.

Groups	<i>t</i>	P value
Inlets, Paranaguá bay	2.55	<b>0.01</b>
Inlets, Laranjeiras bay	2.07	<b>0.01</b>
Inlets, Mixture zone	0.93	Ns
Inlets, Pinheiros bay	1.39	Ns

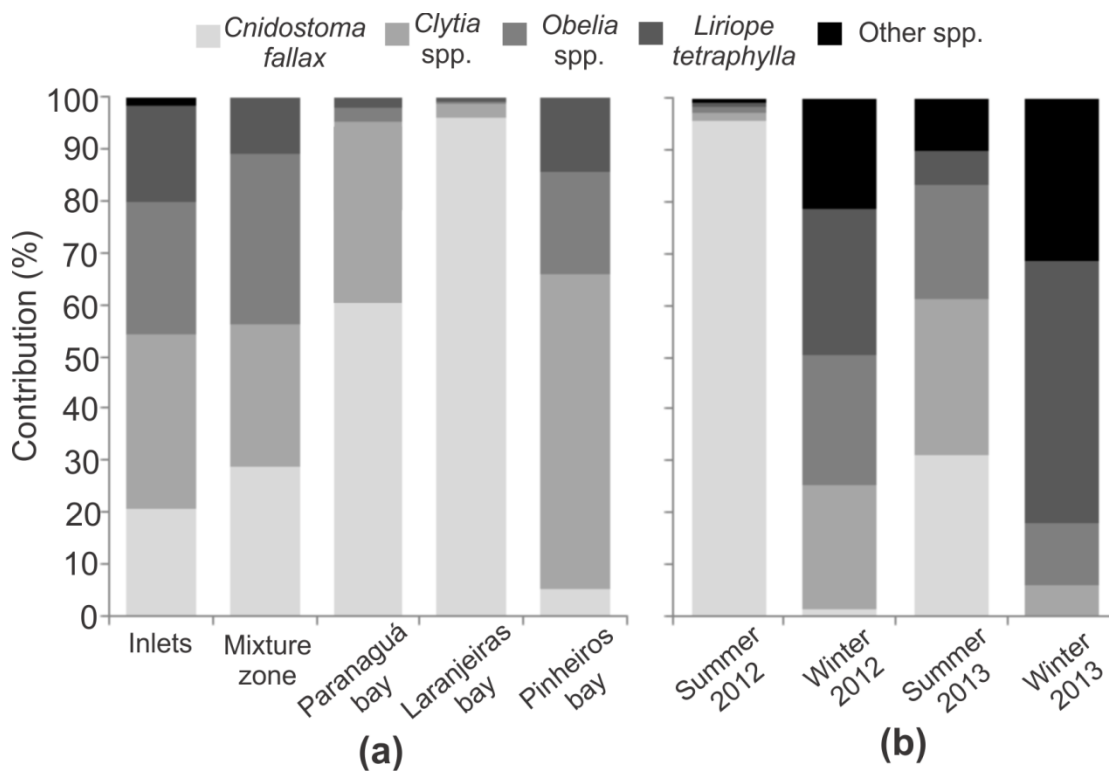
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<b>Paranaguá bay, Laranjeiras bay</b>	1.37	<b>0.04</b>
<b>Paranaguá bay, Mixture zone</b>	1.26	Ns
<b>Paranaguá bay, Pinheiros bay</b>	1.46	<b>0.05</b>
<b>Laranjeiras bay, Pinheiros bay</b>	2.32	<b>0.01</b>
<b>Laranjeiras bay, Mixture zone</b>	2.40	<b>0.01</b>
<b>Mixture zone, Pinheiros bay</b>	1.79	<b>0.05</b>

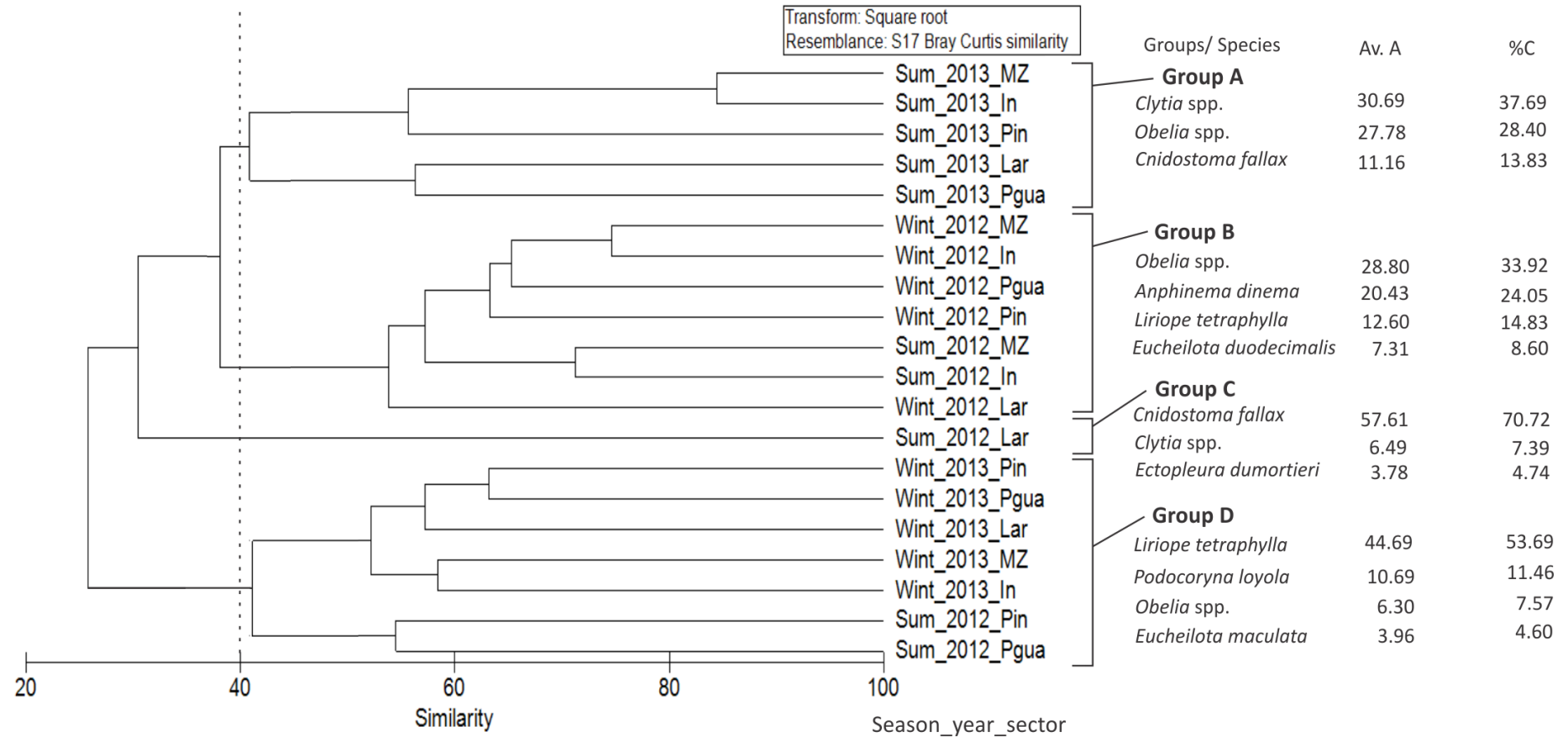
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**Fig. 5.** Structural and temporal distribution of hydromedusae abundance (ind.m<sup>-3</sup>) (a), siphonophores abundance (col.m<sup>-3</sup>) (b) and planktonic hydrozoans species richness (c) in Paranaguá Estuarine System during summer and winter 2012 and 2013. Col = colonies.



**Fig. 6.** a) Contribution (%) of *Cnidostoma fallax*, *Clytia* spp., *Obelia* spp., *Liriope tetraphylla* and other species found in this study for each Paranaguá Estuarine sector (a) and for summer and winter 2012 and 2013 (b).



**Fig. 7.** Cluster dendrogram based Bray-Curtis similarity measures, and similarity percentage analyses of planktonic cnidarians abundance from the Paranaguá Estuarine System. The cluster analysis identified four distinct assemblage groups at the 40% similarity level.

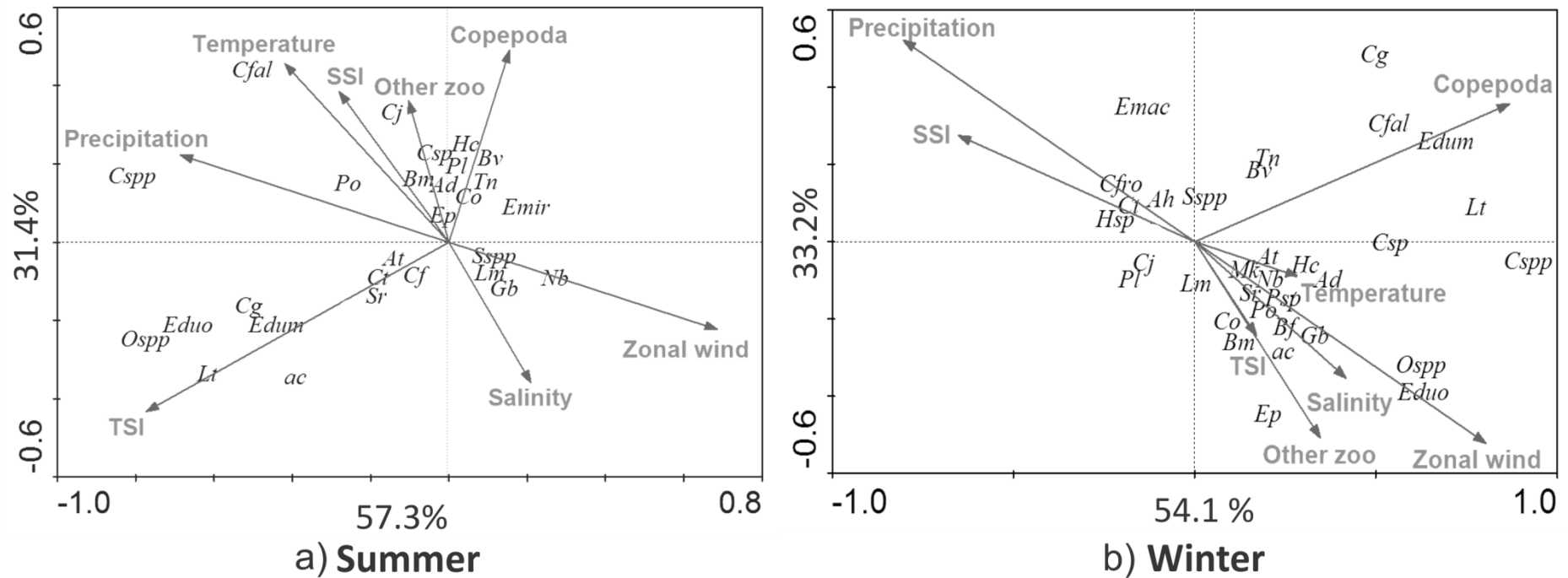
### 3.4 Relationship of planktonic hydrozoans with environmental variables and food availability

The Redundancy analysis (RDA) demonstrates the relationship of each taxa with environmental factors for summer and winter (Fig. 8a; 8b). In the summer RDA, a total of 88.7% of the cumulative variance of the taxa-environment relationship was represented by the first two axes, and the significance test of Monte Carlo showed that there are significant associations between environmental variables and planktonic hydrozoans ( $P = 0.002$ ). The Monte Carlo test detected significant relationships between planktonic hydrozoans and explanatory variable. Subsurface temperature and salinity were respectively positively and negatively related with *C. fallax* (Fig. 8a). Higher precipitation rates and lower wind zonal component were associated with *Clytia* spp., while higher TSI was well related to *L. tetraphylla*, *Obelia* spp., *E. dumortieri* and actinula larvae (Fig. 8a). In winter, these taxa had different relationships with the environmental variables, and the influence of subsurface temperature and salinity and TSI was less pronounced (Fig. 8b).

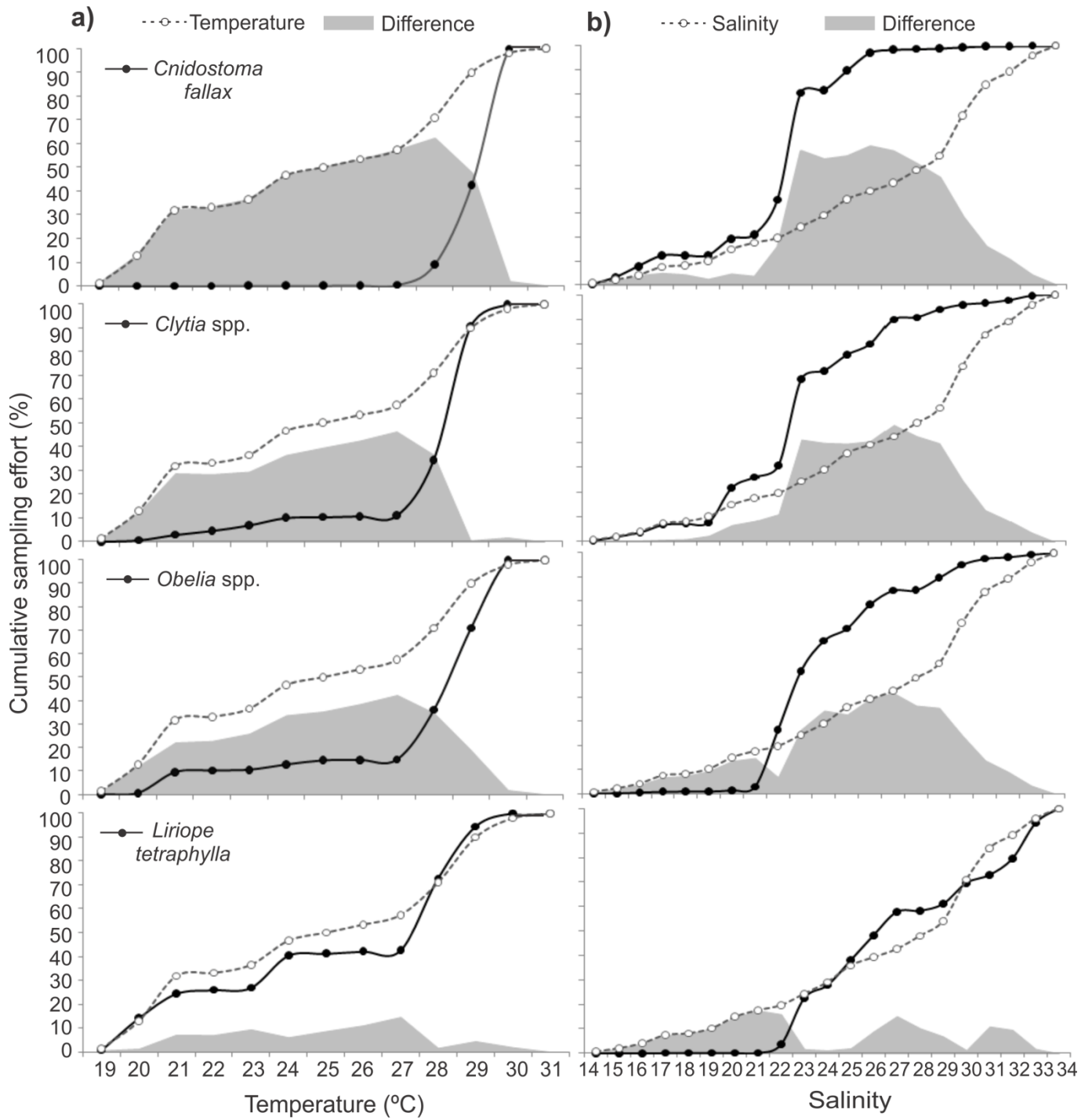
In winter RDA, a total of 87.3% of the cumulative variance of the taxa-environment relationship was represented by the first two axes, and the significance test of Monte Carlo also showed significant associations between environmental variables and planktonic hydrozoans ( $P = 0.002$ ). Water transparency depth and meridional winds were also excluded from the model, because these environmental variables did not have significant relationships between planktonic hydrozoans. *Cnidostoma fallax*, *E. dumortieri* and *C. gracilis* were positively related to copepod abundance, while *Obelia* spp. and *E. duodecimalis* were mainly associated to higher wind zonal component, and *E. paradoxica* was positively related to other zooplankton abundance (Fig. 8b). Those taxa with weak or variable relationships are situated close to the axes origin (Fig. 8a; 8b).

*Clytia* spp. and *Obelia* spp. presented the highest difference between the temperature and abundance curves at 27°C, becoming more abundant from this temperature, and *C. fallax* was only captured at this temperature (Fig. 9a). *Liriope tetraphylla* had abundance curve similar to temperature curve, being captured in all temperature values (Fig. 9a). *Cnidostoma fallax*, *Clytia* spp. had

highest capture percentage at salinity 21, with highest differences between curves from this interval until salinity 29 (Fig. 9b). Both, *Obelia* spp. and *Liriope tetraphylla* occurred only in salinities higher than 21 and 22, respectively, the later being abundant in all salinities higher than this (Fig. 9b).



**Fig. 8.** Ordination diagram of canonical Redundancy Analysis (RDA), axis 1 and 2, in the PES for summer (a) and winter (b) campaigns. Planktonic hydrozoans codes: ac = actinula larvae, Ad = *Amphinema dinema*, Ah = *Aglaura hemistoma*, At = *Abylopsis tetragona*, Bf = *Bougainvillia frondosa*, Bm = *Bougainvillia muscus*, Bv = *Blackfordia virginica*, Cfal = *Cnidostoma fallax*, Cf = *Corymorpha forbesii*, Cg = *Corymorpha gracilis*, Cj = *Corymorpha januarii*, Co = *Cunina octonaria*, Csp = *Cunina* sp., Csp = *Clytia* spp., Ct = *Cirrholovenia tetranema*, Eduo = *Euceilota duodecimalis*, Edum = *Ectopleura dumortieri*, Emac = *Euceilota maculata*, Ep = *Euceilota paradoxica*, Gb = *Gossea brachymera*, Hc = *Hydractinia carica*, Hsp = *Helgicirrho* sp., Lm = *Laodicea minuscula*, Lt = *Liriopha tetraphylla*, Mk = *Muggiaea kochii*, Nb = *Nanomia bijuga*, Ospp = *Obelia* spp., Pl = *Podocoryna loyola*, Po = *Proboscicydactila ornata*, Sr = *Stauridiosarsia reesi*, Sspp = *Solmaris* spp., Tn = *Turritopsis nutricula*. Environmental codes: TSI = Temperature Stratification Index; SSI = Salinity Stratification Index.



**Fig. 9.** Cumulative sampling effort (%) for temperature (a), salinity (b) and the most abundant species (*Cnidostoma fallax*, *Clytia* spp., *Obelia* spp. and *Liriope tetraphylla*) captured in Paranaguá Estuarine System. The shaded area represents the difference is the subtraction of cumulative sampling effort in the temperature and salinity range per % cumulative sampling effort for species density in the same temperature and salinity range.

#### 4. Discussion

Our study showed that planktonic hydrozoans assemblage varied structurally and temporally in PES (Table 3). The high structural sampling resolution adopted allowed to observe marked differences mainly in distant sectors and among those sectors that have different land-ocean influences (Table 4). The structural distribution also varied significantly in time (Table 3), and higher abundances occurred in Laranjeiras bay in summer 2012 and in the inlets and mixture zone in summer 2013 (Fig. 5a). Then, the hypothesis “ii) the temperature increase coupled with the food availability can promote the production and release of jellyfish, then we expected that the planktonic hydrozoans abundance will be higher in the warmest sampling campaigns” was confirmed because summer campaigns had higher temperatures; and the hypothesis “iii) if large concentrations of nutrients in the ‘estuarine turbidity maximum zone’ (ETMZ) in the Paranaguá and Antonina bays during the summer favor the aggregation of copepods and other zooplan” was refuted.

Two abundance peaks were recorded:  $> 2,300 \text{ ind.m}^{-3}$  in summer 2012 and  $1,094 \text{ ind.m}^{-3}$  in summer 2013. Highest abundance in warmest periods were previously recorded for assemblages in temperate regions (e.g. Larson, 1986; Zamponi and Genzano, 1994; Ballard and Myers, 2000; Hosia and Bamstedt, 2007; Hosia and Bamstedt, 2008; Primo et al., 2012). Nevertheless, the structural and temporal distributions of planktonic hydrozoans in PES seem to be mainly related to species preferences towards local and regional environmental factors. These specific environmental preferences favored greater richness in the outer portions of the bay, thus confirming the hypothesis “whether the marine species of hydrozoans are more numerous, and salinity affect their structural distribution, so we expect to find a decrease in the planktonic hydrozoans richness from downstream to upstream in the PES”.

The stress caused by structural and temporal variations in the environmental factors and the low horizontal locomotion capacity of most species (Costello et al., 2008) favored the occurrence of species tolerant to salinity variations in PES. Thus, confirming the hypothesis that most of planktonic hydrozoans in estuarine regions are composed by euryhaline species (Santhakumari et al., 1999), with few species being considered only estuarine or even oceanic. Mostly siphonophores species are referred as truly oceanic (Pugh, 1999), though its presence has already been detected also in bays and estuarine waters (e.g. Byrne, 1995; Sanvicente-Añorve et al., 2009, Primo et al., 2012; Nogueira Júnior, 2012), usually occurring, and in some cases in high abundances (Sanvicente-Añorve et al., 2009, Primo et al., 2012). In the PES, siphonophores were not as diverse and abundant as hydromedusae, and its sporadic presence inside the estuary is probably related to high salinity values and other specific conditions.

Surprisingly, *Cnidostoma fallax* was the dominant species in the present study, representing about 50% of total planktonic hydrozoans abundance, and more than 90% of summer 2012, being responsible for the peak of abundance in this campaign (Table 2; Fig. 6b). Its dominance and higher abundances calls attention, because it was never reported in other studies carried out in coastal subtropical Brazil, where *L. tetraphylla* has recurrently been reported as dominant (Vanucci, 1957, Montú & Cordeiro, 1988, Tronolone, 2007, Nogueira Júnior, 2012, Nagata et al., 2014b, Nogueira Júnior et al., 2014; 2015a). The highest abundance of *L. tetraphylla* in Brazil was registered in shallow waters off PES, with  $> 900 \text{ ind.m}^{-3}$  (Nagata et al., 2014b). Therefore, the maximum abundance of *C. fallax* estimated here is more than two folds higher ( $> 2,000 \text{ ind.m}^{-3}$ ), and is the highest hydromedusae density recorded in Brazilian coast (Montú & Cordeiro, 1988; Tronolone, 2007; Bardi, 2011; Nagata et al., 2014b; Nogueira Júnior et al., 2014, 2015). However, *C. fallax* was never captured in PES (Montú & Cordeiro, 1988; Bardi, 2011) and in adjacent waters (Nagata et al., 2014b), and we distrust that it is an introduced species in PES and nearby estuaries (see Discussion in “Capítulo I”).

The results presented herein strengthen the hypothesis that the species occur in higher abundances in the estuary than in adjacent shelf waters, due to the continental proximity and influences by inputs from the rivers (e.g. Chícharo

et al., 2001; 2006, Resgalla Júnior, 2011). The freshwater input carries nutrients that usually fertilize estuaries, which associated to the sheltered morphology, hydrology and the mixing process within estuaries, favor the development of the primary productivity and plankton community in its environment (Schelske & Odum, 1961; Miranda et al., 2002; Kimmerer, 2002), including planktonic hydrozoans assemblage (e.g. Navas-Pereira, 1980; Benovic and Lucic, 1996; Ballard and Myers, 2000; Primo et al., 2012; Nogueira Júnior, 2012).

Previous studies have shown the importance of the continental drainage as main source of nutrients and organic matter in the PES, mainly in the summer (Machado et al., 1997; Marone et al., 2005; Mizerkowski et al., 2012). Although, ecological process and zooplankton responses to this enrichment are still uncertain (Marone et al., 2005), the increases in the abundance of planktonic hydrozoans and other zooplankton groups in the summer (Fig. 4d; f) were probably associated with an increased in continental drainage and nutrient concentration in this season. Higher planktonic hydrozoans abundance has already been associated with increased precipitation and food availability in tropical regions (Santhakumari, 1999). The second most abundant species in this study, *Clytia* spp., was positively associated to precipitation in RDA summer analysis (Fig. 9a), corroborating this hypothesis. The opposite is also true, since planktonic hydrozoans abundance was considerably lower during winter campaigns (Fig. 5a).

Furthermore, increasing temperature is considered one of the most important factors controlling reproduction and proliferation of planktonic hydrozoans (Carré and Carré, 1990; 1991; Arai, 1992; Bavestrello et al., 2006). Indeed, the most abundant taxa, *C. fallax*, *Clytia* spp. and *Obelia* spp., occurred mainly in greatest abundance in temperatures higher than 27 °C (Fig. 9a) and *C. fallax* was especially related to subsurface temperatures in the summer (Fig. 9a). The majority of the specimens of *C. fallax* collected in the PES had medusae buds. Asexual reproduction through the production of medusae buds in *P. ornata*, *E. paradoxica* and *N. dendrotentaculata* can rapidly produce a dense population (Berril 1950; Carré and Carré 1990; Boero et al. 2008; Kawamura and Kubota, 2008). Laboratory experiments showed high bud production of *P. ornata* in Japan, and *E. paradoxica* in the Mediterranean under specific temperatures: 20 °C (Kawamura and Kubota, 2008) and 24 °C (Carré

and Carré, 1990), respectively. In the Paraná coast, *E. paradoxica* and *P. ornata* were mostly found in higher temperatures (25–27°C; Nagata et al., 2014b). Considering the similar asexual reproduction, *C. fallax* could also perhaps respond to higher and specific temperatures as these species, as shown in the present study, and maybe the higher temperatures registered in summer campaigns may have favored the production of *C. fallax* jellyfish in the PES. Gonads from *C. fallax* were never described (e.g. Bouillon, 1999) and the captured specimens are mostly caught with medusoids shoots (Picard and Rahm, 1954; Kramp, 1959b; Nogueira Júnior, 2012; the present study). These are indications that asexual reproduction is the main strategy of *C. fallax* reproduction, as it is the case of *Proboscycyda ornata* (Kawamura and Kubota, 2008), and probably the standard of higher rate of asexual reproduction at higher temperatures is repeated also for this species.

*Cnidostoma fallax* was the only dominant species in summer 2012 (Fig. 6b). Summer 2012 had higher temperatures and salinities and homogeneous structural distribution of these environmental variables (Fig 2; 3), probably related to the lower precipitation rate than in summer 2013 (Table 1). Higher salinities and homogeneous vertical layer are similar conditions to some winter condition in PES (Mantovanelli et al., 2004; Marone et al., 2005). In fact, according to the cluster analysis, planktonic hydrozoans assemblage structure in summer 2012 was similar to winter campaigns, except for the peak abundance in the Laranjeiras bay, which separates this sector in summer 2012 from the other campaigns (Fig. 7). Besides PES, *C.fallax* also occurred in higher abundances ( $> 11.000 \text{ ind.m}^{-3}$ ; 28°C and salinity 10) in March 2012, in Patos Lagoon, a coastal lagoon ~ 800 km southwards PES, in Rio Grande do Sul. Then, some specific regional environmental characteristics in this period may be also related to these high abundances in coastal systems in southern Brazil. Both coastal systems were under the influence of a La Niña event in March 2012 and probably this large-scale phenomenon caused the lower precipitation rates in the region and influenced especially the *C. fallax* abundance.

On the other hand, summer 2013 presented higher precipitation rates, which consequently caused the stratified condition in this campaign (Fig. 3; 4a; 4b) and may have favored the abundance of hydromedusae which were not as

abundant in the summer 2012 (Table 2; Fig. 6b). As examples *Clytia* spp., *Obelia* spp., *L. tetraphylla*, *Eucheilota duodecimalis*, *Proboscya ornata* and actinula larvae were more abundant in summer 2013, and the first three taxa were particularly important to the abundance peak recorded during this campaign (Fig. 6b). These species are common and abundant in the adjacent shelf (Nagata et al., 2014a; b) and its abundances were higher in outer portions of the estuary, mainly in summer 2013 and in winter campaigns. Some results present in the present study and previous studies corroborate this condition for these species: i) *Liriope tetraphylla*, *Obelia* spp. and *Eucheilota duodecimalis* were related to high TSI in the summer (Fig. 9a), corroborating their positive relationship with major stratifications in the outer portions; ii) *Obelia* spp. and *E. duodecimalis* were also positively related to higher zonal winds in the winter, probably indicating their dispersion inside out estuary; iii) *Proboscya ornata* is a shelf water mass indicator (Vannucci, 1957), being especially abundant in the continental shelf in Brazilian waters (Vannucci, 1957; Navas-Pereira, 1980; Nagata et al. 2014b), as well as, actinula larvae, which apparently are more abundant in the shelf than in estuaries (Nogueira Júnior, 2012, Nogueira Júnior et al., 2014; the present study).

The occurrences of typical neritic species in the PES increased the richness in the summer 2013 and winter campaigns (Fig. 5c). In the winter, the planktonic hydrozoans richness was also influenced by siphonophores species, when their occurrence and richness was higher (Table 2; Fig. 5b). It is likely caused by near-shore accumulation by the arrival of cold fronts with strong south-easterly winds that may cause coastward advection of planktonic populations (Nagata et al., 2014b). Siphonophores are holoplanktonic organisms and have high vulnerability to currents and water mass movements (Pugh, 1999; Mapstone, 2014) and may result in transport inside the estuary. The siphonophore *Muggiaea kochii* occurred only in winter campaigns in the PES. *Muggiaea kochii* is one of the few siphonophores which prefer coastal waters (Abreu and Nogueira, 1989; Cordeiro and Montú, 1991; Nogueira and Oliveira, 1991; Nogueira Júnior, 2012). It is abundant throughout the year in the Paraná continental shelf, however only in the winter it occurred in stations closer to the coast (-10 e -15 m depth) (Nagata et al., 2014b), suggesting that

winter conditions may carry this species to shallow waters and probably favor its entry into the estuary.

Other exclusive temporal occurrences in PES may also be connected to meteorological conditions. *Aglaura hemistoma* occurred only in the PES in summer 2012. In Brazil, *Aglaura hemistoma* is common in the middle and outer shelf and occasionally reaches coastal waters, supporting salinities from 33 to 36.9 (Vannucci, 1957; 1963; Tronolone, 2007; Nagata et al., 2014a; b; Nogueira Júnior et al., 2015a). In summer 2012 was registered the highest salinity values (mean of 34) and the predominance of east winds which may have favored the transport of this species to the estuary. In addition, the incidences of east winds and the high salinities registered in summer 2012 may also favored the siphonophore *Nanomia bijuga* entry more into the estuary than in other campaigns (Fig. 5b). *Bougainvillia frondosa* a rare coastal species found in continental shelf regions (Moreira, 1973; Goy, 1979; Navas-Pereira, 1981; Migotto et al. 2002; Nagata et al., 2014a; b) occurred only in the winter 2012. This hydromedusa was found throughout the year in the Paraná coast (-25 to -40 m depth) (Nagata et al., 2014b). In the present study, the low precipitation (about 0 mm) observed in winter 2012 and higher salinities may have also favored the occurrence of *B. frondosa* in the estuary.

Despite the low zooplankton abundances in the winter apparently indicate low food availability, *Corymorpha gracilis*, *E. dumortieri* and *C. fallax* were positively related to copepod abundance in winter campaigns (Fig. 9b). *Corymorpha gracilis* is a meroplanktonic species previous observed in estuaries in south and southeast Atlantic (Navas-Pereira, 1980; Nogueira Júnior, 2012) which is apparently dependent on the food availability, because its highest concentrations were coincident with high abundances of not gelatinous zooplankton in the south Brazilian Bight (Nogueira Júnior et al., 2014). *Ectopleura dumortieri* was mainly registered in the winter in the PES (Bardi, 2011), in Sepetiba bay (Navas-Pereira, 1980) and in Chesapeake bay (Calder, 1971), which may be related to favorable conditions for jellyfish formation and release, as temperature and food available at this season. However *C. fallax* relationship with the copepods is probably indirect, because apparently copepods are not its food source and both can benefit from other planktonic group(s). Information about *C. fallax* diet is not available, however probably *C.*

*fallax* has the same microphagous feeding habits than *Obelia* spp. (Fulton and Wear, 1985; Boero et al., 2007), considering their similar sizes of mouths. Given the shorter generation times and the higher metabolic rate of microplankton its effects in the following trophic levels are often faster and more efficient than the mesozooplankton (Buskey, 1993; First et al., 2007), and probably caused the higher abundances registered for *C. fallax* in the present study.

Planktonic hydrozoans were more abundant in the Laranjeiras bay and other zooplankton groups were more abundant in the Paranaguá bay (Fig. 4d; 4e; 4f). High abundances of other zooplankton in the Paranaguá bay may have been related to the occurrence of a known ETMZ around the harbor area, between Antonina and Paranaguá bay (Mantovanelli et al., 2004; Cattani and Lamour, 2015). In fact, lowest transparency water depths were in general registered in Paranaguá bay (Fig. 4c). The ETMZ act as a trap favored by a convergence zone, contributing to an accumulation of organic matter (Herman and Heip, 1999; Leonov and Nemirovskaya, 2011), enhancing the trophic transfers and favoring zooplankton concentration by abundant food (Bernát et al., 1994; Dejen et al., 2004) as already observed in the Paranaguá bay (Lopes et al., 1998; Salvador, 2015). The same is true in the La Plata River estuary, where a similar barrier, a bottom saline front associated to a EMTZ (Nagy et al., 2008; Acha et al., 2008), entraps planktonic organisms (Berasategui et al., 2006; Acha et al., 2008; Derisio et al., 2014). Jellyfish aggregation has already been associated to physical barrier (Arai, 1992; Graham et al., 2001), however, apparently this EMTZ between Paranaguá and Antonina bays does not favored the abundance of planktonic hydrozoans in this region and the lowest abundances were recorded in Paranaguá bay in all sampling campaigns.

However, apparently another front zone favored the abundance of planktonic hydrozoans in the present study. The low precipitation rates and easterly winds during summer and winter 2012 may have favored the aggregation of planktonic hydrozoans in inner and shallow portions of the estuary, in the Laranjeiras bay (Fig. 5a). *Cnidostoma fallax* was the most important species of this sector (Fig. 6a; 7). Moreover, the well mixed conditions observed in summer 2012 may have increased the concentration of suspended particles in the water column, acting as an alternative source of nutrients and organic matter to Laranjeiras bay, favoring especially *C. fallax* population.

On the other hand, the horizontal heterogeneity and aggregations in assemblage in summer 2013 must have been caused by advective processes, which are usually dominant under conditions of high vertical stratification (Matonvanelli et al., 2004), and probably it was the responsible for distributing planktonic hydrozoans throughout the estuary and concentrate its abundance in outer stations.

The same pattern of occurrence in outer portions of the estuary was observed for *L. tetraphylla* in the Babitonga bay (Pukanski, 2011) and in another tropical estuary, in India (Santhakumari et al., 1999). In PES, adults *L. tetraphylla* occurred mainly in stations with marine influences (Bardi, 2011; the present study). Its occurrence in outer portions is probably related to coastward transport which brings adult hydromedusae from adjacent shelf waters in addition to nutrient enriched conditions (Brandini et al., 2000; 2007).

Siphonophores occurred only in the inlets and mixture zone and outer portions of Pinheiros bay (Fig. 5b), as well as the hydromedusa *Ectopleura dumortieri* (Bardi, 2011; the present study), *Proboscycodactyla ornata* and actinula larvae. These occurrences may be related to species environmental preferences (as salinity condition), and contributed to the higher richness in the downstream estuary, mainly in the south inlet (Fig. 5c). Indeed, there is an increasing trend of the species richness of planktonic hydrozoans in larger and more stable salinities (Santhakumari, 1999). Nevertheless, typical estuarine species and with brackish waters affinities were mainly or even exclusively captured in the upstream estuary and did not occur in adjacent shallow shelf (Nagata et al., 2014 a; b), as *Blackfordia virginica*, *Cnidostoma fallax*, *Podocoryna loyola*; *Helgicirrha* sp., *Corymorpha januarii*, *Laodicea minuscula* and *Eutima mira*. Despite these exceptions, most species occurred in a wide range of salinities and in various portions of the estuary, probably because most species are euryhaline and due to the environmental factors variations in sectors and time. Making unclear the assemblage division between inner, intermediate and outer portions in the estuary, as already noted in other studies for substrate particle size, chlorophyll, turbidity, salinity, water temperature, suspended particulate matter and fishes assemblages (Lamour et al., 2004; Cattani and Lamour, 2015; Possato, 2015).

The circulation alone often cause or favor planktonic hydrozoans aggregations, however, the interactions between the biology of the animal and physics characteristics of the water are other very important sources of the structural distribution in its abundance and composition, especially at local scales (Graham et al., 2001), as noted in the present study. Planktonic hydrozoans assemblage in PES was similar at the mixture zone and Paranaguá bay, which are nearby areas, probably influenced by the same factors (Fig. 1, Table 4). As well as, in the mixture zone, Paranaguá bay receives pronounced marine influence, due to more intense water circulation because of constant dredging and port activities that enabled the penetration of coastal waters and marine zooplankton further into this bay, as already observed by Miyashita et al. (2012) and Salvador (2015). The inlets are similar to the mixture zone and Pinheiros bay, which have also more marine influences due to direct incoming seawater. Laranjeiras bay planktonic hydrozoans assemblage differs significantly from the other sectors; probably because this bay does not have a direct connection to the ocean and land influences are more pronounced, supporting, in general, lower planktonic hydrozoans diversity and higher abundances.

In general, planktonic hydrozoans were more abundant in the winter in the Paraná coast (Nagata et al., 2014), as well as in Sepetiba bay, Rio de Janeiro (Navas-Pereira, 1980). In a previous study in the Paranaguá bay (Montú and Cordeiro, 1988) and in the Babitonga bay (Pukanski, 2011, Nogueira Júnior, 2012) higher abundances occurred in early spring. However, in the Rio Caeté estuary, Pará (Mesquita et al., 2006), in Rio Sergipe estuary, Sergipe (Araújo et al., 2008) and in other recent study carried out in the PES (Bardi, 2011) higher abundances occurred in the summer, as observed in the present study. These seasonal discrepancies in studies carried out in tropical and subtropical regions may suggest that the temporal variations in the assemblage does not have a seasonal pattern and succession as observed in temperate regions (Mills, 1981; Larson, 1986; Ballard and Myers 2000; Greve et al., 2004; Hosia and Bamistedt, 2007; 2008; Gibbons and Richardson, 2009; Primo et al., 2012), as previously observed by Nagata et al. (2014). Indeed, subtropical coastal environments are considered regions without seasonality

(e.g. McClanahan, 1988), because some environmental factors are not necessarily typical of any season.

Moreover, studies of planktonic hydrozoans distributions are difficult because they have great variability among different species (Bouillon, 1999; Bouillon et al., 2004), responding different to environmental factors. Some species can produce resting stage and release active stages (juvenile and adult) when resources are not limiting and environmental conditions favour population growth (Edwards 1973; Boero et al. 1992; Marcus and Boero, 1998), causing high abundances in a given period, however very little is known about this lifecycle strategy and about which species can produce it. Besides this, changes in life history traits involve alternate periods of rarity and commonness according to resource availability (Boero et al., 2008), as a natural variation of each species. Then, planktonic hydrozoans may activate some resting stage or stimulating reproduction, and favor the proliferation of one species depending on the environment conditions.

Furthermore, the regional and interannual variability of environmental factors makes these comparisons even more complex. In the present study, precipitation rates showed higher interannual variability, with the highest peak abundance occurring in summer 2012, during an atypically dry summer period caused by a La Niña event. Climatic events of large scale were already associated to changes in hydromedusae assemblage in an estuarine environment (Raskoff, 2001) and should also be considered in temporal analysis. Similar interannual variation in meteorological condition was previously related with changes in zooplankton assemblages in the PES (Salvador, 2015) and changes in hydromedusae assemblages in other tropical and subtropical estuaries (Santhakumari et al., 1999; Mesquita et al., 2006).

Here we took into account wide and representative assemblage variability. The mesh size used in the present study (200 $\mu$ m) is appropriate to quantitatively sample planktonic hydrozoan assemblages (Nogueira Júnior et al., 2015b), as well as, the sampling strategy was efficient for both temporal and structural distribution evaluation. However, further studies with shorter sampling intervals (i.e. monthly, weekly, daily) and long-term monitoring programs should be implemented to better account for the interannual variability in PES and better verify distributions patterns. Moreover, studies on anthropogenic factors

(global warming, eutrophication, acidification and biological invasions) need to be carried out to evaluate their effects on the assemblage dynamics.

## CONSIDERAÇÕES FINAIS & CONCLUSÕES

A partir do estudo dos hidrozários planctônicos do Complexo Estuarino de Paranaguá (CEP) e da análise de sua variação espaço-temporal foi possível, pela primeira vez, fazer um levantamento taxonômico-faunístico abrangente da assembléia na região e tão detalhado para a assembléia no Brasil. Tal feito tornou possível preencher lacunas na distribuição geográfica de algumas espécies, conhecer melhor a distribuição espaço-temporal desse importante grupo planctônico, verificar possíveis modificações na fauna, e conhecer quais fatores e processos ambientais influenciam suas distribuições.

*Cnidostoma fallax*, *Amphinema dinema*, *Corymorpha forbesii*, *Corymorpha januarii*, *Stauridiosarsia reesi*, *Eutima mira*, *Laodicea minúscula* e *Helgicirrha* sp. foram registradas pela primeira vez na costa do Paraná (Nagata et al. 2014a). A fauna de hidrozários planctônicos no CEP é similar a fauna encontrada em sistemas estuarinos próximos como a Baía da Babitonga (Nogueira Júnior, 2012), o estuário de Cananéia (Martinez et al., 2015), e à plataforma rasa adjacente (Nagata et al., 2014a). Estas semelhanças se devem provavelmente à proximidade desses ambientes e à comunicação entre o estuário e a plataforma que permitem que as mesmas espécies ocorram.

O CEP é composto principalmente por espécies eurihalinas, como pode ser observado em outras regiões estuarinas (Santhakumari, 1999; Nogueira Júnior, 2012; Primo et al., 2012), as quais ocorrem, em sua maioria, em uma ampla variação de salinidade, embora as maiores diversidades foram observadas em porções mais externas do estuário. Desta forma a hipótese “i) se as espécies marinhas de hidrozários são mais numerosas, e se a salinidade influencia a distribuição espacial dos hidrozários planctônicos, então espero encontrar um decréscimo na riqueza de hidrozários planctônicos de jusante à montante no CEP” foi em parte corroborada, pois apesar de não termos notado um nítido decréscimo na riqueza de hidrozários planctônicos de jusante à montante e da salinidade ter apresentado variações sazonais e interanuais, no geral, as maiores riquezas ocorrem à jusante do estuário.

Hidromedusas meroplanctônicas foram as mais abundantes e freqüentes e aparentemente os picos de abundância dos hidrozários planctônicos no CEP ocorrem nas mesmas condições de regiões temperadas: em estações do

ano mais quentes associadas à maior disponibilidade de alimento (e.g. Larson, 1986; Zamponi & Genzano, 1994; Ballard & Myers, 2000; Hosia & Bamstedt, 2007; Hosia & Bamstedt, 2008; Primo *et al.*, 2012). O incremento na disponibilidade de alimento no CEP provavelmente esteve relacionado aos períodos de maiores precipitações que aumentam a concentração de nutrientes no estuário pelo aumento da drenagem continental. A relação entre o aumento da abundância de hidrozoários planctônicos e da precipitação já foi observado em outros estuários em regiões tropicais (e.g. Shantakumari, 1999). Além disso, as temperaturas de verão parecem favorecer a produção de medusas meroplanctônicas, como *Cnidostoma fallax*, que representou mais de 50% dos hidrozoários e mais de 90% da abundância no verão de 2012, dividindo a dominância com *Clytia* spp. e *Obelia* spp. no verão de 2013. Corroborando assim a hipótese “ii) se o aumento de temperatura aliada à disponibilidade de alimento pode favorecer a produção e liberação de medusas, então a abundância dos hidrozoários planctônicos será maior nas campanhas de verão”.

Em geral, o zooplâncton foi mais abundante no verão, entretanto, não observamos distribuições espaciais semelhantes entre os hidrozoários planctônicos e copépodes, presas comuns desses organismos (Purcell & Arai, 2001; Bouillon *et al.*, 2004). Nas proximidades da cidade de Paranaguá e na Zona da máxima turbidez não ocorreram as maiores concentrações de hidrozoários planctônicos, diferentemente dos outros grupos zooplanctônicos. Maiores concentrações desses organismos foram principalmente encontradas na Baía de Laranjeiras e desembocaduras. A distribuição horizontal dos hidrozoários planctônicos no CEP parece estar mais associada às condições meteorológicas, às áreas abrigadas, à circulação e estratificação estuarina e ao aporte de nutrientes no interior do estuário do que ao acúmulo de matéria orgânica em suas porções medianas. Refutando assim a hipótese “iii) se as grandes concentrações de nutrientes na Baía de Paranaguá e na Zona de Máxima Turbidez durante o verão favorecem a agregação de copépodes e outros zooplâncton nesta região, então espero que o mesmo ocorra para os hidrozoários planctônicos”.

Os resultados gerados neste estudo indicam que possivelmente a fauna de hidrozoários planctônicos no CEP vem sofrendo modificações. Este foi o

primeiro registro de *C. fallax* na região (Montú & Cordeiro, 1988; Lopes, 1988; Bardi, 2011; Nagata *et al.*, 2014a; b) e o primeiro registro de sua dominância e grande abundância no Brasil (abundância máxima 2300 ind.m<sup>-3</sup>) (Nagata *et al.*, 2014b; Nogueira Júnior *et al.*, 2014; Tronolone, 2007). Pouco se sabe sobre a distribuição e a história natural de *C. fallax*, ainda assim, suspeita-se que a espécie tenha sido introduzida na região considerando algumas características como: i) ser tipicamente estuarina e encontrada em regiões com atividades portuárias e de navegação (Vanhöffen, 1911; Picard & Rahm, 1954; Kramp, 1959b, Nogueira Júnior, 2012); ii) possuir características oportunistas, como reprodução assexuada por brotos laterais e abundâncias elevadíssimas em situações favoráveis, conforme observado neste estudo; iii) sua recente detecção de ocorrência no Brasil em diversos estuários com grandes portos e/ou intenso tráfico local de embarcações como Baía da Babitonga (Nogueira Júnior, 2012), CEP (este estudo), estuário de Cananéia (Martinez *et al.*, 2015) e Baía de Santos (M. Nogueira Júnior, dados não publicados). Estudos anteriores já relataram mudanças na composição de organismos pelágicos no CEP devido à introdução de espécies invasoras por água de lastro (Procopiak *et al.* 2006; Nogueira Júnior & Oliveira 2006; Lopes *et al.*, 1998; Salvador, 2015).

Este estudo ressalta a importância de monitoramentos faunísticos no CEP, sendo que a introdução de espécies invasoras é uma questão que precisa receber atenção especial. Também é importante considerar que estudos da distribuição espacial e temporal dos hidrozoários planctônicos bem como dos fatores e processos que as influenciam são fundamentais para: i) compreender processos hidrográficos, pois são organismos que se movem à mercê das correntes; e ii) verificar possíveis mudanças no ecossistema, pois altas abundâncias de hidrozoários planctônicos são conhecidas por alterarem a estrutura e abundância de outros organismos zooplânctônicos, podem afetar atividades pesqueiras e de aquicultura, e modificar teias alimentares e o caminho de energia e carbono nos ecossistemas.

Fornecemos uma lista completa de espécies de hidrozoários planctônicos do CEP baseada em uma ampla e representativa variação espaço-temporal e em alguns registros prévios da literatura. Entretanto, dados ainda mais consistentes seriam produzidos se monitoramentos periódicos em

todas as estações do ano durante uma longa série temporal fossem aplicados. Outras abordagens mais detalhadas também ajudariam a compreender outros aspectos da variação temporal e espacial dos hidrozoários planctônicos, como o estudo da sua variação diária em relação às marés e da sua variação vertical em estratificações na coluna d'água. Além disso, se metodologias mais apropriadas aos hidrozoários planctônicos fossem utilizadas que prevenissem danos e destruição dos organismos, provavelmente o número de espécies coletadas seria maior e suas abundâncias e distribuições seriam mais bem avaliadas. Podemos acrescentar ainda o uso da biologia molecular como fundamental ferramenta para elucidar a origem das populações, as relações entre diferentes populações e validar a identificação taxonômica das espécies. Apesar da maioria das espécies serem consideradas “cosmopolitas”, a biologia molecular ajudaria no questionamento sobre a presença de espécies crípticas entre as chamadas “cosmopolitas”.

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## ANEXO – DADOS BRUTOS

Tabela 1. Dados ambientais do cruzeiro do verão de 2012 (12-16/03/2012).

<b>DATA</b>	<b>PONTO</b>	<b>LAT</b>	<b>LONG</b>	<b>PROF. (m)</b>	<b>TEMP sup (°C)</b>	<b>SAL sup</b>	<b>SECCHI (m)</b>
12/03/2012	1	768421	7170548	13	27	33	1,5
12/03/2012	2	766185	7172314	10	26	32	2,2
12/03/2012	3	763899	7174008	7	26	29	1,8
12/03/2012	4	761056	7171194	15	26	32	1,9
12/03/2012	5	761849	7175967	20	28	29	1,9
12/03/2012	6	759162	7177266	20	28	29	1,9
13/03/2012	7	755758	7178034	15	28	27	1,8
13/03/2012	8	753753	7178018	15	28	28	1,3
13/03/2012	9	751747	7178709	13	29	24	0,8
13/03/2012	10	749742	7177056	15	29	24	1,1
13/03/2012	11	749735	7179056	15	29	24	0,9
13/03/2012	12	747728	7177269	15	27	28	1
13/03/2012	13	747736	7179269	13	27	28	1,1
13/03/2012	14	745742	7178880	13	26	27	1,2
13/03/2012	15	743745	7178899	15	26	24	0,5
13/03/2012	16	741744	7178957	12	29	23	0,6
13/03/2012	17	737747	7180134	13	29	25	0,6
14/03/2012	18	771310	7177427	28,6	28	33	1,4
14/03/2012	19	769972	7178060	30,9	28	32	1,4
14/03/2012	20	768995	7179082	22	28	32	1,4
14/03/2012	21	767169	7179260	12	27	32	1,2
14/03/2012	22	766158	7180292	7,5	28	32	0,8
14/03/2012	23	762741	7180816	2,6	29	32	1,4
14/03/2012	24	763741	7184806	2,9	28	32	1
14/03/2012	25	764159	7188820	5,4	29	32	1,5
14/03/2012	26	765646	7192824	8,4	29	32	2
14/03/2012	27	765576	7194829	4,1	30	32	0,8
14/03/2012	28	768180	7198809	4,4	30	32	0,8
14/03/2012	29	769203	7200861	5,2	30	32	1,3
16/03/2012	30	776578	7181695	8	29	34	1,1
16/03/2012	31	776256	7185427	7	29	34	1,1
16/03/2012	32	777903	7189172	10	30	31	0,7
16/03/2012	33	778199	7191630	5	30	31	1
16/03/2012	34	778367	7193753	10	31	31	1
16/03/2012	35	778457	7195619	5	30	29	1
16/03/2012	36	775687	7195066	3	31	28	0,9
16/03/2012	37	779306	7196610	3	31	28	0,9

Tabela 2. Dados ambientais do cruzeiro do inverno de 2012 (23 e 24/08/2012).

DATA	PONTO	LAT	LONG	PROF. (m)	TEMP sup (°C)	SAL sup	SECCHI (m)
24/08/2012	1	768421	7170548	15,2	24	33	1,8
24/08/2012	2	766185	7172314	12,2	24	34	2,5
24/08/2012	3	763899	7174008	14,3	25	31	2,6
24/08/2012	4	761056	7171194	3,5	24	33	2,1
24/08/2012	5	761849	7175967	11,5	25	31	2,5
24/08/2012	6	759162	7177266	12,8	25	31	2
24/08/2012	7	755758	7178034	3,4	25,5	31	1,8
24/08/2012	8	753753	7178018	18	25	31	1,7
24/08/2012	9	751747	7178709	14,4	24	31	1,6
24/08/2012	10	749742	7177056	10,5	24,5	30	1,3
24/08/2012	11	749735	7179056	11,7	24,5	30	1,4
24/08/2012	12	747728	7177269	5,4	24,5	30	1
24/08/2012	13	747736	7179269	13,2	24,5	30	1,2
24/08/2012	14	745742	7178880	3,6	24	28	1,1
24/08/2012	15	743745	7178899	6,7	23	29	1
24/08/2012	16	741744	7178957	6,2	23	29	0,7
24/08/2012	17	737747	7180134	7	23	27	0,8
23/08/2012	18	771310	7177427	30	19,5	32	1,2
23/08/2012	19	769972	7178060	30	24,5	33	2
23/08/2012	20	768995	7179082	21,4	24	33	2,3
23/08/2012	21	767169	7179260	11,9	24,5	33	1,8
23/08/2012	22	766158	7180292	6,1	24,5	32	2,1
23/08/2012	23	762741	7180816	2,1	23,5	34	1
23/08/2012	24	763741	7184806	2,8	24	33	1,1
23/08/2012	25	764159	7188820	3	24	32	0,9
23/08/2012	26	765646	7192824	7	23,5	28	1,5
23/08/2012	27	765576	7194829	6	22,5	27	0,8
23/08/2012	28	768180	7198809	5,5	22	25	1,1
23/08/2012	29	769203	7200861	3	21,5	24	0,5
23/08/2012	30	776578	7181695	18	20	34	1,4
23/08/2012	31	776256	7185427	19	20	33	1,2
23/08/2012	32	777903	7189172	13	20	32	1,1
23/08/2012	33	778199	7191630	8,5	21	30	1,3
23/08/2012	34	778367	7193753	19	20,5	30	1,2
23/08/2012	35	778457	7195619	6	21,5	30	0,7
23/08/2012	36	775687	7195066	6,5	21,5	29	0,9
23/08/2012	37	779306	7196610	5,5	21	30	0,7

Tabela 3. Dados ambientais do cruzeiro do verão de 2013 (21 e 22/02/2013).

<b>DATA</b>	<b>PONTO</b>	<b>LAT</b>	<b>LONG</b>	<b>PROF. (m)</b>	<b>TEMP sup (°C)</b>	<b>SAL sup</b>	<b>SECCHI (m)</b>
21/02/2013	1	768421	7170548	6,2	28,4	27	3,4
21/02/2013	2	766185	7172314	10,1	28,6	25	2,9
21/02/2013	3	763899	7174008	15,7	29,6	23	2,2
21/02/2013	4	761056	7171194	3,9	30	24	1,9
21/02/2013	5	761849	7175967	14,3	29,6	22	2,1
21/02/2013	6	759162	7177266	13,4	29,6	23	1,8
22/02/2013	7	755758	7178034	12	27,8	19	1,32
22/02/2013	8	753753	7178018	17	27,8	19	1
22/02/2013	9	751747	7178709	13	28	17	1
22/02/2013	10	749742	7177056	10	28	17	0,9
22/02/2013	11	749735	7179056	11	28,3	16	1,1
22/02/2013	12	747728	7177269	5	29	17	1,2
22/02/2013	13	747736	7179269	13	28	21	0,9
22/02/2013	14	745742	7178880	6,5	29	15	1,2
22/02/2013	15	743745	7178899	6,3	29	17	1
22/02/2013	16	741744	7178957	6,3	28	16	1,1
21/02/2013	17	737747	7180134	7,6	29	16	1,1
21/02/2013	18	771310	7177427	24,8	28,6	21	2,35
21/02/2013	19	769972	7178060	30,1	28,5	26	3,4
21/02/2013	20	768995	7179082	21,5	28,3	26	3,04
21/02/2013	21	767169	7179260	12,1	29,5	23	3
21/02/2013	22	766158	7180292	7,5	29,7	21	1,8
21/02/2013	23	762741	7180816	2,6	30	22	1,3
21/02/2013	24	763741	7184806	3,2	30	20	1,33
21/02/2013	25	764159	7188820	5,5	30,9	18	1,3
21/02/2013	26	765646	7192824	8,3	29,5	17	1
21/02/2013	27	765576	7194829	4,5	29,6	20	1,7
21/02/2013	28	768180	7198809	4,8	29,9	15	1,3
21/02/2013	29	769203	7200861	2,8	30,2	14	1
21/02/2013	30	776578	7181695	10,7	28,7	24	1,9
21/02/2013	31	776256	7185427	12,6	29,2	23	1,35
21/02/2013	32	777903	7189172	9,6	29,6	21	1,33
21/02/2013	33	778199	7191630	9	29,8	20	1,6
21/02/2013	34	778367	7193753	15,9	29,6	20	1,05
21/02/2013	35	778457	7195619	7,7	29,7	20	1,3
21/02/2013	36	775687	7195066	5,5	30	20	1
21/02/2013	37	779306	7196610	6,3	29,8	19	1,3

Tabela 4. Dados ambientais do cruzeiro do inverno de 2013 (18 e 19/06/2013).

<b>DATA</b>	<b>PONTO</b>	<b>LAT</b>	<b>LONG</b>	<b>PROF. (m)</b>	<b>TEMP sup (°C)</b>	<b>SAL sup</b>	<b>SECCHI (m)</b>
18/06/2013	1	768421	7170548	6	21	33	3
18/06/2013	2	766185	7172314	9,5	21	32	3,2
18/06/2013	3	763899	7174008	15	21	32	3,3
18/06/2013	4	761056	7171194	4	21	34	2,7
18/06/2013	5	761849	7175967	13	21	31	3
18/06/2013	6	759162	7177266	13	21	31	3,2
19/06/2013	7	755758	7178034	13	20	31	3,4
19/06/2013	8	753753	7178018	18	20	30	2,1
19/06/2013	9	751747	7178709	14	20	30	3,2
19/06/2013	10	749742	7177056	10	20	30	2
19/06/2013	11	749735	7179056	9	20	30	1,4
19/06/2013	12	747728	7177269	5	20	28	2,6
19/06/2013	13	747736	7179269	13	20	29	2,6
19/06/2013	14	745742	7178880	6,1	20	25	2,3
19/06/2013	15	743745	7178899	6	20	25	2,3
19/06/2013	16	741744	7178957	6	20	25	2
19/06/2013	17	737747	7180134	11	19	21	2,3
18/06/2013	18	771310	7177427	24	21	31	2,6
18/06/2013	19	769972	7178060	29	21	30	3
18/06/2013	20	768995	7179082	21	21	30	2,7
18/06/2013	21	767169	7179260	12	21	30	3,2
18/06/2013	22	766158	7180292	7	21	30	3,2
18/06/2013	23	762741	7180816	2,5	21	31	2,9
18/06/2013	24	763741	7184806	3	21	30	2,6
18/06/2013	25	764159	7188820	5,5	21	30	2,4
18/06/2013	26	765646	7192824	9	20	29	2
18/06/2013	27	765576	7194829	5	20	30	2
18/06/2013	28	768180	7198809	5	21	25	1,4
18/06/2013	29	769203	7200861	2,5	20	25	1,4
18/06/2013	30	776578	7181695	12	21	23	2
18/06/2013	31	776256	7185427	13	21	25	2,3
18/06/2013	32	777903	7189172	8	21	31	3
18/06/2013	33	778199	7191630	9	21	31	2,3
18/06/2013	34	778367	7193753	16	21	30	2
18/06/2013	35	778457	7195619	5,5	21	30	1,7
18/06/2013	36	775687	7195066	8	21	31	2,3
18/06/2013	37	779306	7196610	6,5	21	30	1,7

Tabela 5. Dados de abundância das hidromedusas (ind.m<sup>-3</sup>) e sifonóforos (col.m<sup>-3</sup>) do cruzeiro do verão de 2012 (12-16/03/2012).

PONTO	<i>L</i> <i>tetraphylla</i>	<i>A</i> <i>hemistoma</i>	<i>Helgicirrha</i> sp	<i>E</i> <i>duodecimalis</i>	<i>E</i> <i>maculata</i>	<i>E</i> <i>paradoxa</i>	<i>Cunina</i> sp	<i>C</i> <i>octonaria</i>	<i>C</i> <i>gracilis</i>	<i>C</i> <i>forbesii</i>	<i>C</i> <i>januari</i>
1	2,965	0	0	1,22	0	0	0	0	1,45	0	0
2	1,103	0	0	0,12	0	0	0	0	0,23	0	0
3	3,139	0	0	0,86	0	0	0	0	1,76	0	0
4	2,862	0	0	0	0	0	0	0	0,26	0	0
5	1,33	0	0	0,11	0	0,028	0	0	0	0	0
6	4,58	0	0	1,75	0	0	0	0	0	0	0
7	1,698	0	0	1,41	0	0,146	0	0	0,97	0	0
8	0,326	0	0	0	0	0	0	0	0,59	0	0
9	0	0	0	0	0	0	0	0	0	0	0
10	0,148	0	0	0	0	0	0	0	0,15	0	0
11	0	0	0	0	0	0	0	0	0,06	0	0
12	0	0	0	0,04	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0	0
16	0,025	0	0	0	0	0	0	0	0	0	0
17	0,126	0	0	0	0	0	0	0	0,25	0	0
18	1,421	0	0	0,16	0	0	0	0	0	0	0
19	1,187	0	0	0,21	0	0,103	0	0	0	0	0
20	3,163	0	0	0,52	0	0	0	0	0	0	0
21	0,43	0	0	1,18	0	0	0	0	0,86	0	0
22	1,278	0	0	3,65	0	0	0	0	3,1	0	0
23	0,923	0	0	0,5	0	0	0	0	2,77	0	0
24	1,46	0	0	0,46	0	0	0	0	1,28	0	0
25	0,548	0	0	0,27	0	0	0	0	2,46	0	0
26	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0,63	0	0	0	0	2,1	0	0
28	1,198	0	0	0	0	0	0	0	1,4	0	0
29	0	0	0	1,84	0	0	0	0	0	0	0
30	0,45	0	0	0,32	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0
33	0,055	0	0	0	0	0,028	0	0	0,06	0	0
34	0,232	0	0	0,43	0	0	0	0	0	0	0
35	0	0	0	0,17	0	0	0	0	0	0	0
36	0,214	0	0	0	0	0	0	0	0,07	0	0
37	0	0	0	0,09	0	0	0	0	0,05	0	0

Tabela 5 (continuação). Dados de abundância das hidromedusas (ind.m<sup>-3</sup>) e sifonóforos (col.m<sup>-3</sup>) do cruzeiro do verão de 2012 (12-16/03/2012).

PONTO	<i>Obelia</i> spp	<i>B</i> <i>muscus</i>	<i>E</i> <i>dumortieri</i>	<i>Clytia</i> spp	<i>G</i> <i>brachymera</i>	<i>S reesi</i>	<i>E</i> <i>mira</i>	<i>B</i> <i>carolinensis</i>	<i>P</i> <i>loyola</i>	<i>Solmaris</i> sp	<i>P</i> <i>ornata</i>	<i>C fallax</i>
1	2,706	0	0,297	2,82	0	0	0	0	0	0	0	5,189
2	0,416	0,15	0,083	0,48	0	0	0	0	0	0	0	0,687
3	1,474	0	0,428	8,37	0	0	0	0	0	0	0	7,656
4	0,643	0	0,193	0,32	0	0	0	0	0	0	0	0
5	0,481	0	0,198	0,25	0	0	0	0	0	0,11	0	0,566
6	2,538	0	0,583	5,86	0	0	0	0	0	0	0	10,01
7	0,582	0	0	13,2	0	0	0	0	0	0	0	1,601
8	0,196	0	0	1,31	0,065	0,065	0	0	0	0	0	6,007
9	0,821	0	0	0,55	0	0	0	0	0	0	0	4,381
10	0,148	0	0	0,59	0	0	0	0	0	0	0	5,757
11	0,238	0,05	0	0,6	0	0,119	0	0	0	0	0	0,417
12	0,084	0	0	0	0	0	0	0	0	0	0	0,084
13	0,122	0	0	0,18	0	0	0,12	0	0	0	0	0
14	0,187	0	0	0,14	0	0	0	0	0	0	0	0,28
15	0,041	0	0	0	0	0	0	0	0,02	0	0	0,103
16	0	0	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0,13	0	0	0	0	0
18	0,711	0	0	2,61	0	0	0	0	0	0	0	0
19	0,774	0	0,052	0,52	0	0	0	0	0	0,36	0	4,386
20	1,033	0	0,258	1,48	0	0	0	0	0	0	0,065	15,17
21	0,322	0	0,215	1,4	0	0	0	0	0	0	0	2,686
22	15,7	0	1,643	5,48	0	0	0	0	0	0	0	16,43
23	9,944	0	1,137	2,06	0	0	0	0	0	0	0	163,2
24	0	0	0	0,91	0	0	0	0	0	0	0	13,6
25	0,137	0,03	2,054	0,68	0	0	0	0	0	0	0	256,2
26	0,329	0	0	1,53	0	0	0	0	0	0	0	427,9
27	3,353	0	0	4,82	0	0	0	0	0	0	0	809
28	0,999	0	0	2,8	0	0	0	0	0	0	0	2305
29	0	0	3,487	4,31	0	0	0	0	0	0	0	362,1
30	0,212	0	0	0,05	0	0	0	0	0	0	0	0,238
31	0,076	0	0	0	0	0	0	0	0	0	0	0,051
32	0,256	0	0	1,03	0	0	0	0	0	0	0	0,077
33	3,135	1	0,277	1,03	0	0,111	0	0	0	0	0,028	2,025
34	1,721	0	0	1,92	0	0,033	0	0	0	0	0	4,203
35	0,956	0	0	4,46	0	0,029	0	0	0	0	0	1,999
36	0,107	0	0,036	0,21	0	0	0	0	0	0	0	0,391
37	0,465	0	0	1,16	0	0,047	2	0	0	0	0	2,884

Tabela 5 (continuação). Dados de abundância das hidromedusas (ind.m<sup>-3</sup>) e sifonóforos (col.m<sup>-3</sup>) do cruzeiro do verão de 2012 (12-16/03/2012).

PONTO	<i>H</i> <i>carica</i>	<i>A</i> <i>dinema</i>	<i>L</i> <i>minuscule</i>	<i>C</i> <i>tetranema</i>	<i>T</i> <i>nutricula</i>	<i>B</i> <i>virginica</i>	<i>N</i> <i>bijuga</i>	<i>M</i> <i>kochii</i>	<i>A</i> <i>tetragona</i>	NI
1	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0
5	0	0	0,028	0	0	0	0	0	0	0,06
6	0	0	0	0	0	0,047	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0,05
8	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0
11	0,06	0	0	0	0	0	0	0	0	0,06
12	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0,12	0	0	0
14	0	0	0	0	0	0	0	0	0	0
15	0,062	0	0	0	0	0	0,02	0	0	0,02
16	0	0	0	0	0,025	0	0	0	0	0
17	0	0	0	0	0	3,009	0,13	0	0	0
18	0	0	0	0	0	2,986	0	0	0	0
19	0	0	0	0	0	1,976	0	0	0	0
20	0	0	0	0	0,065	4,009	0	0	0	0
21	0	0	0	0	0,107	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0
33	0,028	0	0,083	0	0	0	0	0	0	0
34	0	0	0	0,033	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0
36	0	0	0	0	0	0	0	0	0	0
37	0	0	0	0	0	0	2	0	0	0

Tabela 6. Dados de abundância das hidromedusas (ind.m<sup>-3</sup>) e sifonóforos (col.m<sup>-3</sup>) do cruzeiro do inverno de 2012 (23 e 24/08/2012).

PONTO	<i>L</i> <i>tetraphylla</i>	<i>A</i> <i>hemistoma</i>	<i>Helgicirrha</i> sp	<i>E</i> <i>duodecimalis</i>	<i>E</i> <i>maculata</i>	<i>E</i> <i>paradoxa</i>	<i>Cunina</i> sp	<i>C</i> <i>octonaria</i>	<i>C</i> <i>gracilis</i>	<i>C</i> <i>forbesii</i>	<i>C</i> <i>januari</i>
1	7,6	0,0	0,0	0,3	0,0	0,3	0,1	0,0	0,1	0,0	0,0
2	2,1	0,0	0,0	0,0	0,0	0,0	0,0	0,2	0,0	0,0	0,0
3	1,9	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
4	2,0	0,0	0,0	0,1	0,0	0,0	0,0	0,0	0,1	0,0	0,0
5	1,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
6	1,4	0,0	0,0	0,3	0,0	0,1	0,0	0,0	0,3	0,0	0,0
7	0,9	0,0	0,0	0,7	0,0	0,2	0,0	0,0	0,1	0,0	0,0
8	0,8	0,0	0,0	0,8	0,0	0,7	0,0	0,0	0,1	0,0	0,0
9	0,9	0,0	0,0	0,2	0,0	0,4	0,0	0,0	0,0	0,0	0,0
10	1,6	0,0	0,0	1,4	0,0	0,1	0,0	0,0	0,0	0,0	0,0
11	1,5	0,0	0,0	0,9	0,0	0,4	0,0	0,0	0,0	0,0	0,0
12	0,7	0,0	0,0	1,8	0,0	1,2	0,0	0,0	0,1	0,0	0,0
13	1,3	0,0	0,2	0,6	0,0	0,0	0,1	0,0	0,1	0,0	0,0
14	0,4	0,0	0,0	0,7	0,0	0,4	0,0	0,0	0,0	0,0	0,0
15	0,8	0,0	0,0	1,3	0,0	0,1	0,1	0,0	0,4	0,0	0,0
16	0,9	0,0	0,0	5,1	0,0	0,8	0,0	0,0	0,2	0,0	0,0
17	0,8	0,0	0,0	2,2	0,0	0,2	0,0	0,0	0,0	0,0	0,0
18	5,5	0,0	0,0	0,3	0,0	0,0	0,0	0,1	0,0	0,0	0,0
19	23,6	0,0	0,0	0,4	0,0	0,0	0,0	0,0	0,2	0,0	0,0
20	5,6	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
21	0,6	0,0	0,0	0,7	0,0	0,0	0,0	0,0	0,1	0,0	0,0
22	2,2	0,0	0,0	1,0	0,0	0,0	0,0	0,6	0,4	0,0	0,0
23	2,5	0,0	0,0	0,0	0,0	0,0	0,0	0,0	4,9	0,0	0,0
24	34,1	0,0	0,0	0,0	0,0	0,0	0,0	0,0	22,5	0,0	0,0
25	17,4	0,0	0,0	0,0	0,0	0,0	0,7	0,0	6,9	0,0	0,0
26	2,4	0,0	0,0	1,3	0,0	0,0	0,0	0,0	14,1	0,0	0,0
27	4,5	0,0	0,0	2,6	0,0	0,0	0,8	0,0	0,5	0,0	0,0
28	7,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	55,6	0,0	0,0
29	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
30	26,6	0,0	0,0	1,0	0,0	0,0	0,1	0,0	0,1	0,0	0,0
31	29,4	0,0	0,0	1,8	0,0	0,0	0,5	0,0	0,3	0,0	0,0
32	21,6	0,0	0,0	2,4	0,0	0,0	0,3	0,0	1,2	0,0	0,0
33	5,0	0,0	0,0	5,1	0,0	0,0	0,6	0,0	1,0	0,0	0,0
34	11,1	0,0	0,0	2,8	0,0	0,0	0,2	0,0	0,4	0,0	0,0
35	9,8	0,0	0,0	2,1	0,0	0,4	0,1	0,0	0,6	0,0	0,0
36	10,0	0,0	0,0	2,9	0,0	0,2	0,2	0,0	1,0	0,0	0,0
37	8,5	0,0	0,0	2,7	0,0	0,5	0,1	0,0	0,9	0,0	0,0

Tabela 6 (continuação). Dados de abundância das hidromedusas (ind.m<sup>-3</sup>) e sifonóforos (col.m<sup>-3</sup>) do cruzeiro do inverno de 2012 (23 e 24/08/2012).

PONTO	<i>Obelia</i> spp	<i>B</i> <i>muscus</i>	<i>E</i> <i>dumortieri</i>	<i>Clytia</i> spp	<i>G</i> <i>brachymera</i>	<i>S reesi</i>	<i>E</i> <i>mira</i>	<i>B</i> <i>carolinensis</i>	<i>P</i> <i>loyola</i>	<i>Solmaris</i> sp	<i>P</i> <i>ornata</i>	<i>C fallax</i>
1	2,8	0,0	0,8	8,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	5,2
2	5,9	0,1	1,0	2,2	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,7
3	11,1	0,0	0,1	0,6	0,0	0,0	0,0	0,0	0,0	0,0	0,0	7,7
4	1,2	0,0	1,0	1,5	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
5	9,9	0,0	0,0	0,6	0,0	0,0	0,0	0,0	0,0	0,1	0,0	0,6
6	3,6	0,0	0,0	0,6	0,0	0,0	0,0	0,0	0,0	0,0	0,0	10,0
7	2,0	0,0	0,2	1,3	0,0	0,0	0,0	0,0	0,0	0,0	0,0	1,6
8	2,8	0,1	0,5	2,8	0,0	0,1	0,0	0,0	0,0	0,0	0,0	6,0
9	0,6	0,0	0,0	0,3	0,0	0,0	0,0	0,0	0,0	0,0	0,0	4,4
10	2,2	0,1	0,1	1,6	0,0	0,0	0,0	0,0	0,0	0,0	0,0	5,8
11	6,4	0,1	0,1	2,2	0,0	0,1	0,0	0,0	0,0	0,0	0,0	0,4
12	1,7	0,1	0,0	3,8	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1
13	0,8	0,1	0,2	2,5	0,0	0,0	0,1	0,0	0,0	0,0	0,0	0,0
14	0,9	0,0	0,1	1,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,3
15	1,2	0,0	0,3	13,6	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1
16	1,3	0,1	0,0	12,4	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
17	1,1	0,0	0,0	4,9	0,0	0,0	0,1	0,0	0,0	0,0	0,0	0,0
18	0,2	0,0	0,6	1,5	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
19	2,8	0,0	0,8	5,4	0,0	0,0	0,0	0,0	0,0	0,4	0,0	4,4
20	2,4	0,0	0,8	2,7	0,0	0,0	0,0	0,0	0,0	0,0	0,1	15,2
21	1,0	0,0	0,0	2,4	0,0	0,0	0,0	0,0	0,0	0,0	0,0	2,7
22	3,5	0,0	0,7	3,7	0,0	0,0	0,0	0,0	0,0	0,0	0,0	16,4
23	1,1	0,0	4,0	4,2	0,0	0,0	0,0	0,0	0,0	0,0	0,0	163,2
24	0,3	0,3	2,9	13,8	0,0	0,0	0,0	0,0	0,0	0,0	0,0	13,6
25	4,0	0,0	11,1	17,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	256,2
26	0,0	0,0	34,9	14,4	0,0	0,0	0,0	0,0	0,0	0,0	0,0	427,9
27	3,5	0,0	3,3	5,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	809,0
28	8,3	0,0	0,0	32,8	0,0	0,0	0,0	0,0	0,0	0,0	0,0	2305,2
29	0,7	0,0	0,0	1,3	0,0	0,0	0,0	0,0	0,0	0,0	0,0	362,1
30	4,1	0,0	0,8	4,4	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,2
31	2,8	0,0	0,4	0,9	0,2	0,0	0,0	0,0	0,0	0,0	0,0	0,1
32	1,1	0,2	0,6	2,2	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1
33	1,1	1,0	0,9	3,3	0,1	0,1	0,0	0,0	0,0	0,0	0,0	2,0
34	0,6	0,2	0,0	2,8	0,0	0,0	0,0	0,0	0,0	0,0	0,0	4,2
35	5,1	0,1	0,2	6,7	0,0	0,0	0,0	0,0	0,0	0,0	0,0	2,0
36	76,7	0,0	0,2	24,6	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,4
37	50,4	0,0	0,0	8,9	0,0	0,0	2,0	0,0	0,0	0,0	0,0	2,9

Tabela 6 (continuação). Dados de abundância das hidromedusas (ind.m<sup>-3</sup>) e sifonóforos (col.m<sup>-3</sup>) do cruzeiro do inverno de 2012 (23 e 24/08/2012).

PONTO	<i>H</i> <i>carica</i>	<i>A</i> <i>dinema</i>	<i>L</i> <i>minuscule</i>	<i>C</i> <i>tetranema</i>	<i>T</i> <i>nutricula</i>	<i>B</i> <i>virginica</i>	<i>N</i> <i>bijuga</i>	<i>M</i> <i>kochii</i>	<i>A</i> <i>tetragona</i>	NI
1	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
2	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
3	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
4	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
5	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1
6	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
7	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
8	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
9	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
10	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
11	0,1	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1
12	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
13	0,0	0,0	0,0	0,0	0,0	0,0	0,1	0,0	0,0	0,0
14	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
15	0,1	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
16	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
17	0,0	0,0	0,0	0,0	0,0	3,0	0,1	0,0	0,0	0,0
18	0,0	0,0	0,0	0,0	0,0	3,0	0,0	0,0	0,0	0,0
19	0,0	0,0	0,0	0,0	0,0	2,0	0,0	0,0	0,0	0,0
20	0,0	0,0	0,0	0,0	0,1	4,0	0,0	0,0	0,0	0,0
21	0,0	0,0	0,0	0,0	0,1	0,0	0,0	0,0	0,0	0,0
22	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
23	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
24	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
25	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
26	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
27	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
28	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
29	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
30	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
31	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
32	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
33	0,0	0,0	0,1	0,0	0,0	0,0	0,0	0,0	0,0	0,0
34	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
35	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
36	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
37	0,0	0,0	0,0	0,0	0,0	0,0	2,0	0,0	0,0	0,0







Tabela 8. Dados de abundância das hidromedusas (ind.m<sup>-3</sup>) e sifonóforos (col.m<sup>-3</sup>) do cruzeiro do inverno de 2013 (18 e 19/06/2013).

PONTO	<i>L</i> <i>tetraphylla</i>	<i>A</i> <i>hemistoma</i>	<i>Helgicirrha</i> sp	<i>E</i> <i>duodecimalis</i>	<i>E</i> <i>maculata</i>	<i>E</i> <i>paradoxa</i>	<i>Cunina</i> sp	<i>C</i> <i>octonaria</i>	<i>C</i> <i>gracilis</i>	<i>C</i> <i>forbesii</i>	<i>C</i> <i>januari</i>
1	2,1	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
2	0,2	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
3	0,3	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
4	13,2	0,1	0,0	0,1	0,2	0,0	0,0	0,0	0,0	0,0	0,0
5	1,2	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
6	1,2	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1	0,0	0,0
7	0,1	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
8	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
9	0,3	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1	0,0	0,0
10	0,7	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,5	0,0	0,0
11	10,6	0,0	0,0	0,0	0,5	0,0	0,0	0,0	0,7	0,0	0,0
12	0,3	0,0	0,0	0,1	0,0	0,0	0,0	0,0	0,0	0,0	0,0
13	0,2	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
14	0,1	0,0	0,0	0,0	0,1	0,0	0,0	0,0	0,0	0,0	0,0
15	0,5	0,0	0,1	0,0	0,0	0,0	0,0	0,0	0,3	0,0	0,0
16	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
17	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
18	0,2	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1	0,0	0,0
19	0,5	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
20	0,3	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
21	0,8	0,0	0,0	0,0	0,0	0,0	0,0	0,0	1,2	0,0	0,0
22	4,1	0,0	0,0	0,0	0,0	0,0	0,0	0,0	7,2	0,0	0,0
23	9,4	0,0	0,0	0,1	0,0	0,0	0,0	0,0	5,1	0,0	0,0
24	1,6	0,0	0,0	0,1	0,1	0,0	0,0	0,0	3,0	0,0	0,0
25	0,2	0,0	0,0	0,0	0,2	0,0	0,0	0,0	0,2	0,0	0,0
26	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,3	0,0	0,0
27	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1
28	0,1	0,0	0,0	0,1	0,0	0,0	0,0	0,0	0,3	0,0	0,0
29	0,2	0,0	0,0	0,0	0,1	0,0	0,0	0,0	0,5	0,1	0,0
30	4,8	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1	0,0	0,0
31	0,2	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,4	0,1	0,0
32	0,2	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1	0,0	0,0
33	0,2	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,4	0,0	0,0
34	0,3	0,0	0,0	0,0	2,0	0,0	0,0	0,0	0,4	1,3	0,0
35	1,2	0,0	0,0	0,0	1,1	0,0	0,0	0,0	0,1	0,0	0,0
36	0,7	0,0	0,0	0,0	0,3	0,0	0,0	0,0	0,6	0,0	0,0
37	1,2	0,0	0,0	0,0	0,5	0,0	0,0	0,0	0,3	0,2	0,0



