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# DIVERSIDADE, DISTRIBUIÇÃO E ABUNDÂNCIA DOS CNIDÁRIOS PELÁGICOS DO OCEANO ATLÂNTICO EQUATORIAL SOB INFLUÊNCIA DA PLUMA DO RIO AMAZONAS

Recife
2021

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Tese apresentada ao Programa de Pós-Graduação em Oceanografia da Universidade Federal de Pernambuco, Centro de Tecnologia e Geociências, como requisito parcial para a obtenção do título de Doutor em Oceanografia.

**Área de Concentração**: Oceanografia Biológica.

**Orientador**: Profa. Dra. Sigrid Neumann-Leitão.
**Coorientador**: Prof. Dr. Miodeli Nogueira Júnior.

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# RESUMO

A descarga de água doce do rio Amazonas no oceano Atlântico equatorial provoca uma pluma superficial com baixa salinidade e alta carga de nutrientes e material suspenso que pode ser traçada por centenas de quilômetros no Atlântico norte e Caribe. Essa pluma tem forte influência na ecologia e biogeografia dos animais marinhos, entre eles os cnidários pelágicos. Um grupo que historicamente foi deixado de lado em estudos do zooplâncton. Assim a presente tese buscou explorar aspectos da diversidade, distribuição, abundância da comunidade de cnidários planctônicos e neustônicos do lado oeste do oceano Atlântico equatorial, avaliando os efeitos ecológicos da pluma do rio Amazonas na estrutura da comunidade. Entre os principais resultados relacionados a biodiversidade, foram encontradas duas novas espécies de hidromedusas da família Eirenidae, *Eutima marajoara* e *Helgicirrha angelicae*, as primeiras ocorências para o Brasil das espécies *Cirrholovenia polynema*, *Pegantha laevis* e *Forskalia tholoides*, além de várias outras primeiras ocorrências em nível regional e local. No total foram encontrados 93 táxons na área, uma alta biodiversidade que apresenta indícios de ser ainda maior. Em geral, o oceano aberto apresentou uma maior biodiversidade na área que a plataforma continental, não somente para espécies holoplanctônicas, mas também para grupos meroplanctônicos como Athoathecata, o que pode estar relacionado à circulação e topografia complexas presentes na área. A pluma do rio Amazonas se mostrou o principal processo oceanográfico em mesoescala moldando a distribuição da comunidade de cnidários planctônicos e neustônicos tanto na plataforma continental, onde as diferenças mais marcadas foram observadas, quanto no oceano aberto. Na plataforma continental, espécies como *Persa incolorata*, *Enneagonun hyalinun*, *Muggiaea kochii* e *Diphyes dispar*, foram restritas, ou ocorreram em abundâncias bem mais altas na região sob influência da pluma. Já no oceano aberto as diferenças foram relacionadas a abundância da espécies: enquanto as áreas fora da influência da pluma foram marcadas por abundancias maiores das espécies *Chelophyes appendiculata*, *Bassia bassensis*, *Eudoxoides spiralis* e *Abylopsis tetragona*, a área sob influência da pluma apresentou maior abundância das espécies *Diphyes bojani*, *D. dispar* e *Cytaeis* sp.1. Embora os resultados no plâncton epipelágico e neustôn tenham sido semelhantes, diferenças também foram observadas tanto na composição taxonômica, com ambos os ambientes apresentando espécies exclusivas quanto nos padrões de distribuição espacial na região oceânica, que foram menos marcados na comunidade neustônica.

**Palavras-chave:** biodiversidade; medusas; Sifonóforos; zooplâncton gelatinoso; Costa Amazônica.

# ABSTRACT

The freshwater discharge of the Amazon River in the Equatorial Atlantic Ocean causes a surface plume with low salinity and high nutrients and suspended material that can be traced hundreds of kilometers in North Atlantic and Caribbean. This plume has strong influence on the ecology and biogeography of marine animals, among them, the pelagic cnidarians. A group that historically has been set aside in traditional zooplankton studies. Thus, the present thesis aimed to explore aspects on the diversity, distribution and abundance of the pelagic cnidarian community from the Western Equatorial Atlantic, investigating the ecological effects of the Amazon River Plume on community structure. Among the mains results related to biodiversity, two new hydromedusae species from family Eirenidae were found, *Eutima marajoara* and *Helgicirrha angelicae*. Additionally, we reported the first occurrences in Brazilian waters of the specie *Cirrholovenia polynema*, *Pegantha laevis* and *Forskalia tholoides* and several regional and local new occurrences. In totality, 93 taxa were found the area, a high biodiversity with signs to be even higher. In general, the open ocean in the area presented a higher diversity than the continental shelf, not only for holoplanktonic but also in the meroplanktonic taxa such as Anthoathecata, what can be related to complex circulation and topography present in the area. The Amazon River Plume was the main mesoscale oceanographic process shaping planktonic and neustonic cnidarian community distributions both over the continental shelf, were sharp differences were observed, and in the open ocean. Over the continental shelf, species such *Persa incolorata*, *Enneagonun hyalinun*, *Muggiaea kochii* and *Diphyes dispar* were restricted, or occurred in much larger abundance in the area under influence of the plume. In the open ocean, differences were more related to species abundance: while areas outside the influence of the plume presented higher abundances of the species *Chelophyes appendiculata*, *Bassia bassensis*, *Eudoxoides spiralis* and *Abylopsis tetragona*, the area under influence of the plume presented higher abundance of *Diphyes bojani*, *D. dispar* e *Cytaeis* sp.1. Although results in plankton and neuston were similar, differences were observed in taxonomic composition, where both environments presented exclusive species and in distribution patterns in the oceanic region, which were less pronounced in the neustonic community.

Keywords: biodiversity; medusa; Siphonophores; gelatinous zooplankton; Amazonian Coast.

# SUMÁRIO

# 1 INTRODUÇÃO GERAL

O filo Cnidária surgiu cedo na história dos Metazoa, possivelmente durante o período Criogeniano da era Neoproterozóica (entre 720 e 635 milhões de anos atrás), com os fósseis mais antigos presentes em estratos do período Ediacarano da mesma era (VAN ITEN et al., 2014). Nesse período, o surgimento das cnidas, organelas especializadas em descarregar um filamento em forma de dardo com veneno utilizadas para defesa e captura de presas, diferenciou os cnidários dos outros animais diploblásticos (com dois folhetos embrionários). Embora outras características originais do filo como a simetria radial, larva plânula e estágio polipóide já tenham sido considerados em sua diagnose, elas não estão presentes em todos os táxons atuais. Assim a presença de cnidas é a sinapomorfia atualmente utilizada para a distinção do filo (COLLINS, 2009; DALY et al., 2007).

Desde o surgimento, o grupo se diversificou em uma variedade de formas e modos de vida que se distribuem em 3 grupos principais: Anthozoa, Myxozoa e Medusozoa. A classe Anthozoa incluí linhagens que apresentam apenas o estágio polipóide bentônico e sua vida no ambiente pelágico é restrita a estágios larvais (DALY et al., 2007; VAN ITEN et al., 2014). Esses animais são tipicamente chamados corais e anêmonas, muitos dos quais produzem esqueletos de carbonato que contribuem significativamente para a formação de recifes. O segundo grupo, Myxozoa, é composto por endoparasitas marinhos e de água doce com uma variedade de ciclos de vida complexos e organelas semelhantes às cnidas denominadas cápsulas polares. Até recentemente o grupo era considerado um filo de protistas, contudo, análises moleculares indicaram que o grupo pertence a Cnidária (COLLINS, 2009). O último grupo incluiu as classes de cnidários com formas medusóides no ciclo de vida: Hydrozoa, Cubozoa, Scyphozoa e Staurozoa, os três primeiros sendo representativos no ambiente pelágico marinho (VAN ITEN et al., 2014).

O ciclo de vida típico de Medusozoa apresenta o estágio medusóide pelágico com reprodução sexuada em alternância com o estágio polipóide bentônico com reprodução assexuada. Contudo variações nesse ciclo de vida padrão também são comuns (COLLINS, 2002). Na classe Hydrozoa, várias espécies de hidróides não liberam medusas enquanto os grupos Narcomedusae e Trachymedusae apresentam somente o estágio medusóide que permanece toda a sua vida no ambiente pelágico

(COLLINS, 2002). No grupo também merecem destaque os sifonóforos, colônias de hidrozoários pelágicas altamente especializadas com formas polipóides e medusóides ocorrendo simultaneamente, alguns com alternância entre o estágio com reprodução assexuada e sexuada, denominados poligástrico e eudóxia respectivamente (MACKIE; PUGH; PURCELL, 1988; MAPSTONE, 2014).

No ambiente pelágico, seja na forma de medusa, larva ou colônia pelágica, os cnidários não possuem capacidade natatória suficiente para vencer as correntes marinhas, sendo assim incluídos na comunidade planctônica, ou neustônica, caso presentes nos primeiros centímetros da coluna d'água, o que não é incomum já que várias espécies de sifonóforos apresentam estruturas especializadas para flutuação (IOSILEVSKII; WEIHS, 2009; PURCELL et al., 2015). Em conjunto com outros grupos de animais planctônicos como os Ctenóforos e Tunicados, os cnidários pelágicos são tipicamente incluídos na categoria funcional denominada zooplâncton gelatinoso (HADDOOCK, 2004). Os animais dessa categoria apresentam alta taxa de água em seus tecidos (> 95 % do peso). Essa característica confere aos animais planctônicos uma série de vantagens, entre elas: melhor flutuabilidade e menor gasto de energia para manter a posição na coluna d'água; maior transparência, que favorece a camuflagem no meio pelágico; podem atingir maiores tamanho com baixo investimento em carbono e energia, com os maiores tamanhos podem se alimentar de presas maiores e reduzem o risco de predação por indivíduos menores; plasticidade corporal, aumentando e diminuindo de tamanho facilmente; e rápido crescimento populacional (ACUÑA; LOPEZ-URRUTIA; COLIN, 2011; BIDIGARE; BIGGS, 1980; JOHNSEN, 2001; LARSON, 1986).

Historicamente, os cnidários foram deixados de lado em estudos ecológicos tradicionais do zooplâncton marinho (HADDOOCK, 2004), ou agrupados em uma única categoria, ignorando sua diversidade (ex. GARCÍA-COMAS et al., 2011; LANE et al., 2008). Entre os motivos que justificam essa negligência estão a fragilidade e dificuldade de fixação desses animais em formol, o que muitas vezes danifica seus tecidos impossibilitando a identificação das espécies (BOUILLON, 1999) e ausência de especialistas em sua não tão simples taxonomia. Adicionalmente, a fragmentação das colônias de sifonóforos com os arrastos utilizados para a coleta de plâncton também dificulta a quantificação adequada desses organismos.

No entanto nas últimas décadas a situação tem mudado devido a um melhor entendimento do papel dos cnidários nas teias tróficas pelágicas e seus efeitos no funcionamento dos ecossistemas. Cnidários são predadores de vários grupos do zooplâncton pertencentes a diferentes classes de tamanho, variando de pequenos náuplios de copépodes e protozoários, até decápodes, larvas de peixes e outros cnidários (ARAI, 2005; COLIN et al., 2005; PURCELL, 1997). Para isso várias estratégias de captura são utilizadas, como a filtração da água do mar através dos tentáculos, emboscada, forrageio e busca ativa (ARAI, 2005; COSTELLO; COLIN, 1995; PURCELL, 1997). Além disso, tipicamente os cnidários possuem taxas alimentares altas, que, associadas às explosões populacionais comuns no ciclo de vida de vida de muitas espécies do grupo tem o potencial de controlar as comunidades pelágicas e causar impactos significativos à pesca, não somente devido à predação de larvas de peixes, mas também através da competição por outros recursos alimentares comuns para ambos os grupos (BOERO, 2013; STIBOR; TOKLE, 2003). Adicionalmente, devido à baixa proporção de carbono, os cnidários pelágicos costumavam ser vistos como o final da linha nas teias tróficas pelágicas, porém estudos recentes têm demonstrado que vários animais se alimentam ocasionalmente ou até exclusivamente deles (AYALA et al., 2018; CARDONA et al., 2012; EDUARDO et al., 2020; HAYS; DOYLE; HOUGHTON, 2018).

Outro fator que tem aumentado o interesse em questões ecológicas envolvendo os cnidários pelágicos é a preocupação de que essas populações dos mesmos então aumentando globalmente devido às alterações que os humanos têm causado nos oceanos como as mudanças climáticas, sobrepesca, eutrofização, acidificação e instalação de estruturas offshore (PURCELL, 2012; PURCELL; UYE; LO, 2007). Essa preocupação começou a partir da observação de que as explosões populacionais comuns no ciclo de vida desses organismos estão se tornando mais recorrentes em várias regiões do planeta (MILLS, 2001; PURCELL; UYE; LO, 2007). Contudo evidências das respostas das populações de cnidários às variações no ambiente antrópicas ou não, sobretudo em largas escalas espaciais e temporais, ainda são escassas, o que impede conclusões definitivas sobre o tema (CONDON et al., 2012, 2013; PITT et al., 2018).

Os padrões na diversidade, distribuição e abundância dos cnidários planctônicos estão relacionados a processos oceanográficos ocorrendo em diferentes escalas. Globalmente, os táxons estão distribuídos de acordo com padrões climáticos e massas d’água (BROTZ et al., 2012; GARCÍA-COMAS et al., 2011; GRAHAM, 2001). Processos em mesoescala como correntes, vórtices, frentes, ressurgência e a topografia do fundo costumam delinear a distribuição das espécies (BOERO et al., 2016; GUERRERO et al., 2016, 2018; NOGUEIRA JÚNIOR; BRANDINI; CODINA, 2014; PAGÈS; GILI, 1991), enquanto a ocorrência e abundância local das espécies geralmente é determinada pelas condições da agua do mar (ex. temperatura, salinidade, oxigênio) e disponibilidade de alimento (GIBBONS; BUECHER, 2001; GILI et al., 1988; LUO et al., 2014).

Em regiões de baixa latitude ainda temos uma grande lacuna na compreensão desses padrões de diversidade, distribuição e abundância, particularmente no oeste do oceano Atlântico Equatorial. Nessa região o rio Amazonas descarrega até $2,4 \times 10^5$ $m^3s^{-1}$ de água doce com nutrientes e sedimentos, contribuindo com aproximadamente 1/5 de toda água doce continental lançada no oceano global (DAGG et al., 2004; LENTZ, 1995). Essa descarga provoca uma pluma superficial com alta carga de nutrientes e materiais suspensos, baixa salinidade e períodos de forte estratificação vertical que pode ser traçada por centenas de quilômetros no Atlântico Norte e Caribe (HELLWEGER; GORDON, 2002; JO et al., 2005; SIGNORINI et al., 1999). As características únicas da pluma do rio Amazonas tem forte influência na ecologia e biogeografia da plataforma continental do norte do Brasil e Atlântico equatorial. A alta carga de nutrientes aumenta a produção primária e possivelmente toda a comunidade consumidora por controle *bottom-up* (SMITH; DEMASTER, 1996). O ambiente de baixa salinidade gerado pela pluma na plataforma continental e oceano aberto também tem o potencial de afetar a distribuição espacial dos animais marinhos. Além das restrições de nicho impostas às espécies, a pluma do rio Amazonas também é considerada a principal barreira responsável pelo isolamento biogeográfico e alto grau de endemismo entre as costas do mar do Caribe e nordeste do Brasil (BRIGGS, 1974; FLOETER et al., 2008; ROCHA, 2003).

Também, como um sistema de borda oeste, fortes correntes marinhas (a Corrente Norte do Brasil) fluem paralelas e em direção à costa no oeste do oceano Atlântico equatorial (JOHNS et al., 1998; LODER; BOICOURT; SIMPSON, 1998). Processos similares resultam em intrusões massivas de águas oceânicas oligotróficas e sua fauna de cnidários associada sobre a plataforma continental em outros sistemas análogos (THIBAULT-BOTHA; LUTJEHARMS; GIBBONS, 2004; TOSETTO et al., 2021). Porém no oeste do oceano Atlântico equatorial a plataforma continental larga e a pluma do rio Amazonas podem impedir essas intrusões

(LODER; BOICOURT; SIMPSON, 1998) e até mesmo ocorrer uma situação inversa, onde as espécies costeiras se espalham pelo oceano aberto por influência da pluma.

O aporte de água doce de pequenos rios é um mecanismo importante na estrutura das comunidades de cnidários pelágicos em regiões costeiras, onde as espécies respondem aos gradientes de salinidade de maneiras distintas (Ex. LOMAN-RAMOS; ORDÓÑEZ-LÓPEZ; SEGURA-PUERTAS, 2007; MORALES-RAMÍREZ; NOWACZYK, 2006; NAGATA et al., 2014; SANVICENTE-AÑORVE et al., 2009; VANSTEENBRUGGE et al., 2015). Contudo os efeitos de grandes plumas estuarinas alcançando grandes distâncias no oceano aberto como a pluma do rio Amazonas nunca foram testados, o que dificulta o entendimento adequado do funcionamento do ecossistema, padrões biogeográficos e de diversidade de espécies e também na potencial barreira à dispersão de espécies causada pela pluma do rio Amazonas (ROCHA, 2003).

Nesse contexto a presente tese busca explorar aspectos da diversidade, distribuição, abundância e estrutura da comunidade de cnidários planctônicos e neustônicos nas províncias neríticas e oceânicas do lado oeste do oceano Atlântico equatorial. Apresentando um panorama compreensivo da composição taxonômica e ampliando o conhecimento da biodiversidade na área, bem como identificar os padrões espaciais na distribuição e abundância das espécies, avaliando os efeitos ecológicos da pluma do rio Amazonas e outros processos oceanográficos em meso-escala.

# 2 OBJETIVOS

Explorar aspectos da diversidade, distribuição, abundância e estrutura da comunidade de cnidários planctônicos e neustônicos nas províncias neríticas e oceânicas do lado oeste do oceano Atlântico equatorial.

## 2.1 Objetivos específicos

1. Descrever a composição taxonômica da comunidade de cnidários do plâncton e nêuston, detalhando novas espécies e novos registros locais e regionais
2. Avaliar a distribuição espacial e abundância da comunidade de cnidários planctônicos e neustônicos
3. Verificar a influência da pluma do rio Amazonas e outros processos oceanográficos de meso-escala e das condições ambientais na distribuição e abundância da comunidade de cnidários planctônicos e neustônicos.

# 3 ESTRUTURA DA TESE

Os resultados da tese estão organizados em três capítulos que ainda serão publicados em formato de artigo e quatro apêndices com artigos que já foram publicados. No primero artigo,” *Pelagic cnidarian fauna in the equatorial Atlantic Ocean under influence of the Amazon River Plume*”, a composição taxonômica da comunidade de cnidários pelágicos do oceano Atlântico equatorial sob influência da pluma do rio Amazonas é descrita e discutida, com ênfase aos novos registros locais e regionais. Esse artigo será submetido para o periódico *Marine Biodiversity*.

No segundo artigo, intitulado “*Effects of mesoscale oceanographic processes on the spatial distribution of planktonic cnidarians in the Western Equatorial Atlantic Ocean under influence of the Amazon River plume*” que será submetido ao periódico *ICES Journal of Marine Science*, a distribuição espacial e abundância da comunidade de cnidários planctônicos e sua relação com a pluma do Rio Amazonas e outros processos físicos do oceano foi avaliada. Já no terceiro artigo, “*Influence of the Amazon River Plume in the spatial distribution of neustonic cnidarians in the Western Equatorial Atlantic Ocean*” que será submetido para o periódico *Marine Ecology Progress Series*, a distribuição espacial e abundância dos cnidários da camada neustônica foi avaliada e relacionada com a pluma do rio Amazonas e outros processos físicos.

No primeiro apêndice, com o artigo “*New records of Pegantha spp. (Hydrozoa: Narcomedusae) off Northern Brazil*”, publicado no periódico *Papéis Avulsos de Zoologia*, são discutidos detalhes das ocorrência das narcomedusas *Pegantha laevis*, encontrada pela primeira vez na costa brasileira, e *Pegantha triloba*, que já havia sido encontrada previamente, mas foi omitida em checklists recentes da fauna de cnidários brasileiros. No segundo apêndice, intitulado “*First record of Cirrholovenia polynema (Hydrozoa: Leptothecata) in the Western Atlantic Ocean*”, já aceito e atualmente em processo de publicação no periódico *Ocean and Coastal Research*, a presença da hidromedusa *C. polynema* é reportada pela primeira vez no lado oeste do oceano Atlântico. Previamente a espécie só era conhecida nos oceanos Índico e Pacífico e na costa Atlântica da África.

No terceiro apêndice, “*New species of Eirenidae (Hydrozoa: Leptothecata) from the Amazonian coast (northern Brazil)*”, publicado no periódico *Scientia Marina*, duas espécies de hidromedusa da família Eirenidae novas para a ciência são descritas, *Eutima marajoara* e *Helgicirrha angelicae*. No quarto apêndice, "*Sampling planktonic cnidarians with paired nets: Implications of mesh size on community structure and abundance*", publicado no periódico *Estuarine, Coastal and Shelf Science*, a eficiência das malhas de 120 e 300 µm na amostragem de cnidários planctônicos foi comparada, nos resultados observamos que não houve diferenças significativas entre as duas malhas.

# 4 ARTIGO 1 - PELAGIC CNIDARIAN FAUNA IN THE WESTERN EQUATORIAL ATLANTIC OCEAN UNDER INFLUENCE OF THE AMAZON RIVER PLUME

## Abstract

We surveyed the pelagic cnidarian fauna from the Western Equatorial Atlantic Ocean, an area under influence of the large freshwater discharge of the Amazon River. We analyzed 87 zooplankton and 90 zooneuston samples collected at the neritic and oceanic provinces of the Western Equatorial Atlantic Ocean under the influence of the Amazon River Plume off the north coast of Brazil. 34,772 organisms were studied corresponding to 7 orders, 31 families and 93 species. Ate least two of them were news species, 1 was a new record to western Atlantic, 2 were new records to Brazil and 22 were new regional records. Holoplanktonic siphonophores dominated in terms of species richness and abundance both in the Continental shelf and open ocean, were higher diversity was observed. In conclusion, we observed a highly diverse community and presume this biodiversity is higher since sampling in different seasons, with different gears, and including deeper waters certainly will further increase the number of pelagic cnidarian species in the area.

**Keywords:** Biodiversity, Taxonomy, Jellyfish, Gelatinous zooplankton, Amazonian Coast

## Introduction

Marine habitats from the Caribbean Sea and the tropical coast of Brazil and its oceanic islands are considered distinct biogeographical provinces based on the high endemism of corals, hydrozoans, molluscs and fish (Briggs 1974; Rocha 2003; Floeter et al. 2007; Tosetto et al. under review). The main barrier considered responsible for the endemism is the large freshwater and sediment discharge of the Amazon River, which in glacial periods with low sea level, covers the entire continental shelf, preventing dispersion of neritic species associated with saline waters (Rocha 2003). In high sea level periods, such as the present time, saline water masses are present in the bottom of the continental shelf below the Amazon River plume, and some exchange of organisms between both biogeographical provinces may occur through the area (Rocha 2003). Furthermore, marine environments with riverine run-off such as the Western Equatorial Atlantic Ocean under the influence of the Amazon River plume are extremely productive, with high social and ecological value, playing a major role in the Atmospheric $CO_2$ assimilation and sinking (Smith and Demaster 1996; Körtzinger 2003; Subramaniam et al. 2008). Despite the importance, these systems are subject of increasing anthropogenic pressure, mainly associated with urban development, sewage disposal, predatory fisheries and oil exploitation (Paerl 1997; Silva Junior and Magrini 2014).

The marine biota is directly involved with all above processes and the complex interactions in the estuarine-coastal-oceanic environment. Knowledge on the community inhabiting the Western

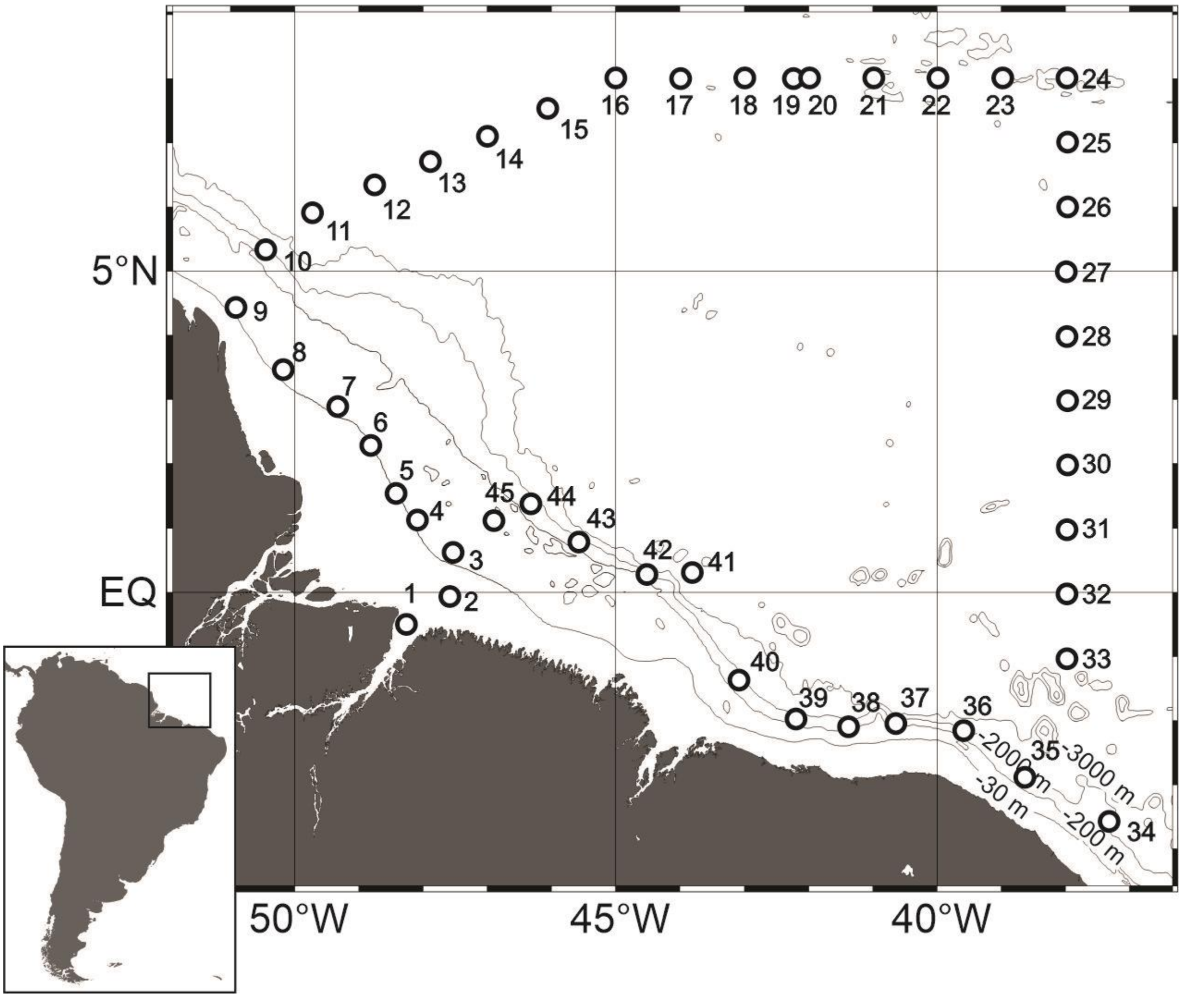
Equatorial Atlantic Ocean, mainly the area under the influence of the Amazon River Plume is poorly known (Moura et al. 2016; Neumann-Leitão et al. 2018; Tosetto et al. 2018, 2019, 2020). This hampers proper understanding of species diversity, ecosystem functioning, biogeographical patterns and the potential dispersal barrier the plume imposes to marine organisms (Rocha 2003). Knowledge in the area is even narrower when considering the pelagic cnidarian community. Although relevant to the dynamics and community structuring of marine ecosystems, pelagic cnidarians are often set aside in traditional zooplankton studies due to their high fragility and complicated taxonomy (e.g. Lane et al. 2008; García-Comas et al. 2011). In recent decades, cnidarians attracted interest from scientists due to their significant role as predators in pelagic environments, where the high feeding rates associated with occasional population blooms have the potential to control the pelagic community and collapse fisheries and other human activities (Purcell et al. 2007; Pitt et al. 2009; Purcell 2012; Hays et al. 2018).

Few studies focused on planktonic cnidarian biodiversity in the North Brazilian Continental Shelf and adjacent open waters (Leloup 1934; Leloup and Hentschel 1938; Ranson 1949; Kramp 1959a; Alvariño 1968; Tosetto et al. 2018, 2019, 2020). Species diversity is an intuitive index of community structure, which can be measured at booth small and large spatial scales (Blake and Loiselle 2000; Rahbek and Graves 2001) and detailed understanding regarding species composition is a critical component of biological science, providing background for other areas such as ecology, modelling, biogeography and conservation biology (Tewksbury et al. 2014; Nogueira Júnior et al. 2018). This study aimed to provide a comprehensive overview of the planktonic cnidarian biodiversity in a mesoscale spatial area, presenting the taxonomic composition from 87 zooplankton and 90 zooneuston samples collected at the neritic and oceanic provinces of the Western Equatorial Atlantic Ocean under the influence of the Amazon River Plume off the north coast of Brazil.

## Materials and methods

Samples were obtained during the oceanographic cruise *Camadas Finas* III, aboard the research vessel NHo. Cruzeiro do Sul - H38 (DHN/Brazilian Navy), along the north Brazilian continental shelf between the Amazon and Oyapok river mouths and adjacent equatorial Atlantic oceanic waters between 8°N, 51°W and 3.5°S, 37°W (Fig. 1). The cruise was performed during October 9-31, 2012, corresponding to the period when most of the Amazon River plume is retroflexed and transported eastward (Molleri et al. 2010).

**Figure 1.** Geographic location of the study area in the North Brazilian continental shelf and adjacent Western Equatorial Atlantic Ocean, showing the sampled stations.



A total of 87 zooplankton samples were obtained at 44 stations along the track of the cruise in oblique hauls, using a Bongo net with 120 and 300 µm mesh size and 0.3 and 0.6 m mouth opening respectively. Stations were sampled from near bottom to surface over the continental shelf, and from 200 m to the surface in the open ocean. These nets were towed at approximately 2 knots, at various times of day and night. In addition, 90 zooneuston samples were obtained at 45 stations along the track of the cruise with a David-Hempel aluminum catamaran (Hydro-Bios, Kiel, Germany) equipped with two superposed nets with rectangular mouth (30x15 cm each one) and a 500 µm mesh size. The upper net was adjusted exactly centered at the air-water interface, sampling the epineuston layer from the surface to 7.5 cm depth, while the lower net sampled the hyponeuston layer from 7.5 cm to 22.5 cm depth. The catamaran was hauled during 20 minutes at a speed of 2-3 knots at each station. Nets were fitted with a flowmeter (Hydro-Bios) to estimate the volume filtered during each trawl. Samples were fixed with 4% formaldehyde buffered with sodium tetraborate (0.5 g.l-1). Samples were classified as neritic (bottom depth <120 m) and oceanic (bottom depth >120 m). At each station temperature (°C) and salinity profiles were recorded with a Seabird SBE 25 Sealogger CTD profiler.

In laboratory, whole zooplankton samples were analyzed under stereomicroscope and specimens were identified (Mainly following Bouillon 1999; Pugh 1999; Bouillon et al. 2006) and counted. For calycophorans, the number of anterior nectophores was used for estimating the polygastric stage abundance, and eudoxid bracts for the eudoxid stage abundance (Hosia and Båmstedt 2007; Hosia et al. 2008). For physonects and the calycophoran *Hippopodius hippopus*, number of colonies were roughly estimated by dividing the number of nectophores by 10 (Pugh 1984). Rarefaction curves and biodiversity estimators Chao 1, Chao 2, Jackknife 1 and Jackknife 2 were computed at EstimateS 9.1.0 Software to predict the expected number of species and compare to the number of species found here.

## Results

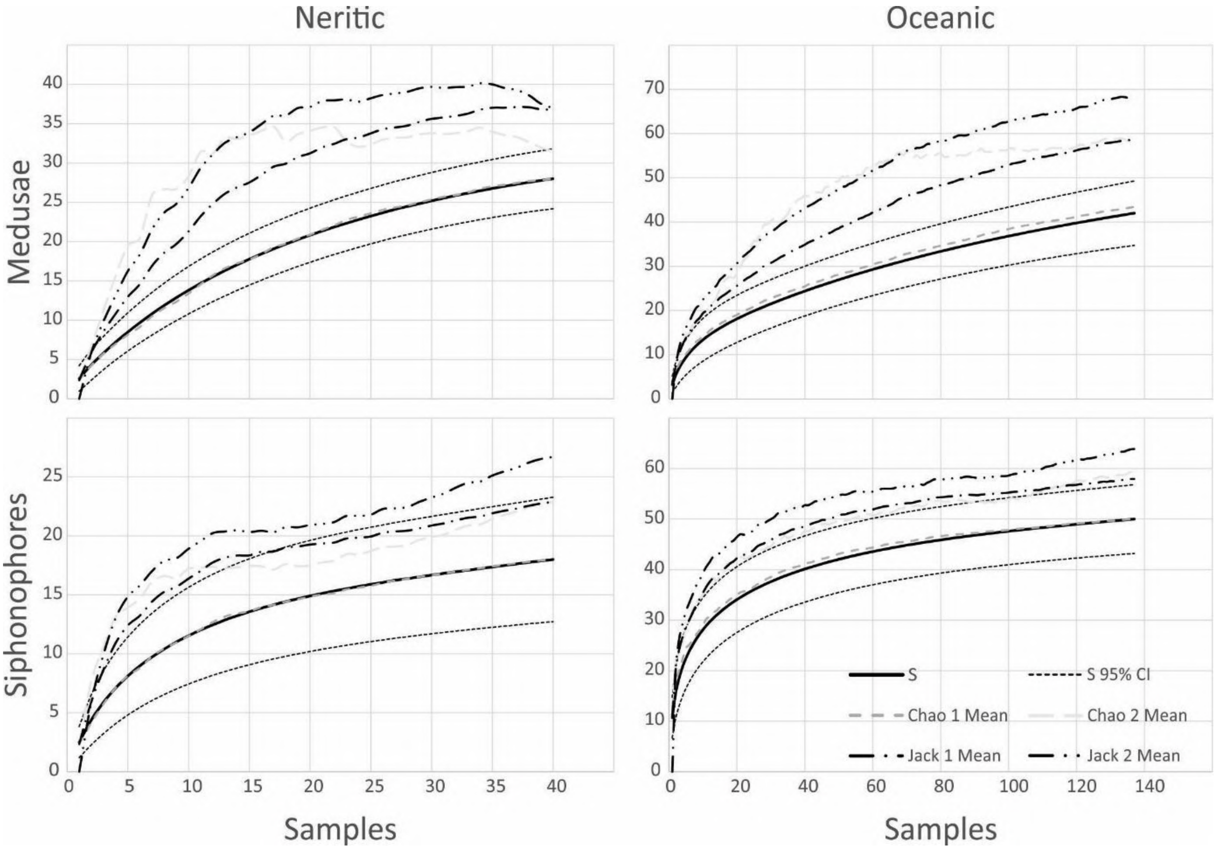
### *Species composition*

In total, 34,772 cnidarians were analyzed in the present survey, corresponding to 93 non-ambiguous taxa, distributed in 31 families and 7 orders (Table 1). Additionally, many unidentifiable larval forms such as cerinula, ephyrae and athorybia were found. Damaged unidentifiable specimens accounted for less than 2% of the total. Zooplankton samples accounted for 83 taxa, averaging 16.2±7.1 taxa per sample while zooneuston samples accounted 52 taxa, averaging 7.8±4.3 taxa. Among these species, 41 were found exclusively in zooplankton samples while 9 were exclusive from zooneuston including floating species such as *Porpita porpita*, *Velella velella* and *Physalia physalis* (Table 1).

Holoplanktonic cnidarians of the order Siphonophora dominated in terms of species richness. All the 45 taxa were found at the oceanic samples, 18 of them were also found at neritic ones. Meroplanktonic hydromedusae of the orders Leptothecata (18 taxa) and Anthoathecata (15 taxa) were also representative. The former presented slightly more taxa over the continental shelf than in the open ocean (15 and 10 respectively) and the later presented more taxa at oceanic samples (13 vs. 5; Table 1). Among holoplanktonic hydromedusae, the order Narcomedusae was represented by six species, all of them present in the open ocean and two over the continental shelf as well. While in the order Trachymedusae four of the five species found were observed in both environments and one was exclusive in the open ocean. The siphonophores *Chelophyes appendiculata*, *Diphyes bojani* and *Eudoxoides mitra* dominated in abundance (4446, 4431 and 2391 colonies respectively) followed by the Trachymedusae *Aglaura hemistoma* (2351) and *Liriope tetraphylla* (2340; Table 1).

The rarefaction curves showed differences among medusae and siphonophores considering neritic and oceanic habitats, but neither became asymptotic at any point. While Chao 1 estimated a number of species similar to the observed in all occasions, Chao 2 and Jackknife 1 and 2 estimators were higher than the observed, the former presenting wide oscillations with increasing number of samples (Fig. 2).

**Figure 2.** Species accumulation plots and richness estimators for medusae and siphonophores in neritic and oceanic provinces from Western Equatorial Atlantic Ocean



From literature, additional 38 species can be included in the pelagic cnidarian checklist from the area of the equatorial Atlantic Ocean located between 12°N to 5°S, and 33 to 55°W (Table 1). Twenty-one taxa previously reported in Brazil were recorded for the first time in the area (Table 1). This is the first time *Forskalia tholoides* was recorded in South America and Brazilian waters. Two new species, *Eutima marajoara* and *Helgicirrha angelicae*, and the first records of *Persa incolorata*, *Cirrholovenia polynema* and *Pegantha laevis* were observed in the same sampling program discussed herein, and already were published in other contexts (Tosetto et al. 2018, 2019, 2020, in press). Taxonomic attention will be directed to new records and other noteworthy taxa.

**Table 1.** Checklist and taxonomic classification of pelagic cnidarian species registered in the Equatorial Atlantic Ocean between 12°N, 55°W and 6°S, 33°W. Number of individuals analyzed from zooplankton and zooneuston samples (Calycophorae species = poligastric/eudoxid stages), occurrence in neritic (N) and oceanic (O) habitats, temperature (°C) and salinity ranges (surface in neuston samples and range in the first 200 m in plankton samples) of species analyzed in this study are given. Species in bold = new records in the area; * New record in South America. Data sources: 1 = this study, 2 = (Alvariño 1968), 3 = (Alvariño 1971), 4 = (Araujo 2012), 5 = (Kramp 1959b), 6 = (Leloup 1934), 7 = (Leloup 1937), 8 = (Leloup 1955), 9 = (Leloup & Hentschel 1938), 10 = (Marques *et al.* 2006), 11 = (Mesquita *et al.* 2006), 12 = (Neumann-Leitão *et al.* 2018b), 13 = (Ranson 1949), 14 = (Thiel 1936), 15 = (Thiel 1938), 16 = (Tosetto *et al.* 2018b), 17 = (Banha *et al.* 2020), 18 = (Tosetto *et al.* 2020), 19 = (Tosetto *et al*. in press), 20 = (Tosetto *et al.* 2019)

| Species | Plankton | Neuston | N | O | Temp | Sal | Source |
|---|---|---|---|---|---|---|---|
| Class cubozoa | | | | | | | |
| Order Chirodropida | | | | | | | |
| Family Chiropsalmus | | | | | | | |
| *Chiropsalmus quadrumanus* (F. Muller, 1859) | | | | | | | 10, 13 |
| Class Hydrozoa | | | | | | | |
| Subclass Hydroidolina | | | | | | | |
| Order Anthoathecata | | | | | | | |
| Suborder Aplanulata | | | | | | | |
| Family Corymorphidae | | | | | | | |
| ***Corymorpha gracilis* (Brooks, 1883)** | | 3 | | 3 | 27.89−28.4 | 35.94−36.12 | 1 |
| Suborder Capitata | | | | | | | |
| Family Corynidae | | | | | | | |
| ***Stauridiosarsia producta* (Wright, 1858)** | | 1 | | 1 | 26.95 | 36.3 | 1 |
| **Corynidae sp.** | 1 | | | 1 | 15.27−26.21 | 35.56−36.33 | 1 |
| Family Porpitidae | | | | | | | |
| *Porpita porpita* (Linnaeus, 1758) | | 119 | 1 | 118 | 26.26−29.78 | 32.78−36.35 | 1, 10 |
| *Velella velella* (Linnaeus, 1758) | | 1 | | 1 | 26.65 | 36.3 | 1, 7 |

**Table1.** Continuation

| Species | Plankton | Neuston | N | O | Temp | Sal | Source |
|---|---|---|---|---|---|---|---|
| Suborder Filifera | | | | | | | |
| Family Bougainvillidae | | | | | | | |
| *Bougainvillia carolinensis* (McCady, 1859) | | | | | | | 2 |
| ***Bougainvillia muscus* (Allman, 1863)** | 1 | | | 1 | 15.27–26.21 | 35.56–36.33 | 1 |
| *Bougainvillia platygaster* (Haeckel, 1879) | | | | | | | 2 |
| Family Cytaeididae | | | | | | | |
| *Cytaeis tetrastyla* Eschscholtz, 1829 | | | | | | | 15 |
| *Cytaeis* sp.1 | 48 | | 1 | 47 | 9.91–29.69 | 32.55–36.33 | 1 |
| *Cytaeis* sp.2 | 1 | | | 1 | 13.48–26.65 | 35.31–36.3 | 1 |
| *Cytaeis* sp.3 | | 389 | | 389 | 26.65–29.69 | 32.78–36.3 | 1 |
| *Cytaeis* sp.4 | 31 | 1 | 32 | | 25.4–27.88 | 31.05–36.29 | 1 |
| Family Pandeidae | | | | | | | |
| *Annatiara affinis* (Hartlaub, 1914) | 21 | 13 | 1 | 33 | 10.46–29.55 | 32.55–36.35 | 1, 5 |
| **Stomotoca sp.** | 1 | | 1 | | 25.4–27.88 | 31.05–36.29 | 1 |
| Suborder undefined | | | | | | | |
| Anthoathecata sp.1 | 3 | | | 3 | 10.74–29.48 | 33.51–35.45 | 1 |
| Anthoathecata sp.2 | 1 | | | 1 | 10.74–29.52 | 34.23–35.03 | 1 |
| Anthoathecata sp.3 | 5 | | | 5 | 10.56–29.6 | 32.78–35.45 | 1 |
| Anthoathecata sp.4 | 1 | | | x | 12.84–27.99 | 35.37–36.29 | 1 |
| Order Leptothecata | | | | | | | |
| Family Aequoridae | | | | | | | |
| ***Aequorea forskalea* Péron & Lesueur, 1810** | 1 | | | 1 | 18.41–26.99 | 36.08–36.24 | 1 |
| ***Aequorea macrodactyla* (Brandt, 1835)** | | 4 | 3 | 1 | 26.52–26.61 | 36.26–36.27 | 1 |
| Aequorea spp. | 3 | | | 3 | 10.74–29.52 | 34.23–36.27 | 1 |
| Family Campanulariidae | | | | | | | |
| Clytia spp. | 14 | 3 | 6 | 11 | 10.56–29.6 | 31.58–36.64 | 1 |

**Table1.** Continuation

| **Species** | **Plankton** | **Neuston** | **N** | **O** | **Temp** | **Sal** | **Source** |
|---|---|---|---|---|---|---|---|
| Obelia spp. | 18 | | 18 | | 28.23 | 18.18 | 1, 6 |
| Campanulariidae sp. | 1 | | | 1 | 10.53−29.78 | 34.33−35 | 1 |
| Family Cirrholoveniidae | | | | | | | |
| Cirrholovenia polynema Kramp, 1959 | 4 | | 0 | 4 | 10.56−29.6 | 32.78−36.08 | 1, 19 |
| **Cirrholovenia tetranema Kramp, 1959** | 11 | | 8 | 3 | 10.46−29.51 | 31.05−36.64 | 1 |
| Family Eirenidae | | | | | | | |
| **Eirene lactea (Mayer, 1900)** | 1 | | 1 | | 24.9−27.81 | 31.58−36.25 | 1 |
| Eirene viridula (Péron & Lesueur, 1810) | | 97 | 97 | | 27.81−28.23 | 18.18−31.58 | 1, 2 |
| Eutima marajoara Tosetto, Neumann-Leitão, Nogueira Junior, 2020 | 175 | | 175 | | 28.23 | 18.18 | 1, 18 |
| Helgicirrha angelicae Tosetto, Neumann-Leitão, Nogueira Junior, 2020 | 67 | | 67 | | 24.9−27.88 | 31.05−36.29 | 1, 18 |
| Eirenidae sp. | | 1 | | 1 | 26.38 | 36.3 | 1 |
| Family Laodiceidae | | | | | | | |
| **Laodicea undulata (Forbes & Goodsir, 1853)** | 2 | 2 | 2 | 2 | 26.5−26.62 | 36.26−36.31 | 1 |
| Family Lovenellidae | | | | | | | |
| Eucheilota maculata Hartlaub, 1894 | 9 | | 5 | 4 | 11.24−29.48 | 18.18−36.3 | 1 |
| Eucheilota spp. | 2 | 2 | 3 | 1 | 18.41−28.23 | 18.18−36.24 | 1 |
| **Mitrocomium cirratum Haeckel, 1879** | 1 | | 1 | | 24.9−27.81 | 31.58−36.25 | 1 |
| Lovenellidae sp. | 2 | | | 2 | 13.75−27.91 | 35.36−36.27 | 1 |
| Family Malagazziidae | | | | | | | |
| Malagazzia carolinae (Mayer, 1900) | 2 | 3 | 4 | 1 | 25.4−29.55 | 31.05−36.29 | 1, 4 |
| **Octophialucium bigelowi Kramp, 1955** | 2 | | 2 | | 24.9−27.81 | 31.58−36.25 | 1 |
| Octophialucium haeckeli (Vannucci & Soares Moreira, 1966) | 1 | 1 | 2 | | 24.9−27.81 | 31.58−36.25 | 1, 11 |
| Family Mitrocomidae | | | | | | | |
| **Mitrocomella sp.** | | 3 | | 3 | 27.63 | 36.29 | 1 |

**Table1.** Continuation

| Species | Plankton | Neuston | N | O | Temp | Sal | Source |
|---|---|---|---|---|---|---|---|
| Order Siphonophorae | | | | | | | |
| Suborder Calycophorae | | | | | | | |
| Family Abylidae | | | | | | | |
| Abyla haeckeli Lens & van Riemsdijk, 1908 | | | | | | | 2, 3, 4, 7 |
| Abyla trigona Quoy & Gaimard, 1827 | 3/0 | | | 3/0 | 9.91−29.78 | 18.18−37.08 | 1, 2, 4 |
| Abyla sp. | 0/3 | 0/2 | | 0/5 | 10.56−29.6 | 32.78−36.33 | 1 |
| Abylopsis eschscholtzii (Huxley, 1859) | 39/713 | 4/324 | 1/6 | 42/1031 | 9.91−29.78 | 32.55−36.48 | 1, 2, 3, 4, 6 |
| Abylopsis tetragona (Otto, 1823) | 566/377 | 76/46 | 4/3 | 638/420 | 9.91−29.78 | 18.18−36.35 | 1, 2, 3, 4, 6, 7, 9, 12 |
| Bassia bassensis (Quoy & Gaimard, 1833) | 499/1440 | 43/304 | 3/8 | 539/1736 | 9.91−29.78 | 31.05−36.35 | 1, 2, 3, 4, 6, 7, 9, 12, 20 |
| Ceratocymba dentata (Bigelow, 1918) | | | | | | | 2, 3, 4 |
| Ceratocymba leuckartii (Huxley, 1859) | 31/56 | 3/10 | | 34/66 | 9.91−29.78 | 32.55−36.35 | 1, 2, 3, 4 |
| Enneagonum hyalinum Quoy & Gaimard, 1827 | 769/1997 | 9/29 | 777/2026 | 1/0 | 12.57−27.98 | 31.05−36.29 | 1, 2, 3, 4, 7, 20 |
| Family Clausophyidae | | | | | | | |
| Chuniphyes multidentata Lens & van Riemsdijk, 1908 | | | | | | | 6, 9 |
| Chuniphyes problematica Moser, 1925 (nomen dubium) | | | | | | | 6, 9 |
| Chuniphyes sp. | 5 | | | 5 | 11.89−29.23 | 33.69−36.33 | 1 |
| Heteropyramis maculata Moser, 1925 | | | | | | | 4, 6, 9 |
| Family Diphyidae | | | | | | | |
| Chelophyes appendiculata (Eschscholtz, 1829) | 1608/1727 | 281/830 | 21/12 | 1868/2545 | 9.91−29.78 | 31.58−36.35 | 1, 2, 3, 4, 6, 7, 9, 8, 12, 20 |
| Chelophyes contorta (Lens & van Riemsdijk, 1908) | | | | | | | 12 |
| Dimophyes arctica (Chun, 1897) | 4/0 | | | 4/0 | 11.43−29.11 | 34.09−35.11 | 1, 2, 3, 4, 6, 9 |
| Diphyes bojani (Eschscholtz, 1825) | 1540/2171 | 324/396 | 12/65 | 1852/2502 | 9.91−29.78 | 18.18−36.64 | 1, 2, 3, 4, 6, 7, 9, 12, 20 |
| Diphyes dispar Chamisso & Eysenhardt, 1821 | 325/676 | 198/281 | 293/643 | 230/314 | 9.91−29.78 | 18.18−36.51 | 1, 2, 3, 4, 7, 12, 20 |

**Table1.** Continuation

| **Species** | **Plankton** | **Neuston** | **N** | **O** | **Temp** | **Sal** | **Source** |
|---|---|---|---|---|---|---|---|
| Eudoxoides mitra (Huxley, 1859) | 900/1491 | 0/15 | 2/4 | 894/1502 | 9.91–29.78 | 31.05–36.35 | 1, 2, 3, 4, 6, 7, 9, 8, 12, 20 |
| Eudoxoides spiralis (Bigelow, 1911) | 530/737 | 27/32 | 1/2 | 556/767 | 9.91–29.78 | 32.55–36.35 | 1, 2, 3, 4, 6, 7, 9, 12 |
| Lensia achilles Totton, 1941 | | | | | | | 4 |
| Lensia campanella (Moser, 1917) | 80/0 | 13/0 | 5/0 | 88/0 | 9.91–29.69 | 31.05–36.3 | 1, 2, 4, 6, 9 |
| Lensia conoidea (Keferstein & Ehlers, 1860) | 4/0 | 7/0 | | 11/0 | 11.43–29.11 | 34.09–36.33 | 1, 2, 4, 6, 9 |
| Lensia cossack Totton, 1941 | 4/0 | 2/0 | | 6/0 | 10.56–29.6 | 32.55–36.33 | 1, 2, 4 |
| Lensia fowleri (Bigelow, 1911) | 4/0 | | | 4/0 | 11.43–29.11 | 34.09–36.29 | 1, 4, 6, 9 |
| Lensia grimaldii Leloup, 1933 | | | | | | | 9 |
| Lensia hardy Totton, 1941 | 7/0 | | | 7/0 | 10.04–29.69 | 34–36.35 | 1, 4 |
| Lensia havock Totton, 1941 | | | | | | | 4 |
| Lensia hotspur Totton, 1941 | 5/0 | | | 5/0 | 10.4–29.69 | 34.4–34.98 | 1, 3, 4 |
| Lensia leloupi Totton, 1954 | 1/0 | | | 1/0 | 18.41–26.99 | 36.08–36.24 | 1, 2, 4 |
| Lensia meteori (Leloup, 1934) | 101/0 | | | 101/0 | 9.91–29.78 | 32.55–36.33 | 1, 4, 9 |
| Lensia multicristata (Moser, 1925) | | | | | | | 2, 4, 6 |
| Lensia subtilis (Chun, 1886) | 18/0 | 1/1 | 0/1 | 19/0 | 10.04–29.78 | 34–36.51 | 1, 2, 4, 6, 9 |
| Lensia subtiloides (Lens & van Riemsdijk, 1908) | 2/0 | 0/1 | | 0/3 | 12.57–27.98 | 35.22–36.28 | 1, 4 |
| Lensia tottoni Daniel & Daniel, 1963 (taxon inquirendum) | | | | | | | 2, 4 |
| Lensia spp. | 0/18 | | | 0/18 | 10.04–29.52 | 34–36.29 | 1 |
| Muggiaea atlantica Cunningham, 1892 | | | | | | | 4 |
| Muggiaea kochii (Will, 1844) | 991/114 | 57/0 | 986/34 | 62/0 | 10.74–29.52 | 31.05–36.35 | 1, 2, 3, 4, 20 |
| Sulculeolaria biloba (Sars, 1846) | 49/0 | 2/0 | | 51/0 | 9.91–29.69 | 32.55–36.31 | 1, 2, 4, 6, 7, 9 |
| Sulculeolaria chuni (Lens & van Riemsdijk, 1908) | 570/0 | 128/0 | 22/0 | 676/0 | 9.91–29.78 | 32.55–36.35 | 1, 2, 3, 4 |
| Sulculeolaria monoica (Chun, 1888) | 9/0 | 24/0 | | 33/0 | 11.46–29.55 | 32.55–36.3 | 1, 2, 4, 7 |
| Sulculeolaria quadrivalvis de Blainville, 1830 | 1/0 | | | 1/0 | 15.27–26.21 | 35.56–36.33 | 1, 4 |
| Sulculeolaria turgida (Gegenbaur, 1854) | 65/0 | 17/0 | | 82/0 | 9.91–29.78 | 32.55–36.33 | 1, 2, 3, 4 |

**Table1.** Continuation

| **Species** | **Plankton** | **Neuston** | **N** | **O** | **Temp** | **Sal** | **Source** |
|---|---|---|---|---|---|---|---|
| Family Hippopodiidae | | | | | | | |
| Hippopodius hippopus (Forsskål, 1776) | 16 | 1 | | 17 | 10.04−29.78 | 32.55−36.33 | 1, 2, 3, 4, 6 |
| Vogtia glabra Bigelow, 1918 | | | | | | | 2, 4 |
| Vogtia pentacantha Kölliker, 1853 | | | | | | | 2 |
| Family Prayidae | | | | | | | |
| Amphicaryon acaule Chun, 1888 | | | | | | | 2 |
| Amphicaryon ernesti Totton, 1954 | | | | | | | 2, 3, 4 |
| **Amphicaryon peltifera (Haeckel, 1888)** | 1/0 | | | 1/0 | 11.46−29.48 | 33.51−35.16 | 1 |
| Amphicaryon sp. | 0/23 | | | 0/23 | 9.91−29.69 | 32.55−36.3 | 1 |
| Rosacea plicata Bigelow, 1911 | 8/0 | | | 8/0 | 10.04−29.78 | 32.78−36.3 | 1, 2, 4 |
| Rosacea sp. | 0/1 | | | 1 | 9.91−29.55 | 32.55−34.92 | 1 |
| Family sphaeronectidae | | | | | | | |
| **Sphaeronectes koellikeri Huxley, 1859** | 3/0 | | | 3/0 | 10.56−29.6 | 32.78−36.3 | 1 |
| Suborder Cystonectae | | | | | | | |
| Family Physaliidae | | | | | | | |
| Physalia physalis (Linnaeus, 1758) | | 3 | | 3 | 26.52−29.78 | 34.23−36.27 | 1, 4, 10 |
| Suborder Physonectae | | | | | | | |
| Family Agalmatidae | | | | | | | |
| Agalma elegans (Sars, 1846) | 35 | 12 | | 47 | 10.04−29.69 | 32.78−36.3 | 1, 4 |
| Agalma okenii Eschscholtz, 1825 | 90 | 52 | 1 | 141 | 9.91−29.78 | 32.55−36.35 | 1, 2, 3, 4 |
| **Athorybia rosacea (Forsskål, 1775)** | 10 | 2 | 1 | 11 | 9.91−29.69 | 31.58−36.29 | 1 |
| Halistemma rubrum (Vogt, 1852) | 15 | 3 | | 18 | 9.91−29.69 | 32.55−36.33 | 1, 4 |
| Lychnagalma utricularia (Claus, 1879) | 44 | | 14 | 30 | 9.91−29.78 | 31.05−36.33 | 1, 4 |
| Nanomia bijuga (Delle Chiaje, 1844) | 184 | 37 | 34 | 187 | 9.91−29.78 | 18.18−36.51 | 1, 2, 4 |
| Family Cordagalmatidae | | | | | | | |
| Cordagalma ordinatum (Haeckel, 1888) | 25 | 11 | 1 | 35 | 10.4−29.78 | 34.23−36.31 | 1, 4 |
| Family Forskaliidae | | | | | | | |
| Forskalia contorta (Milne Edwards, 1841) | 3 | | | 3 | 10.56−29.6 | 32.78−35.03 | 1, 4 |

**Table1.** Continuation

| **Species** | **Plankton** | **Neuston** | **N** | **O** | **Temp** | **Sal** | **Source** |
|---|---|---|---|---|---|---|---|
| Forskalia edwardsii Kölliker, 1853 | 3 | | | 3 | 9.91−29.55 | 32.55−36.3 | 1, 2, 4 |
| **Forskalia tholoides Haeckel, 1888 *** | 21 | | | 21 | 9.91−29.6 | 32.55−36.29 | 1 |
| Family physophoridae | | | | | | | |
| Physophora hydrostatica Forsskål, 1775 | 1 | 4 | | 5 | 10.04−29.38 | 34−36.29 | 1, 4 |
| Family Resomidae | | | | | | | |
| Resomia convoluta (Moser, 1925) | | | | | | | 4 |
| Subclass Trachylinae | | | | | | | |
| Order Limnomedusae | | | | | | | |
| Family Olindiidae | | | | | | | |
| **Olindias sp.** | 1 | | 1 | | 24.9−27.81 | 31.58−36.25 | 1 |
| Order Narcomedusae | | | | | | | |
| Family Aeginidae | | | | | | | |
| Aegina citrea Eschscholtz, 1829 | | | | | | | 2 |
| Aeginura grimaldii Maas, 1904 | | | | | | | 2 |
| Aeginura lanzarotae (Haeckel, 1879) (taxon inquirendum) | | | | | | | 14 |
| Family Cuninidae | | | | | | | |
| Cunina duplicata Maas, 1893 | | | | | | | 5 |
| **Cunina frugifera Kramp, 1948** | 4 | | | 4 | 13.28−28.26 | 35.33−36.3 | 1 |
| Cunina octonaria McCrady, 1859 | 61 | 256 | 56 | 261 | 12.95−29.6 | 31.05−36.48 | 1, 3 |
| Solmissus marshalli Agassiz & Mayer, 1902 | | | | | | | 5 |
| Family Solmarisidae | | | | | | | |
| Pegantha laevis H.B. Bigelow, 1909 | | 1 | | 1 | 27.91 | 36.17 | 1, 16 |
| **Pegantha martagon Haeckel, 1879** | 2 | | | 2 | 11.89−29.23 | 33.69−36.3 | 1 |
| Pegantha triloba Haeckel, 1879 | 1 | 8 | | 9 | 10.4−29.69 | 34.4−36.29 | 1, 5, 13, 16 |
| Solmaris flavescens (Kölliker, 1853) | | | | | | | 14 |
| Family Solmundaeginidae | | | | | | | |
| Solmundella bitentaculata (Quoy & Gaimard, 1833) | 74 | 16 | 7 | 83 | 9.91−29.69 | 31.05−36.3 | 1, 7 |

**Table1.** Continuation

| **Species** | **Plankton** | **Neuston** | **N** | **O** | **Temp** | **Sal** | **Source** |
|---|---|---|---|---|---|---|---|
| Order Trachymedusae | | | | | | | |
| Famiy Geryoniidae | | | | | | | |
| Liriope tetraphylla (Chamisso & Eysenhardt, 1821) | 2340 | 1646 | 2635 | 1351 | 9.91−29.78 | 18.18−37.08 | 1, 2, 11, 12, 20 |
| Family Halicreatidae | | | | | | | |
| Halicreas minimum Fewkes, 1882 | | | | | | | 2, 14 |
| Family Rhopalonemathidae | | | | | | | |
| Aglaura hemistoma Péron & Lesueur, 1810 | 2351 | 58 | 41 | 2368 | 9.91−29.78 | 31.58−37.06 | 1, 2, 12, 20 |
| Colobonema sericeum Vanhöffen, 1902 | | | | | | | 5 |
| Persa incolorata McCrady, 1859 | 1476 | 8 | 1480 | 4 | 12.35−28.4 | 18.18−36.29 | 1, 20 |
| Rhopalonema velatum Gegenbaur, 1857 | 65 | 5 | 2 | 68 | 9.91−29.6 | 32.55−36.35 | 1, 2, 13 |
| **Sminthea eurygaster Gegenbaur, 1857** | 150 | | | 150 | 10.04−29.78 | 32.78−36.33 | 1 |
| Subclass undefined | | | | | | | |
| Hydromedusae sp. | 1 | | | 1 | 20.86−28.26 | 36.29−36.3 | 1 |
| Class Scyphozoa | | | | | | | |
| Order Coronatae | | | | | | | |
| Family Atollidae | | | | | | | |
| Atolla wyvillei Haeckel, 1880 | | | | | | | 2 |
| Family Nausithoidae | | | | | | | |
| **Nausithoe aurea Da Silveira & Morandini, 1997** | 1 | 1 | | 2 | 14.4−29.69 | 34.4−36.29 | 1 |
| Nausithoe punctata Kölliker, 1853 | 30 | | 2 | 28 | 10.04−29.69 | 33.51−36.64 | 1, 5 |
| Order Rhyzostomeae | | | | | | | |
| Suborder Daktyliophorae | | | | | | | |
| Family Lychnohizidae | | | | | | | |
| Lychnorhiza lucerna Haeckel, 1880 | | | | | | | 10, 17 |
| Family Stomolophidae | | | | | | | |
| Stomolophus fritillarius Haeckel, 1880 | | | | | | | 13, 17 |

**Table1.** Continuation

| **Species** | **Plankton** | **Neuston** | **N** | **O** | **Temp** | **Sal** | **Source** |
|---|---|---|---|---|---|---|---|
| Stomolophus meleagris Agassiz, 1862 | | | | | | | 10 |
| Suborder Kolpophorae | | | | | | | |
| Family Mastigiidae | | | | | | | |
| Phyllorhiza punctata Lendenfeld, 1884 | | | | | | | 10 |
| Order Semaeostomeae | | | | | | | |
| Family Pelagiidae | | | | | | | |
| Chrysaora lactea Eschscholtz, 1829 | | | | | | | 10, 17 |
| Chrysaora quinquecirrha (Desor, 1848) | | | | | | | 2 |
| Pelagia noctiluca (Forsskål, 1775) | | | | | | | 13 |

*Species description*

**Class Hydrozoa**

**Subclass Hydroidolina**

**Order Anthoathecata**

**Suborder Aplanulata**

**Family Corymorphidae**

***Corymorpha gracilis* (Brooks, 1883)**

**Material examined**. 38.01316°W, 4.9965°N: 2 medusae; 50.42683°W, 5.3385°N: 1 medusa.

**Description**. Umbrella with long pointed apical projection. Up to 2 mm wide, 3 mm high (not considering the apical projection). Apical canal as long as apical projection. Manubrium as long as bell cavity. One long tentacle with prominent swellings, opposite tentacle short, cone-shaped, two other reduced to bulbs.

**Remarks**. Among Corymorphidae Allman, 1872, the genus *Euphysora* Mass, 1905 included species with one fully developed tentacles and the three remaining being short or rudimentary (Bouillon 1999; Bouillon et al. 2006). However, *Euphysora* is currently considered a synonym of *Corymorpha* M. Sars, 1835 (Schuchert 2021) where the studied specimens were assigned. *C. gracilis* is a quite characteristic species and the sampled specimens fit in the diagnosis of *C. gracilis* (Bouillon 1999; Nagata et al. 2014). Among the species of the genus found in South Atlantic and Caribbean waters (Bouillon 1999; Segura-Puertas et al. 2003; Oliveira et al. 2016), *Corymorpha forbesii* (Mayer, 1894), *Corymorpha gigantea* (Kramp, 1957) and *Corymorpha abaxialis* (Kramp, 1962) have no apical process and bear only one tentacle (Kramp 1962; Bouillon 1999), *Corymorpha furcata* (Kramp, 1948) has a short and broad apical projection and the long tentacle is bifurcated at the end (Bouillon 1999) and *Corymorpha januarii* Steenstrup, 1855 produces only eumedusoids without tentacles or a functional mouth (Genzano et al. 2009).

**Distribution**. The species was found in both sides of the Atlantic Ocean (Bouillon 1999; Nagata et al. 2014). It was previously recorded in Northeast, Southeast and South Brazilian waters at latitudes higher than 8°S (Oliveira et al. 2016) and in the Caribbean Sea (Segura-Puertas et al. 2003). This is the first report in the area.

**Suborder Capitata**

**Family Corynidae**

***Stauridiosarsia producta* (Wright, 1858)** (Fig. 3a)

**Material examined**. 43.8153°W, 0.33916°N: 1 medusa.

**Description**. Umbrella bell shaped 1.5 mm wide and high. Mesoglea thick. Four radial canals bearing tentacles. Manubrium cylindrical as long as bell cavity with distinct conical apical chamber. Undivided gonads completely surrounding manubrium.

**Remarks**. Corynidae is an uncertain family (probably paraphyletic) and currently genus distinctions are based on molecular sequences (Nawrocki et al. 2010). However, among the species of the family with manubrium as long as (or longer than) bell cavity and undivided gonads completely surrounding manubrium known from the Atlantic coast of South America and/or Caribbean Sea, *S. producta* is distinguished by the distinct conical apical chamber (Forbes 1848; Bouillon 1999).

**Distribution**. Distributed in the Atlantic, Mediterranean and Indo-Pacific (Bouillon 1999). It was previously recorded in Southeast and South Brazilian waters at latitudes higher than 24°S (Oliveira et al. 2016). This is the first report in the area.

**Suborder Filifera**

**Family Bougainvilliidae**

***Bougainvillia muscus* (Allman, 1863)** (Fig. 3b)

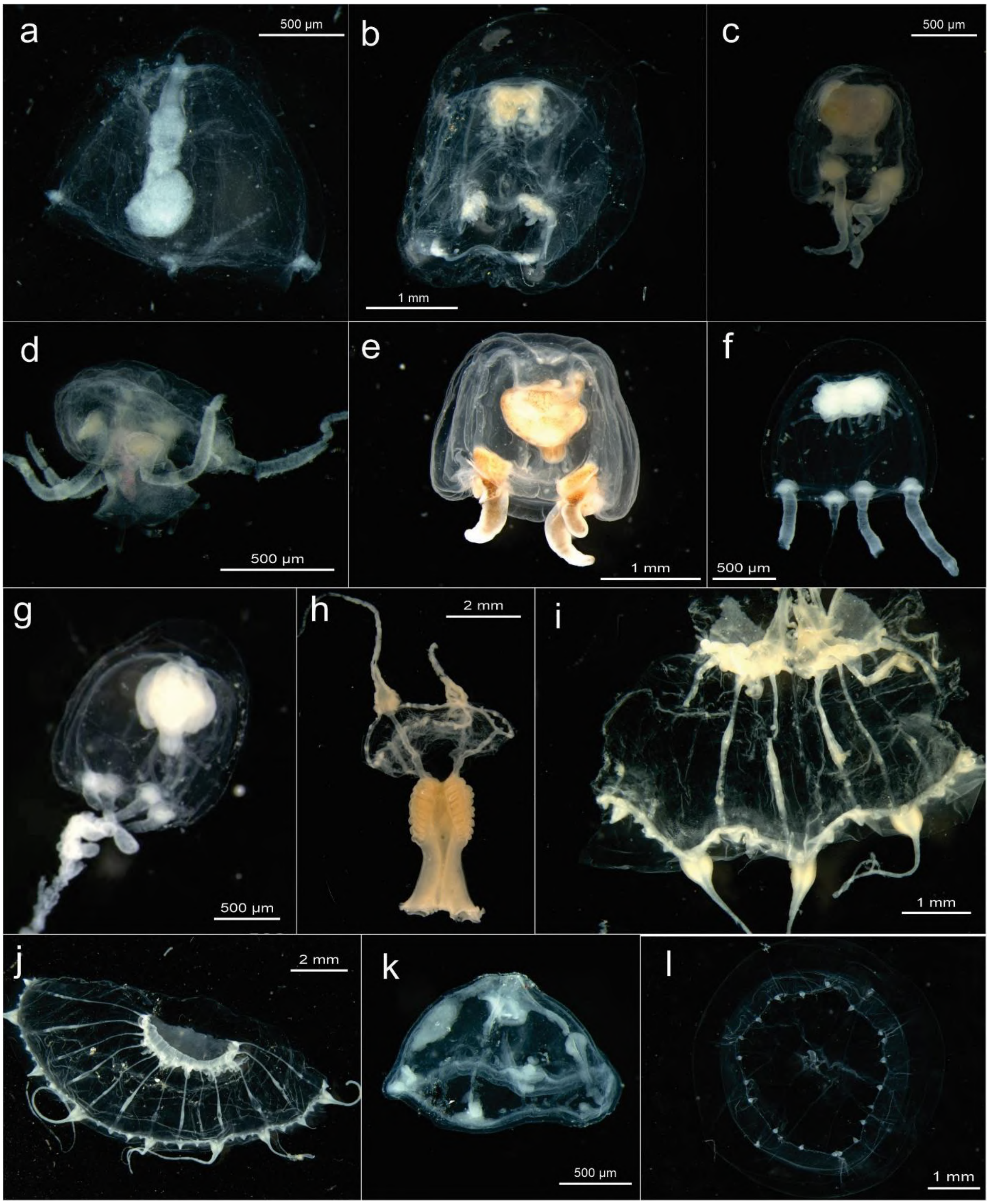
**Material examined**. 38.66°W, 2.83516°S: 1 medusa.

**Description**. Globular umbrella 2 mm wide and 3 mm high. Mesoglea thick. Manubrium short. Peduncle absent. Interradial gonads reaching perradii. Oral tentacles with long basal trunk divided two times. Each marginal bulb with five or six tentacles and the same number of adaxial ocelli.

**Remarks**. *Bougainvillia* Lesson, 1830 medusae are easily recognized by the branched oral tentacles inserted above mouth rim and presence of clusters of marginal tentacles borne on 4 perradial bulbs. Species on the genus are mainly distinguished by the presence/absence of gastric peduncle and ocelli, position and shape of gonads, and length and branching of basal trunk of oral tentacles (Bouillon 1999; Nogueira Júnior et al. 2013). Present specimen, without peduncle, interradial gonads reaching perraddi, ocelli and long basal trunks perfectly fits in *B. muscus* characteristics (Nogueira Júnior et al. 2013).

**Distribution**. Distributed in the Atlantic, Artic, Mediterranean and Indo-Pacific (Bouillon 1999). The species was previously recorded in Brazilian waters at latitudes higher than 9°S (Oliveira et al. 2016, Tosetto et al. in press) and Caribbean Sea (Segura-Puertas et al. 2003). This is the first report in the area.

**Figure 3.** Examples of pelagic cnidarians from Western Equatorial Atlantic Ocean. S*tauridiosarsia producta* (a); *Bougainvillia muscus* (b); *Cytaeis* sp.1 (c); *Cytaeis* sp.2 (d); *Cytaeis* sp.3 (e); *Cytaeis* sp.4 (f, g); *Stomotoca* sp. (h); *Aequorea forskalea* (i); *Aequorea macrodactyla* (j); *Cirrholovenia tetranema* (k); *Eirene lactea* (l).



**Family Cytaeididae**

***Cytaeis* spp.**

**Material examined**. ***Cytaeis* sp.1:** 2.83516°S, 38.66°W : 10 medusae; 0.998°S, 38.00483°W: 6 medusae; 0.30116°N, 44.5235°W: 4 medusae; 5.3385°N, 50.42683°W: 4 medusae; 6.33916°N, 48.7376°W: 4 medusae; 0.33916°N, 43.8153°W: 2 medusa; 3.00183°N, 38.0013°W: 2 medusa; 3.5216°S, 37.349°W: 2 medusae; 6.70616°N, 47.87383°W: 2 medusae; 7.00016°N, 37.9996°W: 2 medusae; 1.14°N, 46.8875°W: 1 medusa; 1.331°S, 43.091°W: 1 medusa; 3.9963°N, 38.00416°W: 1 medusa; 5.9126°N, 49.7035°W: 1 medusa; 7.0965°N, 46.9906°W: 1 medusa; 7.9935°N, 42.2525°W: 1 medusa; 7.9946°N, 41.9995°W: 1 medusa; 7.9993°N, 39.0035°W: 1 medusa; 8.00083°N, 38.00316°W: 1 medusa; 8°N, 44.9983°W: 1 medusa. ***Cytaeis* sp.2:** 44.5235°W, 0.30116°N: 1 medusa. ***Cytaeis* sp.3:** 7.9935°N, 42.2525°W: 1 medusa; 6.70616°N, 47.87383°W: 1 medusa; 7.5223°N, 46.0556°W: 2 medusae; 5.9126°N, 49.7035°W: 2 medusae; 3.9963°N, 38.00416°W: 3 medusae; 0.30116°N, 44.5235°W: 3 medusae; 6.0013°N, 37.9956°W: 4 medusae; 7.00016°N, 37.9996°W: 6 medusae; 2.00283°N, 38.00083°W: 6 medusae; 0.0013°N, 38.0073°W: 6 medusae; 8.0025°N, 42.9973°W: 72 medusae; 7.9946°N, 41.9995°W: 78 medusae; 7.9993°N, 39.0035°W: 98 medusae; 7.99°N, 43.9995°W: 107 medusae. ***Cytaeis* Sp.4:** 4.44°N, 50.896°W: 32 specimens.

**Description**. ***Cytaeis* sp.1:** Umbrella bell shaped, up to 1 mm wide and 1.5 mm high, with fragile mesoglea. Very short gastric peduncle. Manubrium pearl shaped with large mouth. Up to 12 unbranched capitated oral tentacles in adnate position very near mouth rim. Gonads encircling upper portion of manubrium. Four marginal tentacles with triangular bulbs attached to exumbrella above bell margin (Fig. 3c). ***Cytaeis* sp.2:** Umbrella globular, 0.5 mm wide and high, with fragile mesoglea. Very short gastric peduncle. Manubrium pearl shaped with large mouth. Four unbranched capitated oral tentacles in adnate position very near mouth rim. Four marginal tentacles with globular bulbs attached to exumbrella above bell margin (Fig. 3d). ***Cytaeis* sp.3:** Umbrella bell shaped, up to 4 mm wide and 5 mm high. Distinctive gastric peduncle. Manubrium pearl shaped. Up to 32 unbranched capitated oral tentacles in adnate position very near mouth rim. Gonads encircling upper portion of manubrium. Some specimens with medusa buds. Four marginal tentacles with prominent triangular bulbs attached to exumbrella above bell margin (Fig. 3e). ***Cytaeis* sp.4:** Umbrella bell-shaped with a solid, nearly hemispherical apical projection representing about 1/4 of total umbrellar height; 0.8-1.8 mm high and 0.6-1.4 mm wide. Short gastric peduncle in adults, absent in all smaller specimens (<1 mm width), but also absent on some individuals up to 1.4 mm. Manubrium about 1/2 the length of subumbrellar cavity, with oral tube; 8 to 16 unbranched oral tentacles arising above mouth rim each with a terminal cluster of nematocysts; developed gonads completely surrounding the proximal part of manubrium, thicker interrradially, and with milky coloration in the formalin-fixed material. Less developed gonads restricted to interradial region of manubrium. No young specimens were found.

Four simple radial canals; four perradial hemispherical tentacular bulbs each with a single marginal tentacle; ocelli absent; velum narrow (Fig. 3 f, g).

**Remarks.** There are 12 valid described species of this genus (Schuchert 2021), however morphologic characters of the medusa stage of *Cytaeis* Eschscholtz, 1829 species diagnosis overlap and currently there is no way to morphologic distinguish them (Bouillon et al. 2004). Therefore, the past hypothesis that the circumglobally spread *Cytaeis tetrastyla* Eschscholtz, 1829 (and reported for our study area) may actually represent a complex of species (Ress 1962) is still valid and yet to be tested. Due to these taxonomical constraints we did not attempt to determine specific names to the present material. Nevertheless, the specimens studied here could be clearly distinguished into four different morphotypes, differentiated mostly based on the length of gastric peduncle, gonads, number of oral tentacles, shape of tentacle bulbs and mesoglea. It is noteworthy that specimens with intermediate characters were not observed yet a relatively large number of specimens were studied (except *Cytaeis* sp.2), also suggesting they represent different species. Both *Cytaeis* sp.1 and sp.4 presented triangular bulbs, however, while the former presented a very short gastric peduncle and fragile mesoglea, the later presented a long peduncle and robust mesoglea and tentacles. Cytaeis sp.2 differed from both in the shape of bulbs and from sp.1 in the longer peduncle and from sp. In the fragile mesoglea.

Among the four morphotypes, *Cytaeis* sp.4 is noteworthy: Unlike the others, these specimens have the oral tentacles perpendicularly inserted quite distinctly above the mouth rim (Fig. 3 g). This characters would also fit them in the diagnosis of family Bougainvillidae. In fact, actual distinctions between the medusa stage of Cytaeididae and Bougainvillidae are quite ambiguous: Cytaeididae have oral tentacles situated on/or very near mouth rim (usually drawn as a continuous extension of mouth rim in species schematic drawings) and Bougainvillidae have oral tentacles distinctly inserted above mouth rim (Bouillon et al. 2006). The genus in Bougainvillidae with unbranched oral tentacles and four radial canals is *Nubiella* Bouillon, 1980. It was originally described with only four perradial oral tentacles (Bouillon 1980) as in other Bougainvillidae genera (Bouillon et al. 2006). But recently, many species in this genus were described with more than four oral tentacles as in our specimens (Xu et al. 2009; Huang et al. 2012; Guo et al. 2018; Wang et al. 2019), thus if we followed this concern, *Cytaeis* sp4. would fit in *Nubiella* and represent a new species due to the combination of gastric peduncle, gonads encircling manubrium, more than four oral tentacles and apical projection. However, as discussed above, *Nubiella* (according the original description), hasonly four perradial oral tentacles. Further molecular studies are necessary to completely elucidate this question. However, at the moment, present specimens and those *Nubiella* species with more than four oral tentacles should tentatively be included in the family Cytaeididae.

### Family Pandeidae

***Stomotoca* sp.** (Fig. 3h)

**Material examined.** 4.44°N, 50.896°W – 10/21/2012 - 1 specimen: MZUSP 8515

**Description.** Umbrella with a thick and short conical apical projection 3 mm high and 4 mm wide. Manubrium large, far surpassing umbrellar cavity, flask-shaped, cruciform. Mouth with slight crenulated margin and four small recurved lips. Eight adradial gonads on manubrium wall forming eight-nine oblique transversal folds. Two opposite tentacles with conical hollow bulbs. About 10 small rudimentary marginal tentaculae per quadrant, all with similar size. No ocelli. Presence of peduncle in manubrium apparent but uncertain.

**Remarks.** Currently three genera are recognized among Pandeidae Haeckel, 1879 medusae with two well-developed marginal tentacles, radial canals without diverticula and absence of centripetal canals: *Stomotoca* L. Agassiz, 1862, *Larsonia* Boero, Bouillon & Gravili, 1991 and *Amphinema* Haeckel, 1879 (Bouillon et al. 2006; Schuchert 2021). *Larsonia* differs from *Stomotoca* and present specimen in their gonads, which are complexly transversely folded in eight adradial rows (see fig. 97e in Bouillon et al. 2006). Actually, the distinction among *Stomotoca* and *Amphinema* is the presence of gastric peduncle, which was not certain in the present specimen due to the condition of the single animal sampled. Thus, two hypothesis are possible. In the first case, the penduncle is present in its initial stage of development, which would assign the specimen to the genus *Stomotoca*. Boero & Bouillon (1989) described the complete life cycle of *Stomotoca atra* L. Agassiz, 1862, the only current species in the genus, and twenty-day-old medusa presented a wide and short peduncle, 5 rudimentary bulbs each quadrant and four perdadial gonads, each formed by 2 series (equivalent to eight adradial) of folds, which would differ from our specimen just in the number of rudimentary bulbs.

In the case of absence of gastric peduncle, the specimen would be assigned to the genus *Amphinema*. The currently 18 valid species in *Amphinema* are mainly characterized by the shape of gonads and presence of marginal structures (table 1 at Fuentes et al. 2012). The specimen found presented a unique combination of characters that did not fit in any of the currently 18 valid described species (Schuchert 2021) and in this hypothesis it would be a new species. The most distinctive characteristic of our specimen is the obliquely folded gonads. Six *Amphinema* species present folded gonads (Kao et al. 1958; Fuentes et al. 2012). Gonads of *Amphinema australis* (Mayer, 1900), *Amphinema bouilloni* Schuchert, 2007 and *Amphinema platyhedos* Arai & Brickmann-Voss, 1983 have complex folds all in different shapes from our specimen (Mayer 1900; Arai and Brinckmann-Voss 1983; Schuchert 2007), clearly not matching. The remaining three species present gonads in a similar pattern. However, *A. rugosum* and *A. tsingtauensis* differ in the number of folds, not surpassing four, and the considerably smaller number of tentaculae, 40 in the present material and up to 24 and 20 in *A. rugosum* and *A. tsingtauensis*, respectively (Kao et al. 1958; Fuentes et al. 2012). Although the number of folds is not mentioned for *Amphinema physophorum* (Ushida, 1927), the specimen at the artwork is represented with six folds (Ushida 1927). In addition, this species also differs from our specimen by smaller number of tentaculae (14 vs. 40) and a long, narrow and pointed apical projection (Kramp 1968), apart from far distinct distribution, supporting the differentiation of both species.

More specimens in different development stages would be necessary for a definitive conclusion on the presence of peduncle and correct genus assignment of the studied species. However, based on the development of *S. atra* (Boero and Bouillon 1989) and its current distribution - Gulf of Mexico and Southeast Brazil (Segura-Puertas et al. 2003; Oliveira et al. 2016) -, we think that the more conservative hypothesis that present specimen is a young stage of *S. atra* is more plausible.

**Order Leptothecata**

**Family Aequoreidae**

***Aequorea forskalea* Péron & Lesueur, 1810** (Fig. 3i)

**Material examined**. 45.57483°W, 0.8045°N: 1 medusa.

**Description**. Umbrella and manubrium damaged. Tentacles with elongated conical bulbs, about half as many as radial canals. Three to four rudimentary bulbs between successive tentacles. Excretory pores on short papillae. Gonads nearly on the entire length of radial canals.

**Remarks**. Leptothecata medusae with closed statocysts, many simple radial canals, excretory pores and wide manubrium are assigned to the genus *Aequorea* Péron & Lesueur, 1810 (Bouillon 1999; Bouillon et al. 2006). Although the single specimen was torn, the gonads on most length of the radial canals distinguish the species from *Aequeorea conica* Browne, 1905, and the proportion of tentacles and canals and shape of bulbs from other congenerics present in South Atlantic and Caribbean Sea (Bouillon 1999; Segura-Puertas et al. 2003; Oliveira et al. 2016).

**Distribution**. Widespread in tropical and temperate waters of the Atlantic, Mediterranean and Indo-Pacific (Bouillon 1999; Nagata et al. 2014), the species was previously recorded in Northeast, Southeast and South Brazilian waters at latitudes higher than 8°S (Oliveira et al. 2016). This is the first report in the area.

***Aequorea macrodactyla* (Brandt, 1835)** (Fig. 3j)

**Material examined**. 46.8875°W, 1.14°N: 3 medusae; 43.091°W, 1.331°S: 1 medusa.

**Description**. Umbrella 11 mm wide, thicker in the center. Tentacles with broad bulb with abaxial keel. About four times as many radial canals as tentacles. Three to five rudimentary bulbs between successive tentacles. Prominent excretory papillae. Gonads on the nearly entire length of radial canals.

**Remarks**. The assignment of the genus was discussed in the previous species. As in *A. forskalea*, the gonads on most length of radial canals distinguish the species from *A. conica* and mostly shape of bulbs with abaxial keel and prominent excretory papillae from other congenerics present in South Atlantic and Caribbean Sea (Bouillon 1999; Segura-Puertas et al. 2003; Oliveira et al. 2016).

**Distribution**. Widespread in tropical and temperate waters of Atlantic and Indo-Pacific (Bouillon 1999; Nogueira Júnior et al. 2016) the species was previously recorded in Southeast Brazilian waters and Caribbean Sea (Nogueira Júnior et al. 2016). This is the first report in the area.

### Family Cirrholoveniidae

***Cirrholovenia tetranema* Kramp, 1959** (Fig. 3k)

**Material examined**. 46.8875°W, 1.14°N: 3 medusae; 47.5243°W, 0.6455°N: 3 medusae; 50.896°W, 4.44°N: 1 medusa; 50.42683°W, 5.3385°N: 1 medusa; 38.00316°W, 8.00083°N: 1 medusa; 42.2525°W, 7.9935°N: 1 medusa; 48.4135°W, 1.56616°N: 1 medusa.

**Description**. Umbrella up to 1.5 mm wide. Thin mesoglea. Manubrium small with short lips. Thick cylindrical gonads along almost the entire length of radial canals. Four peradial marginal tentacles with broad bulbs. Rudimentary bulbs absent. Up to eight marginal cirri and one or two statocysts each quadrant.

**Remarks**. The genus *Cirrholovenia* Kramp, 1959 is distinguished from other Leptothecata medusae by the presence of four simple radial canals, marginal cirri, at least four closed statocysts and absence of gastric peduncle (Bouillon et al. 2006). Two species in the genus present only four marginal tentacles: *C. tetranema* and *Cirrholovenia reticulata* Xu & Huang, 2004. The studied specimens differ from *C. reticulata* by the absence of reticular papillae covering the exumbrella and number of marginal cirri and statocysts (Xu and Huang 2004), which completely fit with the description of *C. tetranema* (Kramp 1959b). Other species of the genus present in the study is *Cirrholovenia polynema* Kramp, 1959, which differed from *C. tetranema* by the larger number of tentacles (up to 12 in the area; Tosetto et al. in press).

**Distribution**. Distributed in the Atlantic, Mediterranean and Indo-Pacific (Bouillon 1999; Nagata et al. 2014), the species was previously recorded in Northeast, Southeast and South Brazilian waters at latitudes higher than 8°S (Oliveira et al. 2016). This is the first report in the area.

### Family Eirenidae

***Eirene lactea* (Mayer, 1900)** (Fig. 3l)

**Material examined**. 3.47516°N, 50.16°W: 1 medusa.

**Description**. Umbrella 5 mm wide with thick mesoglea at the aboral pole and thin at the margin. Short gastric peduncle. Manubrium damaged. Four radial canals. 20 short tentacles with large bulbs. One or two statocysts between successive tentacles. Gonads linear, situated at a short distance of the junction of radial and circular canals.

**Remarks**. *Eirene* Eschscholtz, 1829 species are distinguished from other Leptothecata by the presence of more than eight closed statocysts (in adults), gastric peduncle and absence of marginal or lateral cirri. Species in the genus are distinguished by the position and shape of gonads, presence of excretory papillae and number of structures such as tentacles, statocysts and radial canals (Bouillon and Barnett 1999). Among the species with gonads in the distal portion of radial canals, *Eirene pyramidalis* (Agassiz, 1862), *Eirene mollis* Torrey, 1909, *Eirene conica* Du, Xu, Huang & Guo, 2010, *Eirene kambara* Agassiz & Mayer, 1899 and *Eirene proboscidea* Bouillon & Barnett, 1999, the numbers of bulbs and tentacles are quite different (100, 150-180, 28-38, 32 and 12 tentacles, respectively; Kramp 1961; Bouillon and Barnett 1999; Du et al. 2010) than the 20 found in the present specimen. The present specimen presents a shorter gastric peduncle than the one represented in the original description of *E. lactea* (Mayer 1900). Yet, this is expected given the small size of the medusa studied here suggests it was not completely developed. Indeed, gastric peduncle was short or absent in *E. lactea* medusae <6 mm in bell diameter raised in laboratory (Brinckmann-Voss 1973).

**Distribution**. First described from Florida (Mayer 1900), the species was also found in Bermuda and Caribbean Sea (Ramos and Segura-Puertas 2004), South Carolina estuaries (Zingmark 1978) Colombian Pacific (Chaparro and Peralta 2013). The species was reported in Brazilian waters in the coast of Paraná state around 27°S (Oliveira et al. 2016).

### Family Laodiceidae

#### ***Laodicea undulata* (Forbes & Goodsir, 1853)** (Fig. 4a)

**Material examined**. 6.0013°N, 37.9956°W: 2 medusae; 1.14°N, 46.8875°W: 2 medusae.

**Description**. Umbrella 6 to 8 mm wide with thick mesoglea. Manubrium quadrate with crenulated lips, small lobes attached to subumbrella perradially. Sinuous gonads along radial canals contiguous with manubrium. Up to 120 marginal tentacles with basal adaxial spurs. Usually one cordylus and one or two cirri between successive tentacles. Adaxial ocelli present on most tentacles.

**Remarks**. Laodiceidae Agassiz, 1862 medusae are distinguished from other Leptothecata by the presence of cordyli and gonads along the radial canals (Bouillon et al. 2006). Although the absence of perradial lobes was included in recent keys to distinguish the family from Tiarannidae Russell, 1940, they are present in Laodiceidae and distinctions among then are in the position of gonads, which in

Tiarannidae are on interradial walls of manubrium and/or adradial to pouches (Bouillon et al. 2006; Maronna et al. 2016). The genus *Laodicea* Lesson, 1843 is distinguished in the family by the four simple radial canals and presence of adaxial ocelli (Bouillon 1999). Species in the genus are mainly distinguished by the shape of gonads, presence of perradial lobes and basal spurs, and proportion of tentacles, cordyli, ocelli and cirri (Kramp 1961; Bouillon 1999). Among species with basal spurs on every tentacle, *L. undulata* differs from *Laodicea fertilis* (Lendenfeld, 1885) by having more than eight tentacles and spurs (Kramp 1961) and from *Laodicea fijiana* Agassiz & Mayer, 1899 by having one cordylus on each tentacle (Bouillon 1999).

**Distribution**. Distributed in the Atlantic, Mediterranean and Indo-Pacific (Bouillon 1999), the species was previously recorded in Northeast, Southeast and South Brazilian waters at latitudes higher than 8°S (Oliveira et al. 2016) and in the Caribbean Sea (Segura-Puertas et al. 2003). This is the first report in the area.

**Family Lovenellidae**

***Eucheilota maculata*** **Hartlaub, 1894**

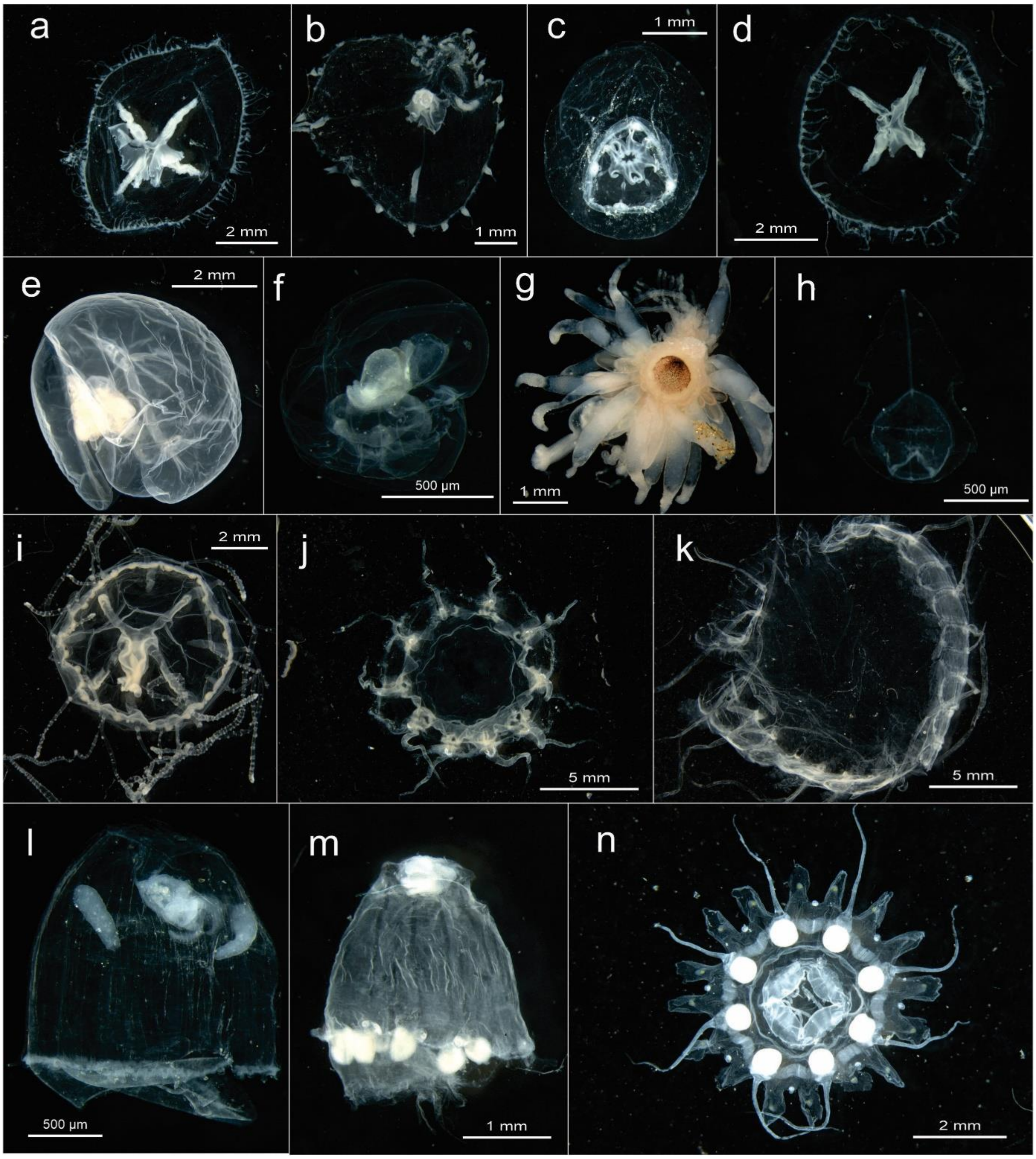
**Material examined**. 3.47516°N, 50.16°W: 3 medusae; 6.0013°N, 37.9956°W: 2 medusae; 0.4645°S, 48.2495°W: 2 medusae; 6.70616°N, 47.87383°W; 6.70616°N, 47.87383°W: 1 medusa; 7.99°N, 43.9995°W: 1 medusa.

**Description**. Umbrella 2 to 7 mm wide. Short manubrium with four developed lips. Gonads on distal 2/3 of radial canals. Up to 20 marginal tentacles and 1-3 rudimentary bulbs between successive tentacles. Marginal tentacles and rudimentary bulbs with lateral cirri. Few statocysts.

**Remarks**. The family Lovenellidae Russell, 1953 is distinguished among Leptothecata due to the presence of closed statocysts, narrow manubrium without gastric peduncle, tentacle bulbs with lateral cirri and without excretory pore and usually 4 or 8 radial canals (Bouillon et al. 2006). In the family, species with no more than 8 statocysts are placed in the genus *Eucheilota* McCrady, 1859. Among *Eucheilota* species known from South Atlantic and Caribbean(Bouillon 1999; Segura-Puertas et al. 2003; Oliveira et al. 2016), three of them have 16 or more marginal tentacles (Wang et al. 2018). Although, the different proportion of tentacles and rudimentary bulbs and position of gonads were used to distinguish *E. maculata* from *Eucheilota foresti* Goy, 1979 and *Eucheilota ventricularis* McCrady, 1859 (Bouillon 1999; Wang et al. 2018), these character may vary with medusa development and validity of these species were previously questioned (Vannucci 1957; Nagata et al. 2014). Further studies based on molecular data are required to test their validity.

**Distribution**. Distributed in the Atlantic and Indo-Pacific (Bouillon 1999; Nagata et al. 2014), the species was previously recorded in Southeast and South Brazilian waters at latitudes higher than 8°S (Oliveira et al. 2016). This is the first report in the area.

**Figure 4.** Examples of pelagic cnidarians from Western Equatorial Atlantic Ocean. *Laodicea undulata* (a); *Mitrocomium cirratum* (b); *Octophialucium bigelowi* (c); *Mitrocomella* sp. (d); *Amphicaryon peltifera* (e); *Sphaeronectes koellikeri* (f); *Athorybia rosacea* (g); *Forskalia tholoides* (h); *Olindias* sp. (i); *Cunina frugifera* (j); *Pegantha martagon* (k); *Persa incolorata* (l); *Sminthea eurygaster* (m); *Nausithoe aurea* (n).



***Mitrocomium cirratum* Haeckel, 1879** (Fig. 4b)

**Material examined**. 3.47516°N, 50.16°W: 1 medusa.

**Description**. Umbrella 4.5 mm wide with part of the margin damaged. Manubrium short. Linear gonads on the distal half of radial canals. Approximately 20 marginal tentacles with large bulbs with lateral cirri. 3-4 rudimentary marginal warts between successive tentacles. Approximately 16 statocysts.

**Remarks**. Systematics of the genera *Mitrocomium* Haeckel, 1879 and *Lovenella* Hincks, 1868 is complicated and unresolved: morphology of medusae is similar, but they differ in hydroid stage (Boero et al. 1996; Schuchert 2003), and the former has even been considered as synonym of *Lovenella* by some authors (e.g. Bouillon et al. 2006). Since no morphological characters could distinguish medusae of both genera, *M. cirratum* is the only Lovenellidae species with 16 statocysts described for the South Atlantic, and present specimens completely match with its diagnosis (e.g. Bouillon 1999).

**Distribution**. Distributed in the Atlantic, Mediterranean and Indo-Pacific (Bouillon 1999), the Species was previously recorded in Southeast and South Brazilian waters at latitudes higher than 20°S (Oliveira et al. 2016). This is the first report in the area.

### Family Malagazziidae

***Octophialucium bigelowi* Kramp, 1955** (Fig. 4c)

**Material examined**. 3.47516°N, 50.16°W: 2 medusae.

**Description**. Umbrella 1 to 3 mm wide and high, almost spherical, with very thick mesoglea. Subumbrellar cavity occupies less than half the umbrella height. Short manubrium with eight pointed lips. Eight radial canals. Linear gonads at initial stage in the middle of radial canals. Eight tentacles with spherical bulbs and one marginal wart between successive bulbs.

**Remarks**. The family Malagazziidae Bouillon, 1984 is distinguished from other Leptothecata by the presence of closed statocysts, narrow manubrium without gastric peduncle and tentacle bulbs with excretory pore (Bouillon et al. 2006). Species in the family with eight symmetrical radial canals are placed in the genus *Octophialucium* Kramp, 1955 with two known species from the South Atlantic and one from Caribbean (Segura-Puertas et al. 2003; Bouillon et al. 2006; Oliveira et al. 2016). *Octophialucium medium* Kramp, 1955, with 16 tentacles, *Octophialucium haeckeli* (Vannucci & Soares Moreira, 1966), with four lips and tentacles and *O. bigelowi* with eight lips and tentacles (Kramp 1955; Bouillon 1999). Although the gonads of *O. bigelowi* are in the entire length of radial canals, the ones of the present specimens were restricted to the middle portion. Small length of umbrella and gonads, and tentacles and bulbs in different developmental stages suggest that the present specimens are in the initial stages of development.

**Distribution**. Distributed in the Atlantic and Indo-Pacific (Bouillon 1999), the species was previously recorded in Northeast, Southeast and South Brazilian waters at latitudes higher than 9°S (Oliveira et al. 2016). This is the first report in the area.

**Family Mitrocomidae**

***Mitrocomella* sp.** (Fig. 4d)

**Material examined**. 7.9993°N, 39.0035°W: 3 medusae.

**Description**. Umbrella up to 5 mm wide with thick mesoglea. Manubrium cruciform extending perradially. Four radial canals. About 100 marginal tentacles with small bulbs. 5-8 marginal cirri between successive tentacles. Few open statocysts.

**Remarks**. Leptothecate medusae with four radial canals, marginal cirri and less than 16 open statocysts without ocelli are placed in the genus *Mitrocomella* Haeckel, 1879 (Bouillon et al. 2006). The higher number of tentacles differentiate it from *Mitrocomella brownei* (Kramp, 1930), which only have 16 (Bouillon 1999), and is the only species of the genus previously recorded in Brazil (Oliveira et al. 2016). However, the immature stage of the specimen studied hinders the possibility of advancing the identification to species level since *Mitrocomella frigida* (Browne, 1910) and *Mitrocomella millardae* Pagès, Gili and Bouillon, 1992, the other two species from South Atlantic with 8 statocysts differs mainly in the shape and position of gonads

**Distribution**. *M. brownei* was the only species in the genus found in Brazil, previously recorded at latitudes higher than 29°S (Oliveira et al. 2016). Since characteristics don´t match, it is the first record of the genus in the area and probably a new species record to Brazil.

**Order Siphonophorae**

**Suborder Calycophorae**

**Family Abylidae**

***Amphicaryon peltifera* (Haeckel, 1888)** (Fig. 4e)

**Material examined**. 7.99°N, 43.9995°W: 1 colony.

**Description**. Larval nectophore rounded, 5 mm high; nectosac occupies half its height; radial canals simple and strait. Vestigial nectophore plate-like and not completely embraced by the larval one; with three finger like radial canals and nectosac absent.

**Remarks**. The genus *Amphicaryon* Chun, 1888 is recognizable due the two rounded nectophores differing in size, with the larger larval nectophore partially enclosing the reduced definitive nectophore (Bouillon et al. 2006). Polygastric stage of the three species in the genus is recognized mostly by the proportion of larval and vestigial nectophores, and shape of nectosac and canals. *A. peltifera* is the only species in the genus without nectosac and presenting three finger like radial canals (Pugh 1999), matching with present specimen.

**Distribution**. Although (Pugh 1999) considered the species to inhabit the Atlantic Ocean from 55°N to 38°S, it was recorded in Brazilian waters only in Southeast Brazil (Dias 1994; Oliveira et al. 2016). This is the first report in the area.

**Family Sphaeronectidae**

***Sphaeronectes koellikeri* Huxley, 1859** (Fig. 4f)

**Material examined**. 0.8045°N, 45.57483°W: 1 nectophore; 6.70616°N, 47.87383°W: 1 nectophore; 7.5223°N, 46.0556°W: 1 nectophore.

**Description**. Delicate rounded larval nectophore, up to 1 mm high. Nectosac occupies the basal half of nectophore. Long and narrow hydroecium bending over one half of the nectosac. Somatocyst irregular over the nectosac.

**Remarks**. Polygastric stage of the genus *Sphaeronectes* Huxley, 1859 is distinguished by the single fragile spherical nectophere. *S. koellikeri* is the single species in the genus with the characteristic hydroecium bending over the nectosac and extending above its apex (Pugh 2009; Grossmann et al. 2012) such as the one observed in the studied specimens.

**Distribution**. Distributed in tropical, subtropical and temperate waters (Pugh 1999), the species was previously recorded in South Brazilian waters at latitudes higher than 26°S (Oliveira et al. 2016). This is the first reported occurrence in the area.

**Suborder Physonectae**

**Family Agalmatidae**

***Athorybia rosacea* (Forsskål, 1775)** (Fig. 4g)

**Material examined**. 8°N, 44.9983°W: 4 colonies; 4.9965°N, 38.01316°W: 2 colonies; 8.0025°N, 42.9973°W: 1 colony; 3.47516°N, 50.16°W: 1 colony; 7.0965°N, 46.9906°W: 1 colony; 7.9993°N, 39.0035°W: 1 colony; 7.9946°N, 41.9995°W: 1 colony; 3.9963°N, 38.00416°W: 1 colony.

**Description**. Large red pigmented pneumatophore with cormidia arranged in spiral. Nectophores and nectosome absent. Many detached elongated flimsy bracts found in the sample.

**Remarks**. The genus *Athorybia* Eschscholtz, 1829 is distinguished from other physonects by the absence of nectosome and the siphosome reduced do a dense corn (Bouillon et al. 2006). Two species are currently described in the genus. *A. rosacea* is mainly distinguished from *Athorybia lucida*

Biggs, 1978 by color and proportional size of pneumatophore, which represents less than 10% of the overall stem length and coloration is absent in the later (Biggs 1978).

**Distribution**. Although (Pugh 1999) considered the species to inhabit the Atlantic Ocean from 18°N to 36°S, it was recorded in Brazilian waters only once around Fernando de Noronha Archipelago (Alvariño 1971) and In Caribbean Sea (Gasca 2002). This is the first reported occurrence in the area.

### Family Forskaliidae

***Forskalia tholoides* Haeckel, 1888** (Fig. 4h)

**Material examined**. 0.99549°N, 38.0093°W: 5 nectophores; 2.00283°N, 38.00083°W: 3 nectophores; 3.00183°N, 38.0013°W: 14 nectophores; 4.9965°N, 38.01316°W: 17 nectophores; 6.0013°N, 27.9956°W: 8 nectophores; 7.00016°N, 37.9996°W: 2 nectophores; 7.0965°N, 46.9906°W: 47 nectophores; 7.5223°N, 46.0556°W: 22 nectophores; 7.9935°N, 42.2525°W: 30 nectophores; 8°N, 44.9983°W: 10 nectophores.

**Description**. Symmetrical elongated and narrow nectophores, flattened in the lateral plane, measuring up to 2.5 mm in length and 1 mm in width, tapering toward the apex, without axial wings. Pronounced lateral processes. Small baso-lateral pockets formed between basal ridges. Large lenticular nectosac occupying the basal third of the nectophore. Long pedicular canal.

**Remarks**. The genus *Forskalia* Kölliker, 1853 is recognizable by the nectophores dorso-ventrally flattened with nectosac restricted to basal half (Pugh 1999, 2003; Bouillon et al. 2006). All sampled nectophores match the diagnosis of *F. tholoides*, the only known forskaliid being bilaterally symmetrical, long and narrow, tapering apically, without axial wings, more or less pronounced lateral process and nectosac in basal third (Pugh 2003).

**Distribution**. Described from specimens collected off Canary Islands, *F. tholoides* was recorded in several parts of the North Atlantic Ocean and also off South Africa and India in the Indian Ocean (Pugh 2003). This is the first record of the species off Brazilian waters.

### Subclass Trachylinae

### Order Limnomedusae

### Family Olindiidae

***Olindias* sp.** (Fig. 4i)

**Material examined**. 3.47516°N, 50.16°W: 1 medusa.

**Description**. Umbrella 3 mm wide. Four radial canals. 1-3 centripetal canals per quadrant. About three primary tentacles per quadrant issuing above bell margin, with distal adhesive pads and cnidocysts in transverse clasps and four secondary tentacles on bell margin per quadrant. Eight spherical statocysts enclosed in mesoglea of umbrella margin. Numerous marginal clubs.

**Remarks**. *Olindias* Müller, 1861 is recognizable by the presence of centripetal canals, spherical statocysts enclosed in mesoglea of umbrella margin and two kinds of tentacles, the primary ones issuing above bell margin, with distal adhesive pads and the secondary on umbrella margin, without pads (Bouillon 1999; Bouillon et al. 2006). Species in the genus are mainly characterized by the number of centripetal canals, primary and secondary tentacles and marginal clubs (Bouillon 1999). Since the number of structures commonly increase with development in hydromedusae (Tosetto et al. 2020), it is difficult to identify younger individuals such as the present specimen down to species level. There are two species of *Olindias* along western Atlantic coast, *O. sambaquiensis* F. Müller, 1861 and *O. tenuis* (Fewkes, 1882). It is unlikely that the currents specimens would correspond to the former species which is restricted to temperate to subtropical waters (Oliveira et al. 2016). More material, preferably more developed specimens, are necessary to confirm if they can be assigned to *O. tenuis* or represent an undescribed species.

**Distribution**. *O. sambaquiensis* was previously recorded in Southeast and South Brazilian waters at latitudes higher than 23.5°S (Oliveira et al. 2016) and *O. tenuis* in the Caribbean Sea (Segura-Puertas et al. 2003), it is the first record of the genus in the area.

**Order Narcomedusae**

**Family Cuninidae**

***Cunina frugifera* Kramp, 1948** (Fig. 4j)

**Material examined**. 4.9965°N, 38.01316°W: 2 medusae; 6.70616°N, 47.87383°W: 1 medusa; 6.33916°N, 48.7376°W: 1 medusa.

**Description**. Umbrella up to 8 mm wide. 10 tentacles, manubrial pouches and marginal lappets. Perradial manubrial pouches tapering from brad base, separated by wide triangular spaces. Marginal lappets square with broad peripheral canal system. Four linear otoporpae per marginal lappet.

**Remarks**. *Cunina* Eschscholtz, 1829 is distinguished among narcomedusae by the presence of perradial manubrial pouches and otoporpae (Bouillon 1999). Three species in the genus have manubrial pouches tapering from broad base. Among them, *Cunina simplex* Gili, Bouillon, Pagès, Palanques, Puig & Heussner, 1998, have only four pouches, tentacles and lappets (Gili *et al.* 1998) and *Cunina tenella* (Bigelow, 1909) have a broad ectodermal pad bellow the base of the tentacles (Kramp 1961), both differing from present specimens which match the description of *C. frugifera* (Bouillon 1999).

**Distribution**. Distributed in the Atlantic, Mediterranean and Indo-Pacific (Bouillon 1999), the Species was previously recorded in Southeast and South Brazilian waters at latitudes higher than 20°S (Oliveira et al. 2016). This is the first report in the area.

**Family Solmarisidae**

***Pegantha martagon* Haeckel, 1879** (Fig. 4k)

**Material examined**. 6.70616°N, 47.87383°W: 1 medusa.

**Description**. Umbrella 15 mm wide, with very thick and vaulted mesoglea. Approximately 22 marginal lappets. Lateral portion of peripheral canals broad at base, tapering outwards. Five otoporpae per lappet short and narrow, about twice as long as width of transverse portion of peripheral canal.

**Remarks**. *Pegantha* Haeckel, 1879 is distinguished among narcomedusae by the presence of peripheral canal system and otoporpae and absence of manubrial pouches (Bouillon 1999). Two species of the genus present a broad peripheral canal system: *Pegantha laevis* H. B. Bigelow, 1909, previously reported in the area (Tosetto et al. 2018), and *P. martagon.* Both species diverge mainly in the shape of peripheral canals, which are broader in *P. laevis*, mainly in the lateral portions, being as wide as the space between them. Differently, peripheral canals in *P. Martagon* tapers towards the margin(Kramp 1957; Bouillon 1999), as observed in the present material. Differences also are observed at the exumbrella, which is fairly thicker in *P. matagon* (Bouillon 1999).

**Distribution**. Distributed in the Atlantic, Indo-Pacific and Southern oceans (Bouillon 1999), the species was previously recorded in South Brazilian waters at latitudes higher than 38°S and Caribbean Sea (Segura-Puertas et al. 2003; Oliveira et al. 2016). This is the first report in the area.

**Order Trachymedusae**

**Family Rhopalonematidae**

***Persa incolorata* McCrady, 1859** (Fig. 4l)

**Material examined**. 4.44°N, 50.896°W: 766 medusae; 3.47516°N, 50.16°W: 713 medusae; 5.3385°N, 50.42683°W: 4 medusae; 0.4645°S, 48.2495°W: 1 medusa

**Description**. Umbrella up to 2 mm wide and 3 mm high. Tubular manubrium with gastric peduncle. Eight radial canals. Two sausage-shaped pendent gonads near middle point of subumbrellar portions of two opposite radial canals.

**Remarks**. The genus *Persa* McCrady, 1859 is easily recognizable by the two opposite sausage-shaped gonads such as the ones present in the studied specimens. *P. incolorata* is the single species in the genus (Bouillon 1999), and the diagnosis match with the studied material.

**Distribution**. Previously found in the Atlantic Ocean, Mediterranean Sea and Indo-Pacific (Bouillon 1999). In Brazil, it was only recorded in the Southern Region at latitudes higher than 29°S (Oliveira et al. 2016). This occurrence was reported in the area in Tosetto et al (2019).

***Sminthea eurygaster* Gegenbaur, 1857** (Fig. 4m)

**Material examined**. 0.0013°N, 38.0073°W: 10 medusae; 0.99549°N, 38.0093°W: 1 medusa; 0.998°S, 38.00483°W: 2 medusae; 1.331°S, 43.091°W: 14 medusae; 1.401°N, 46.32°W: 3 medusae; 1.9369°S, 42.20916°W: 1 medusa; 2.00283°N, 38.00083°W: 6 medusae; 2.83516°S, 38.66°W: 2 medusae; 3.00183°N, 38.0013°W: 1 medusa; 3.5216°S, 37.349°W: 9 medusae; 3.9963°N, 38.00416°W: 5 medusa; 4.9965°N, 38.01316°W: 5 medusa; 5.9126°N, 49.7035°W: 7 medusae; 6.0013°N, 37.9956°W: 17 medusae; 6.33916°N, 48.7376°W: 15 medusae; 6.70616°N, 47.87383°W: 4 medusae; 7.00016°N, 37.9996°W: 5 medusae;7.0965°N, 46.9906°W: 1 medusa; 7.5223°N, 46.0556°W: 8 medusae; 7.99°N, 43.9995°W: 1 medusa; 7.9946°N, 41.9995°W: 6 medusae; 7.99916°N, 41.00016°W: 1 medusa; 7.9993°N, 39.0035°W: 12 medusae; 7.9995°N, 40.007°W: 6 medusae; 8.00083°N, 38.00316°W: 8 medusae.

**Description**. Umbrella up to 3 mm wide and 2 mm high. With small apical projection. Short manubrium without gastric peduncle. Eight radial canals. Globular gonads on radial canals close to circular canal. Eight perradial tentacles. Velum broad.

**Remarks**. Two valid species are currently recognized in the genus (Schuchert 2021). Present specimens completely fit in the diagnosis of *S. eurygaster* which is distinguished from *Sminthea apicigastrica* Xu, Huang & Du, 2009 mainly by the absence of the pair of gelatinous papillae flanked on the basis of each tentacle (Du et al. 2009).

**Distribution**. Distributed in the Pacific, Indian and Atlantic Ocean (Kitamura et al. 1997), the species was previously recorded in Southeast and South Brazilian waters at latitudes higher than 20.5°S and Carribbean Sea (Segura-Puertas et al. 2003; Oliveira et al. 2016). This is the first report in the area.

**Class Scyphozoa**

**Order Coronatae**

**Family Nausithoidae**

***Nausithoe aurea* Da Silveira & Morandini, 1997** (Fig. 4n)

**Material examined**. 5.9126°N, 49.7035°W: 1 medusa; 7.9993°N, 39.0035°W: 1 medusa.

**Description**. Umbrella up to 4 mm wide. Exumbrella flat and smooth. 16 truncated lappets. Alternate clefts between lappets having rhopalium or tentacle, all with similar depth. Eight conspicuous rhopalium and eight tentacles. Stomach 4-lobed with cross-shaped mouth, typically three gastric filaments in each quadrant, one larger flanked by two smaller laterals. Gonads spherical.

**Remarks**. *N. aurea* differs from *Nausithoe punctata* Kölliker, 1853 by the absence of warted surface on exumbrella and the coronal groove less crenated; and from *Nausithoe rubra* Vanhöffen, 1902 by the clefts of rhopalium and tentacles all in the same size and also by the coronal groove, which is circular and prominent in *N. rubra* (Mianzan and Cornelius 1999).

**Distribution**. Previously known from the eastern Atlantic at Cabo Verde Archipelago and Canary Islands (Herrera et al. 2017), and in Southeast and South Brazilian waters at latitudes higher than 21°S (Oliveira et al. 2016). This is the first report in the area.

## Discussion

This is the most comprehensive faunistic inventory of pelagic cnidarians performed in the Northern Brazilian coast and Western Equatorial Atlantic Ocean under the influence of the Amazon River Plume, covering a large spatial scale with heterogeneous habitats, what resulted in a total of 93 taxa, 22 of them represent new records for the area, 1 new records for Brazil, 1 for the Western Atlantic and at least two were new species (Tosetto et al. 2018, 2019, 2020, in press). Therefore, this survey contributes to the sparsely knowledge of pelagic cnidarians distribution along the Brazilian coast and its connectivity with North Atlantic and Caribbean Sea environments, and provides a useful background for future assessments.

Due to several reasons such as differences in sampling effort, depth sampled, and gears used is difficult to compare the number of taxa found in different studies. Yet, the 93 taxa of pelagic cnidarians found in the area is higher than most surveys with similar spatial scale (Thibault-Botha et al. 2004; Hosia et al. 2008; Chen and Liu 2010; Morita et al. 2017) which recorded between 64 and 85 taxa, and similar to the observed in the East China Sea, near the mouth of the Yangtze River (Xu et al. 2008). Our study area has a complex and seasonal oceanographic dynamics (Nittrouer and DeMaster 1996; Molleri et al. 2010) and therefore more sampling dates (as performed in most of these abovementioned studies) would increase the number of species. Furthermore our samples included only epipelagic layers, and therefore the pelagic cnidarian biodiversity in the Western Equatorial Atlantic under influence of the Amazon River Plume is likely to be higher than found here. Indeed, the species accumulation curves and diversity estimators did not reach an asymptote and clearly suggested the occurrence of a considerably higher number of cnidarian pelagic taxa (Fig. 2). The inability to distinguish species of some genera such as *Obelia*, *Clytia* and *Cytaeis* based on morphology of the medusa stage (Cornelius 1990; Bouillon 1999; Lindner et al. 2011), the difficulty in properly identifying larval and young specimens in many groups, and the fragility of gelatinous zooplankton organisms which get easily damaged in the sampling and fixation resulting in many unidentifiable specimens (Nogueira Júnior 2012; Nagata et al. 2014; Nogueira Júnior et al. 2018) may also have further contributed to diminish the number of species found.

The high biodiversity in the area is a consequence of several factors. Samples were obtained from estuarine, coastal, neritic (with a large reef system) and epipelagic oceanic waters, with a wide salinity range (18.1 to 37.1) caused by the Amazon River Plume and other oceanographic mesoscale processes such as eddies and opposite currents (Johns et al. 1990; Nittrouer and DeMaster 1996; Molleri et al. 2010; Moura et al. 2016). This heterogeneity of habitats was certainly the main accountable for the diversity of species in the area. Sampling in the neustonic layer of the water column also contributed with additional floating species which usually would not occur in zooplankton samples such as *P. porpita*, *V. velella* and *P. physalis*. Additionally, the high sampling effort, each station being sampled with different meshes to reduce effect of mesh selectivity (Tosetto et al. 2019) and samples being analyzed in totality contributed for the catch and observation of rare species.

The geographical location of the area, between Caribbean Sea and tropical Brazilian coast as well as North and South Atlantic, holds up species from both biogeographical provinces, enhancing the local biodiversity. Example is the new record of *Forskalia tholoides* in South American waters, a species with distribution until now restricted to the North Atlantic. Based on Ocean Biogeographic Information System data, other species we observed in the area (some for the first time) are widely distributed in the North Atlantic, Caribbean Sea and Gulf of Mexico, but rare in the Brazilian coast (considering official records) are *Aequorea forskalea*, *Aequorea macrodactyla*, *Amphicaryon peltifera*, *Athorybia rosacea*, *Eirene lactea*, *Eutonina scintillans*, *Laodicea undulata*, *Persa incolorata*, *Sphaeronectes koellikeri*, *Dimophyes arctica* (Chun, 1897) and *Lychnagalma utricularia* (Claus, 1879). Otherwise, the Equatorial Atlantic seems the northern limit of *Cunina frugifera* Kramp, 1948 and *Cirrholovenia polynema* Kramp, 1959 distribution in the Atlantic Ocean (OBIS 2021).

The diversity of siphonophores and narcomedusae were quite higher in the oceanic habitat, with the distribution of many species restrict to this environment, an expected condition, since species from the groups are holoplanktonic and do not require shallow waters for their life cycle (Mapstone 2014; Tosetto et al. 2018). Since Anthoathecata and Leptothecata are typically meroplanktonic, with a benthic polypoid stage, it would be expected a higher diversity over the continental shelf (Bouillon 1999; Mapstone 2014), instead, both groups were representative in the oceanic habitat, particularly Anthoathecata which presented three times more species there. The presence of meroplanktonc medusae in open oceanic waters may be a consequence of the complex circulation and strong currents in the area (Johns et al. 1990; Molleri et al. 2010), which could disperse individuals released over the continental shelf far away towards open ocean and also the presence of seamounts from the North Brazilian ridge (Hayes and Ewing 1970), which could supply the dependence on shallow substrates for hydroids.

The continental shelf influenced by the Amazon River Plume has received attention in recent years due to a complex carbonate system resulting in hard-bottom reefs (Moura et al. 2016). Representative inhabitants of this system are still poorly known, however, much of the rich biodiversity found in this study was present in the area (Table 1) and some species until now are known exclusively there, such as *Helgicirrha angelicae*, which could be an endemic representative of the system. Besides the typical anthropogenic impacts estuarine and coastal systems are exposed, such as urban development, untreated sewage deposal and overfishing (Paerl 1997), the environmental integrity of the area is also threatened by oil exploitation in the North Brazilian Continental Shelf (Silva Junior and Magrini 2014). Oil exploitation is responsible for many direct and indirect impacts to the marine ecosystems (Silva Junior and Magrini 2014) and the large scale exploration in close proximity to the bottom reefs in the area may cause potential loses in the rich biodiversity of pelagic cnidarians observed in this survey and other still poorly known organisms inhabiting this unique ecosystem. Therefore, it should be considered in further studies on marine spatial planning in the area.

In conclusion, we observed a highly diverse pelagic cnidarian community inhabiting the Northern Brazilian coast and Western Equatorial Atlantic Ocean under the influence of the Amazon River Plume and presume this biodiversity is higher as indicated by the rarefaction curves. Sampling in different seasons, with different gears, and including deeper waters certainly will further increase the number of pelagic cnidarian species in the area. We extended the known geographic distribution of many species. We also concluded that the open ocean in the area presented a higher diversity than the continental shelf, not only for holoplanktonic but also in the meroplanktonic taxa such as Anthoathecata, what can be related to complex circulation and topography present in the area.

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# 5 ARTIGO 2 - EFFECTS OF MESOSCALE OCEANOGRAPHIC PROCESSES ON THE SPATIAL DISTRIBUTION OF PLANKTONIC CNIDARIANS IN THE WESTERN EQUATORIAL ATLANTIC OCEAN UNDER INFLUENCE OF THE AMAZON RIVER PLUME

## Abstract

An oceanographic cruise was performed at October, 2012, sampling a large area (between 8°N, 51°W and 3.5°S, 37°W) off the north Brazilian coast to follow the surface freshwater plume of the Amazon River over neritic and oceanic provinces in the Western Equatorial Atlantic Ocean and its and other mesoscale influences on the assemblage of planktonic cnidarians. The area presente a complex and dynamic system, with strong currents and eddies dispersing the Amazon River Plume over a large spatial range. Contrasting differences in the planktonic cnidarian communities were observed between neritic and oceanic provinces and the plume was the main mesoscale physical process shaping the structure in both habitats as evidenced by the Cluster, SIMPER and RDA analysis. Over the continental shelf and outside the influence of the plume, the hydromedusae Liriope tetraphylla was dominant and occurred almost alone. Neritic habitat under the influence of the plume presented high species diversity and large abundances of Persa incolorata, Enneagonun hyalinun, Muggiaea kochii and Diphyes dispar. Divergences in the oceanic province where less pronounced but still expressive. Chelophyes appendiculata, Bassia bassensis, Eudoxoides spiralis and Abylopsis tetragona were more abundant outside the influence of the plume while Diphies bojani was clearly more abundant under its influence.

**Keywords:** Medusae. Siphonophores. Jellyfish. Gelatinous zooplankton. Amazonian Coast.

## Introduction

The Amazon River is one of the largest rivers of the world. It discharges up to 2.4 × $10^5$ $m^3s^{-1}$ of freshwater, nutrients and sediments into the Western Equatorial Atlantic Ocean (~20% of global freshwater run-off;(Lentz, 1995; Dagg *et al.*, 2004), creating a surface plume of low-salinity, high nutrients, and suspended and dissolved materials that can be traced thousands of kilometers in the North Atlantic and Caribbean (Signorini *et al.*, 1999; Hellweger and Gordon, 2002; Jo *et al.*, 2005). Environmental factors including strong ocean currents, wind fields and high tidal variation in the North Brazilian Continental Shelf and adjacent oceanic waters affect dynamics and dispersion of the Amazon River plume (hereafter, ARP) resulting in a highly energetic system with large spatial and temporal variability (Geyer, 1995; Lentz, 1995; Lentz and Limeburner, 1995; Geyer *et al.*, 1996; Nittrouer and DeMaster, 1996; Molleri *et al.*, 2010). ARP is also a region with intense land-ocean interaction, characterized by strong currents transport (Varona *et al.*, 2019), with the development of mesoscale cyclonic and anticyclonic eddies (Fratantoni and Richardson, 2006; Castelão and Johns, 2011), changes in mixed layer depth (Silva *et al.*, 2005; Coles *et al.*, 2013) and high carbon sequestration (Ibánhez *et al.*, 2016; Araujo *et al.*, 2017).

These unique characteristics have a strong influence on the ecology of the north Brazilian continental shelf, equatorial Atlantic and Caribbean. The large discharge of nutrients enhances primary production and phytoplankton concentration and possibly the whole aquatic community by a bottom-up effect (Smith and Demaster, 1996). And the low salinity brackish environment may affect the spatial distribution of marine animals such as planktonic cnidarians, which usually are associated to specific environmental conditions and water masses (Pagès, 1992; Hosia *et al.*, 2008; Nogueira Júnior *et al.*, 2014).

Planktonic cnidarians often are set aside in zooplanktonic studies. However, their high feeding rates and significant role as predators in the trophic web, associated with large population blooms, which occur in many species life cycles, have the potential to control the pelagic community and collapse fisheries and other human activities (Pitt *et al.*, 2009; Purcell, 2012). Therefore, interest in pelagic cnidarians ecology and their responses to environmental conditions, mainly related to issues triggering blooms, increased recently (Purcell *et al.*, 2007; Purcell, 2012; Roux *et al.*, 2013).

Global diversity, distribution and abundance patterns of planktonic cnidarians are closely related to oceanographic dynamics and water masses, and to climate patterns (Graham *et al.*, 2001; García-Comas *et al.*, 2011; Brotz *et al.*, 2012). Currents, eddies, fronts, upwelling, cross-shelf characteristics and other physical processes can drive their distribution in mesoscale dimensions (Pagès and Gili, 1991a; Graham *et al.*, 2001; Nogueira Júnior *et al.*, 2014; Boero *et al.*, 2016; Guerrero *et al.*, 2016, 2018). Finally, responses to small-scale changes in the environment, such as prey availability and local temperature and salinity, may determine species occurrence and abundance (Gili *et al.*, 1988; Gibbons and Buecher, 2001; Luo *et al.*, 2014).

The influence of freshwater run-off in the structure of planktonic cnidarians community was previously observed mainly for small rivers in coastal areas (Zamponi, 1983; Santhakumari and Nair, 1999; Morales-Ramírez and Nowaczyk, 2006; Loman-Ramos *et al.*, 2007; Sanvicente-Añorve *et al.*, 2007; Andrade, 2012a, 2012b; Rodríguez-Sáenz *et al.*, 2012; Chaparro and Peralta, 2013; Gutiérrez-Aguirre *et al.*, 2015; Vansteenbrugge *et al.*, 2015) where species had distinct responses to the salinity gradient. Some works described the Jellyfish community in the large Yangtze River estuary and adjacent areas at the shelf of East China Sea (Chen and Liu, 2010; Gao *et al.*, 2015; Wang *et al.*, 2016) and in the Equatorial Atlantic off Amazon (Alvariño, 1968), however these authors did not evaluate in detail the effect of these major river plumes in oceanic areas. Thus, in this study we evaluated the structure of the planktonic cnidarian community from neritic and oceanic provinces in the Western

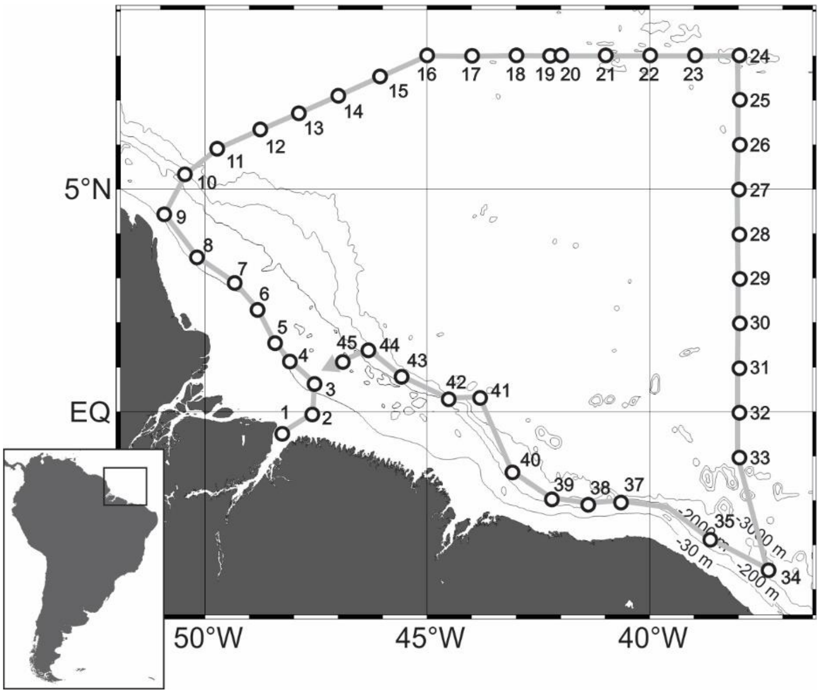
Equatorial Atlantic and its relation with physical environment, particularly considering the ARP and the potential high diversity of this understudied tropical and highly productive ecosystem. The study was based on the hypothesis that the plantonic cnidarian community is structured according to processes induced by the spread of Amazonian freshwaters into the shelf and open ocean environments.

## Materials and Methods

### *Study area*

The study area was along the north Brazilian continental shelf between the Amazon and Oyapok river mouths and equatorial Atlantic oceanic waters between 8°N, 51°W and 3.5°S, 37°W (Fig.1). The continental shelf in the area reaches up to 300 km wide and the shelf break occurs around 120 m depth (Coutinho, 1995; Nittrouer and DeMaster, 1996). The large freshwater discharge of the Amazon River in the region creates an extensive surface plume mainly affected by the discharge volume, the North Brazilian Current (NBC) and wind fields (Geyer, 1995; Lentz, 1995; Lentz and Limeburner, 1995; Geyer *et al.*, 1996; Nittrouer and DeMaster, 1996; Molleri *et al.*, 2010). Three general patterns occurs throughout the year. Between January and April, the ARP flow continuously northwest along the Brazilian coast carried mainly by NE winds. From April to July the ARP reaches the Caribbean region due to the higher discharge, NBC transport and SE winds. From August to December, the retroflection of the NBC, around 5°N and 10°N, disperses the ARP to the east feeding the North Equatorial Counter Current (NECC; Molleri *et al.*, 2010; Coles *et al.*, 2013). During this period, the plume that can exceed $10^6$ km$^2$, reaching longitudes as far as 25°W (Bruto *et al.*, 2017).

**Figure 1.** Geographic location of the study area in the North Brazilian continental shelf and adjacent Western Equatorial Atlantic Ocean, showing the sampled stations.



*Sampling*

Data and samples were obtained during the oceanographic cruise *Camadas Finas* III, aboard the research vessel NHo. Cruzeiro do Sul - H38 (DHN/Brazilian Navy). It was performed during October 9-31, 2012, corresponding to the period when most of the ARP is retroflexed and transported eastward by the NECC (Molleri *et al.*, 2010; Coles *et al.*, 2013). Zooplankton samples were obtained at 44 stations in oblique hauls, using a Bongo net with 120 and 300 µm mesh and 0.3 and 0.6 m mouth opening respectively. Stations were sampled from near bottom to surface on the continental shelf, and from 200 m to the surface in the open ocean. These nets were towed at approximately 2 knots. Nets were fitted with a flowmeter (Hydro-Bios) to estimate the volume filtered during each trawl. Samples were fixed with 4% formaldehyde buffered with sodium tetraborate (0.5 $gL^{-1}$). Current speed and directions were recorded along all the track of the ship by a Teledyne RD Ocean Surveyor ADCP. Data from the first 100 m of the water column were integrated each 30 kms along the track. Salinity, temperature (°C), density ($\sigma_t$), dissolved oxygen ($mgL^{-1}$) and fluorescence vertical profiles were recorded at stations zooplankton was sampled with a Seabird SBE 25 Sealogger CTD profiler (Araujo *et al.*, 2017).

In laboratory, whole zooplankton samples were analyzed under stereomicroscope and specimens were identified (mainly following Bouillon, 1999; Pugh, 1999) and counted. Abundances were standardized as number of individuals per 100 $m^{-3}$ for medusae and number of colonies per 100 $m^{-3}$ for siphonophores. For calycophorans, the number of anterior nectophores was used for estimating the polygastric stage abundance, and eudoxid bracts for the eudoxid stage abundance (e.g. Hosia and Båmstedt, 2007; Hosia *et al.*, 2008). For physonects and the calycophora *Hippopodius* *hippopus*, number of colonies were roughly estimated by dividing the number of nectophores by 10 (Pugh, 1984). Wet weight from whole 120 and 300 µm mesh samples measured by gravimetry after removing the water excess with blotted paper (Omori and Ikeda, 1984) were used as an indirect estimator zooplankton biomass (mostly copepods, cladocerans and other crustaceans).

*Data analysis*

The ARP was delimited by the isohaline of 35 and density < 22. Tropical Surface Water (TSW) and South Atlantic Central Water (SACW) masses were delimited by the isobar of 24.5 (Silva *et al.*, 2005, 2009; Molleri *et al.*, 2010). Cyclonic and anticyclonic eddies were respectively visually identified by negative and positive sea levels anomalies at dailly L4 satellite data, measured by multi-satellite altimetry observations over Global Ocean, produced by SSALTO/DUACS and distributed by E.U. Copernicus Marine Service Information. Dominant current in each station was defined by the overall direction observed in the ADCP data and classified as North Brazilian Current (NBC), retroflection area (RETRO) and North Equatorial Counter Current (NECC).

The abundance, diversity and structure of the planktonic cnidarian community was statistically similar in both meshes used (Tosetto *et al.*, 2019), and thus we considered both samples from each station as replicates. Spatial patterns in planktonic cnidarian community abundance were identified by hierarchical cluster analysis (Bray-Curtis similarity matrix; data transformed by log[x+1]). A Similarity Percentage (SIMPER) analysis was performed in order to identify key species and their contribution to similarity within the groups defined in the cluster.

To identify associations between representative planktonic cnidarian taxa (species occurring in more than 21 stations and species with high abundance in few stations) and the environment, a constrained ordination analysis was performed. Detrended Canonical Correspondence Analysis (DCCA) revealed a small length of variable gradients (< 3), indicating that a linear method was appropriate to use on this occasion, and thus Redundancy Analysis (RDA) was selected (Lepš and Šmilauer, 2003). Species data were transformed by log (x+1). Mesoscales physical processes were included as dummy categorical explanatory variables (neritic and oceanic habitats, presence of ARP, predominant current, precense of cyclonic and anticyclonic eddies). Total zooplankton biomass (mean of both meshes; considered as food availability), max value of fluorescence (as an indirect measure of biological productivity) and dissolved oxygen in the first 200 m of the water column, and surface temperature and salinity were included as continuous explanatory variables.

Station 1 and station 39 were excluded from all analysis due to the absence of replicates. Environmental and biological distribution maps were produced in Ocean Data View 5.0 and Qgis 3.2.1. Cluster, SIMPER and PERMANOVA analysis were performed in Primer v.6 + PERMANOVA. DCCA and RDA were performed in CANOCO 4.5.

## Results

### *Environmental background*

The south of the studied area (reaching station 29 at 3°N, 38°W) was dominated by the North Brazilian Current (NBC), flowing west and in direction to the coast. After station 9 (around 5°N), the NBC is retroflexed northwards, where faster current speeds occurred. From station 15 (7.5°N, 46°W) to station 28 (4°N, 38°W) the North Equatorial Counter Current (NECC), flowing east, predominated (Fig. 2a). One cyclonic eddy, causing surface divergence, occurred near the mouth of the Amazon River during the sampled period, stations 4, 5 and 6 were sampled under its influence. Stations 8, 13, 14, 17, 18 were sampled under the influence of three anticyclonic eddies and surface convergence (Fig. 2b). Although another cyclonic eddy occurred in the west side of the study area, it was already dissipated in the day those stations were sampled.

**Figure 2. (a)** Surface currents vectors and indicators of the predominant current in the area (NBC = North Brazilian Current; RETRO = North Brazilian Current retroflection; NECC=North Equatorial Counter Current). **(b)** Sea level anomalies and indicators of cyclonic and an anticyclonic eddies. **(c)** Sea surface salinity and estimated position of 35 isohaline delimitating the Amazon River plume (ARP) and tropical surface water (TSW). **(d)** Sea surface temperature **(e)** Surface density **(e)** Surface pH. All data from October 2012.

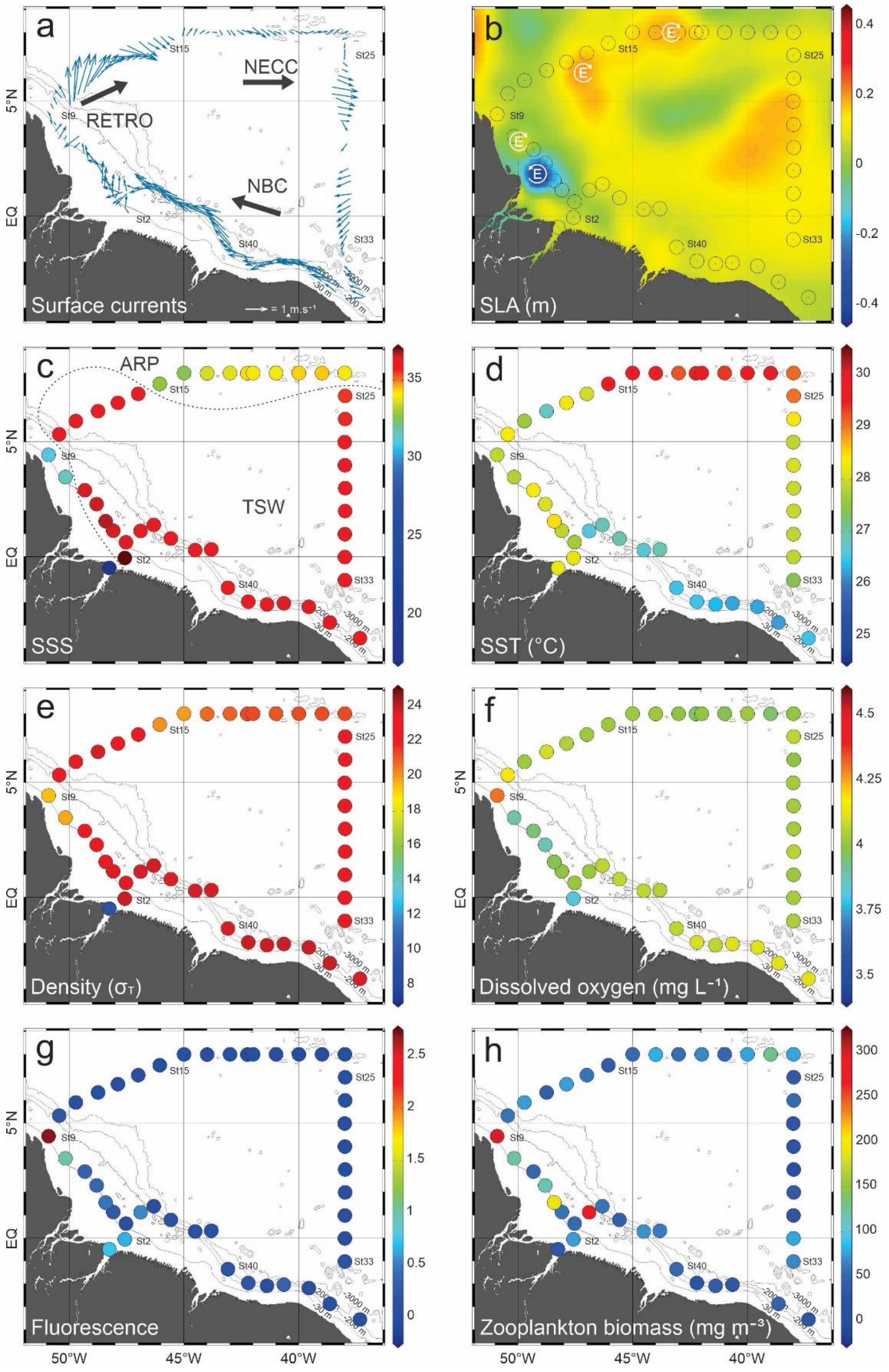


**Figure 3.** Vertical profiles and contours of **(a)** Salinity , traced line is the position of 35 isohaline delimitating the Amazon River plume **(b)** **T**emperature **(c)** **D**ensity **(d)** Dissolved oxygen **(e)** Fluorescence. Upper bars indicate the main mesoscale processes observed in the area. All data from October 2012.

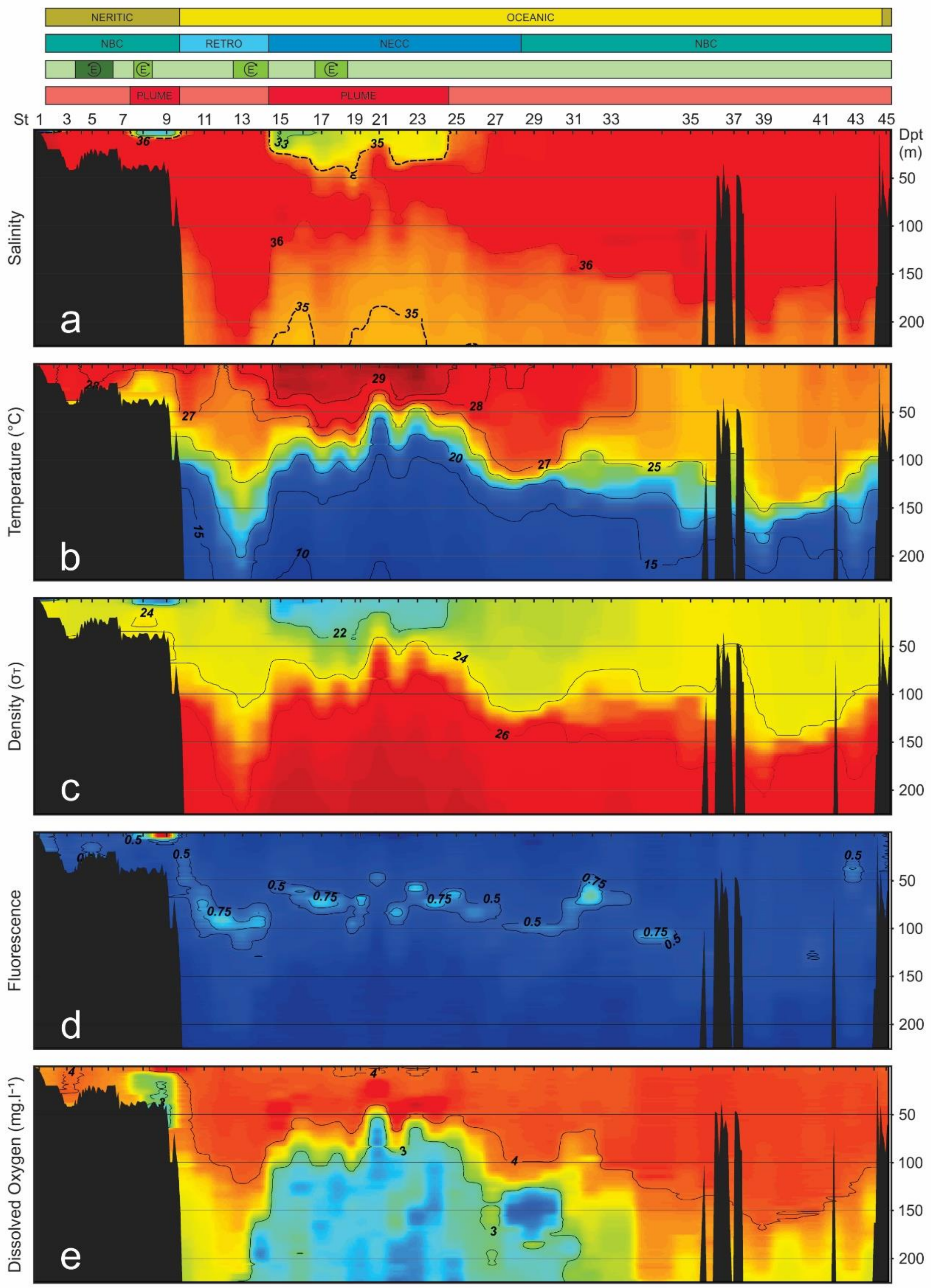
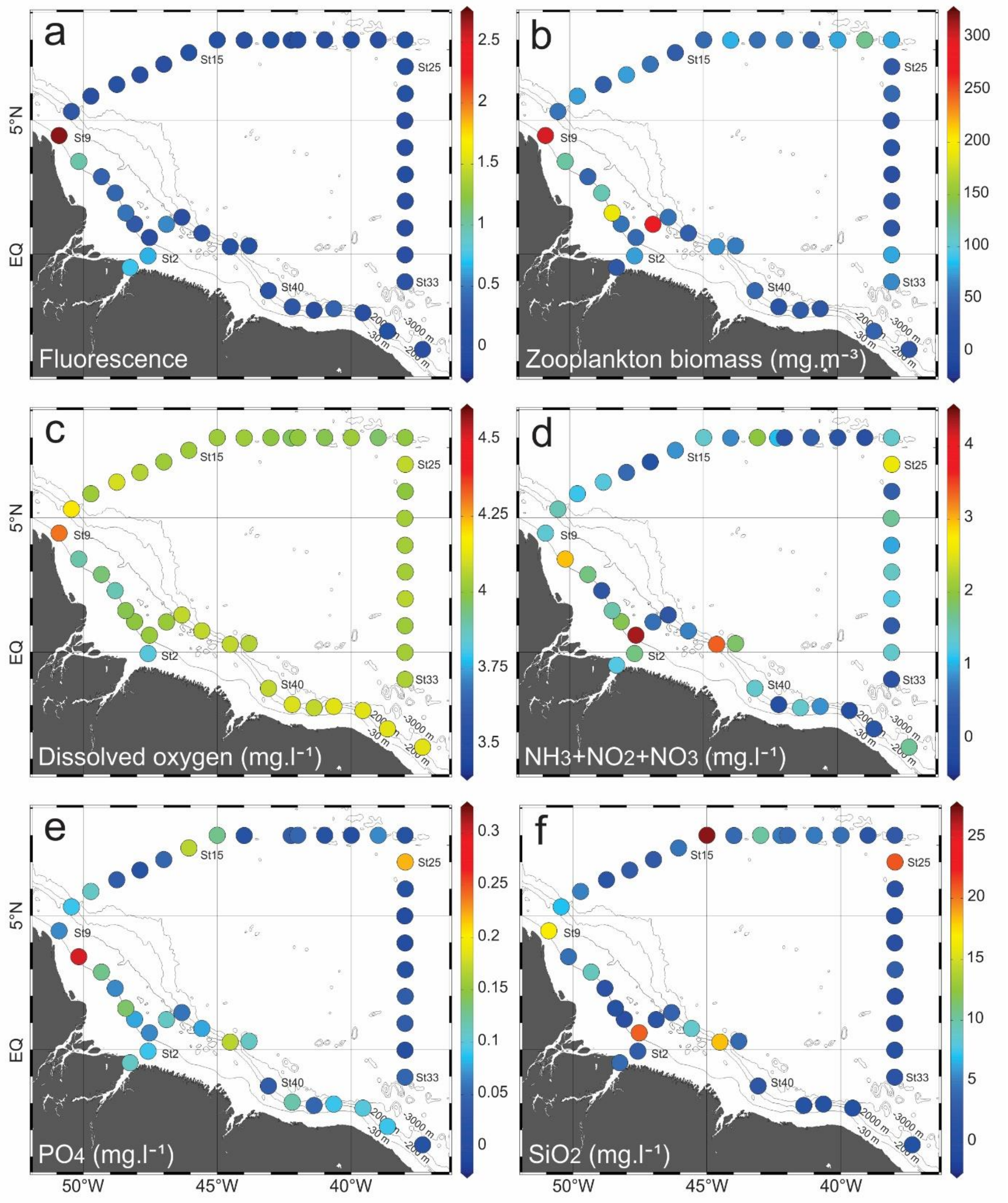


**Figure 4.** **(a)** Surface Fluorescence **(b)** Total zooplankton biomass found in the first 200 m of the water column (mean of 120 and 300 µm meshes). **(c)** Surface dissolved oxygen **(d)** Surface dissolved ammonia ($NH_3^+$), nitrite ($NO_2^-$) and nitrate ($NO_3^-$), **(e)** Surface dissolved phosphate ($PO_4^-$) **(e)** Surface reactive silicate ($SiO_2^-$). All data from October 2012.



Over the continental shelf, surface waters of stations 8 and 9 were influenced by the Amazon River Plume (ARP) resulting in salinities below 35 in the first 8 m of the water column (Fig. 2c; 3a). In the oceanic province, stations 15 to 24 were influenced by the ARP, where 35 isohaline ranged from 14 m depth at station 21 to 59 m depth at station 19. Outside the ARP, surface salinity was around 36 in all stations (Fig. 2c).

Coastal surface waters were slightly warmer than adjacent oceanic stations, reaching 28.5 °C at station 5. In the oceanic waters, surface temperature oscillated mainly with latitude and higher temperatures occurred in the northern stations reaching 29.8 °C at station 22 (Fig. 2d). Colder waters (< 18 °C) occurred commonlly around 120 m depth, however intrusions in the upper layers were observed at stations 21 to 24 were it reached up to 60 m depth. On the other hand, warm surface water transposed 150 m depth at stations 12 to 14, and 35 to 44 over the continental slope (Fig. 3b). These upwelling and downwelling events reflect the complex circulation system in the area. Following the temperature and salinity gradients, three water masses were observed in the first 200 m of the water column in the area, ARP waters ($\sigma_T < 22$), Tropical Surface Waters (TSW) ($\sigma_T$ between 22 and 24.5) and South Atlantic Central Waters (SACW) ($\sigma_T > 24.5$; Fig. 2e; 3c).

Higher primary production, evidenced by the fluorescence, occurred in the surface layer of neritic stations influenced by the ARP, mainly in station 9, were it reached 2.7. An increment in the fluorescence was also observed at station 5, which was sampled under the influence of a cold core cyclonic eddy. In the oceanic stations, a deep fluorescence maximum layer was observed in the limit between TSW and SACW (Fig. 3d). Higher value of zooplankton biomass also occurred at station 9, no clear pattern was observed in other stations (Fig. 4b). Dissolved oxygen did not present significant oscillations in the surface layer. In the oceanic stations under the influence of the ARP an oxygen minimum layer (< 3) was observed between 50 and 200 m depth (Fig. 3e; 4c).

### *Species composition*

A total of 91 taxa of planktonic cnidarians were observed in the area, corresponding to two scyphomedusae, 41 hydromedusae and 48 siphonophores. Furthermore, many unidentified cerinula, ephyrae and athorybia larval forms were found. *Liriope tetraphylla* was the most frequent medusa, being present all over the study area in 88.5% of the samples, followed by *Aglaura hemistoma* (78.2%) and *Sminthea eurygaster* (41.4%). Among Siphonophores, the most frequent were *Diphyes bojani* (88.5%), *Bassia bassensis* (80.5%), *Chelophyes appendiculata* (78.2%), *Abylopsis tetrago*na (75.9%), *Nanomia bijuga* (74.7%) and *Eudoxoides mitra* (75.6%; Table 1).

**Table 1.** Basic statistics of planktonic cnidarian species from neritic and oceanic provinces in the Western Equatorial Atlantic Ocean off north Brazil. Mean abundance (ind. 100 m$^{-3}$) per station and standard deviation, range of abundance and frequency of occurrence (f; considering both provinces).

| Species | Neritic | | Oceanic | | f |
|---|---|---|---|---|---|
| | Mean ± SD | Range of non-zero abundances | Mean ± SD | Range of non-zero abundances | |
| **Siphonophorae** | | | | | |
| *Diphyes bojani* (Eschscholtz, 1825) | 19.72 ± 61.4 | 0.63 - 263.26 | 50.58 ± 81.37 | 2.78 - 471.4 | 88.51 |
| *Bassia bassensis* (Quoy & Gaimard, 1833) | 3.11 ± 8.33 | 1.56 - 30.53 | 19.7 ± 14.35 | 1.78 - 73.09 | 80.46 |
| *Chelophyes appendiculata* (Eschscholtz, 1829) | 8.59 ± 33.4 | 22.9 - 148.8 | 37.73 ± 35.65 | 3.01 - 161.88 | 78.16 |
| *Abylopsis tetragona* (Otto, 1823) | 2.13 ± 5.98 | 0.78 - 22.89 | 8.63 ± 8.33 | 0.89 - 40.47 | 75.86 |
| *Nanomia bijuga* (Delle Chiaje, 1844) | 3.28 ± 6.85 | 0.92 - 28.74 | 2.46 ± 2.94 | 0.1 - 13.51 | 74.71 |
| *Eudoxoides mitra* (Huxley, 1859) | 0.97 ± 2.94 | 0.78 - 11.45 | 34.13 ± 40.13 | 0.3 - 214.61 | 73.56 |
| *Abylopsis eschscholtzii* (Huxley, 1859) | 1.86 ± 7.67 | 2.93 - 34.34 | 6.96 ± 12.32 | 0.3 - 92.75 | 68.97 |
| *Sulculeolaria chuni* (Lens & van Riemsdijk, 1908) | 7.44 ± 28.35 | 22.9 - 125.91 | 7.65 ± 8.35 | 0.19 - 33.39 | 68.97 |
| *Eudoxoides spiralis* (Bigelow, 1911) | 1.72 ± 7.68 | 34.34 - 34.34 | 13.32 ± 21.35 | 0.7 - 123.1 | 60.92 |
| *Diphyes dispar* Chamisso & Eysenhardt, 1821 | 72.07 ± 187.61 | 0.7 - 768.71 | 1.71 ± 2.91 | 0.29 - 15.18 | 57.47 |
| *Agalma okenii* Eschscholtz, 1825 | 0.38 ± 1.71 | 7.63 - 7.63 | 1.14 ± 1.38 | 0.1 - 6.81 | 54.02 |
| *Sulculeolaria turgida* (Gegenbaur, 1854) | - | - | 0.92 ± 1.46 | 0.1 - 6.98 | 37.93 |
| *Ceratocymba leuckartii* (Huxley, 1859) | - | - | 1.03 ± 1.5 | 0.15 - 5.95 | 36.78 |
| *Lensia campanella* (Moser, 1917) | 0.44 ± 1.63 | 1.56 - 7.18 | 0.99 ± 1.74 | 0.3 - 7.56 | 34.48 |
| *Agalma elegans* (Sars, 1846) | - | - | 0.65 ± 1.21 | 0.3 - 6.75 | 29.89 |
| *Sulculeolaria biloba* (Sars, 1846) | - | - | 0.82 ± 1.45 | 0.38 - 5.41 | 29.89 |
| *Cordagalma ordinatum* (Haeckel, 1888) | - | - | 0.49 ± 0.87 | 0.3 - 3.89 | 27.59 |
| *Lensia meteori* (Leloup, 1934) | - | - | 0.97 ± 2.34 | 0.3 - 14.94 | 25.29 |
| *Lychnagalma utricularia* (Claus, 1879) | 0.69 ± 2.37 | 3.59 - 10.17 | 0.55 ± 1.22 | 0.46 - 7.38 | 25.29 |
| *Hippopodius hippopus* (Forsskål, 1776) | - | - | 0.32 ± 0.73 | 0.1 - 2.78 | 18.39 |
| *Forskalia tholoides* Haeckel, 1888 | - | - | 0.25 ± 0.63 | 0.3 - 2.94 | 16.09 |

**Table 1.** Continuation

| Species | Neritic | | Oceanic | | f |
|---|---|---|---|---|---|
| | Mean ± SD | Range of non-zero abundances | Mean ± SD | Range of non-zero abundances | |
| *Amphicaryon* sp. | - | - | 0.35 ± 0.85 | 0.44 - 3.55 | 14.94 |
| *Halistemma rubrum* (Vogt, 1852) | - | - | 0.19 ± 0.47 | 0.39 - 1.91 | 14.94 |
| *Lensia subtilis* (Chun, 1886) | - | - | 0.25 ± 0.74 | 0.1 - 3.4 | 11.49 |
| *Lensia* spp. | - | - | 0.2 ± 0.76 | 0.59 - 4.64 | 8.05 |
| *Muggiaea kochii* (Will, 1844) | 95.69 ± 282.86 | 70.04 - 1185.39 | 0.24 ± 1.29 | 1.91 - 9.14 | 8.05 |
| *Athorybia rosacea* (Forsskål, 1775) | 0.08 ± 0.36 | 1.59 - 1.59 | 0.15 ± 0.69 | 0.44 - 4.73 | 6.9 |
| *Rosacea plicata* Bigelow, 1911 | - | - | 0.15 ± 0.52 | 0.6 - 2.46 | 6.9 |
| *Sulculeolaria monoica* (Chun, 1888) | - | - | 0.14 ± 0.52 | 0.48 - 2.42 | 6.9 |
| *Enneagonum hyalinum* Quoy & Gaimard, 1827 | 207.06 ± 589.06 | 152.82 - 2227.1 | 0.02 ± 0.18 | 1.45 - 1.45 | 5.75 |
| *Chuniphyes* sp. | - | - | 0.08 ± 0.53 | 0.1 - 4.25 | 4.6 |
| *Lensia cossack* Totton, 1941 | - | - | 0.03 ± 0.12 | 0.44 - 0.56 | 4.6 |
| *Lensia fowleri* (Bigelow, 1911) | - | - | 0.06 ± 0.28 | 0.3 - 1.61 | 4.6 |
| *Abyla* sp. | - | - | 0.03 ± 0.18 | 0.1 - 1.13 | 3.45 |
| *Abyla trigona* Quoy & Gaimard, 1827 | - | - | 0.05 ± 0.26 | 0.85 - 1.64 | 3.45 |
| *Forskalia edwardsii* Kölliker, 1853 | - | - | 0.06 ± 0.29 | 1.18 - 1.55 | 3.45 |
| *Lensia conoidea* (Keferstein & Ehlers, 1860) | - | - | 0.04 ± 0.22 | 0.47 - 1.55 | 3.45 |
| *Lensia hardy* Totton, 1941 | - | - | 0.15 ± 0.86 | 0.67 - 6.55 | 3.45 |
| *Sphaeronectes koellikeri* Huxley, 1859 | - | - | 0.06 ± 0.32 | 0.94 - 1.94 | 3.45 |
| *Forskalia contorta* (Milne Edwards, 1841) | - | - | 0.04 ± 0.27 | 0.49 - 2.14 | 2.3 |
| *Lensia subtiloides* (Lens & van Riemsdijk, 1908) | - | - | 0.01 ± 0.05 | 0.3 - 0.3 | 2.3 |
| *Amphicaryon peltifera* (Haeckel, 1888) | - | - | 0.03 ± 0.28 | 2.33 - 2.33 | 1.15 |
| *Dimophyes arctica* (Chun, 1897) | - | - | 0.09 ± 0.76 | 6.18 - 6.18 | 1.15 |
| *Lensia hotspur* Totton, 1941 | - | - | 0.12 ± 1 | 8.19 - 8.19 | 1.15 |

**Table 1.** Continuation

| Species | Neritic | | Oceanic | | f |
|---|---|---|---|---|---|
| | Mean ± SD | Range of non-zero abundances | Mean ± SD | Range of non-zero abundances | |
| *Lensia leloupi* Totton, 1954 | - | - | 0.03 ± 0.24 | 1.94 - 1.94 | 1.15 |
| *Physophora hydrostatica* Forsskål, 1775 | - | - | 0.04 ± 0.3 | 2.42 - 2.42 | 1.15 |
| Rosacea sp. | - | - | 0.02 ± 0.14 | 1.18 - 1.18 | 1.15 |
| *Sulculeolaria quadrivalvis* de Blainville, 1830 | - | - | 0 ± 0.01 | 0.1 - 0.1 | 1.15 |
| **“Hydromedusae”** | | | | | |
| *Liriope tetraphylla* (Chamisso & Eysenhardt, 1821) | 322.1 ± 582.18 | 2.85 - 2199.57 | 9.24 ± 14.62 | 0.28 - 99.31 | 88.51 |
| *Aglaura hemistoma* Péron & Lesueur, 1810 | 10.31 ± 31.27 | 11.56 - 125.91 | 33.02 ± 37.63 | 0.15 - 192.66 | 78.16 |
| *Sminthea eurygaster* Gegenbaur, 1857 | - | - | 2.48 ± 3.98 | 0.19 - 16.71 | 41.38 |
| *Rhopalonema velatum* Gegenbaur, 1857 | 0.57 ± 2.56 | 11.45 - 11.45 | 1.07 ± 1.87 | 0.1 - 7.94 | 35.63 |
| *Solmundella bitentaculata* (Quoy & Gaimard, 1833) | 0.6 ± 1.73 | 1.56 - 7.18 | 1.15 ± 2 | 0.53 - 9.33 | 34.48 |
| *Cytaeis* sp.1 | 0.38 ± 1.71 | 7.63 - 7.63 | 0.54 ± 0.99 | 0.3 - 5.54 | 29.89 |
| *Annatiara affinis* (Hartlaub, 1914) | 0.38 ± 1.71 | 7.63 - 7.63 | 0.41 ± 1.52 | 0.56 - 10.63 | 12.64 |
| *Clytia* spp. | 0.51 ± 1.25 | 3.18 - 3.51 | 0.12 ± 0.4 | 0.46 - 1.91 | 11.49 |
| *Cunina octonaria* McCrady, 1859 | 5.59 ± 17.24 | 4.78 - 75.43 | 0.14 ± 0.69 | 0.46 - 4.51 | 9.2 |
| *Cirrholovenia tetranema* Kramp, 1959 | 2.18 ± 7.66 | 2.11 - 34.34 | 0.09 ± 0.46 | 1.03 - 3.01 | 8.05 |
| *Persa incolorata* McCrady, 1859 | 222.67 ± 646.69 | 3.63 - 2701.26 | 0.18 ± 1.47 | 12.04 - 12.04 | 6.9 |
| *Eucheilota maculata* Hartlaub, 1894 | 0.59 ± 2.36 | 1.25 - 10.54 | 0.07 ± 0.35 | 0.92 - 2.27 | 5.75 |
| *Cirrholovenia polynema* Kramp, 1959 | - | - | 0.05 ± 0.2 | 0.44 - 1.07 | 4.6 |
| Aequorea spp. | - | - | 0.05 ± 0.22 | 0.93 - 1.2 | 3.45 |
| *Cunina frugifera* Kramp, 1948 | - | - | 0.08 ± 0.39 | 1 - 2.7 | 3.45 |
| *Helgicirrha angelicae* Tosetto, Neumann-Leitão, Nogueira Junior, 2020 | 9.63 ± 39.26 | 4.78 - 176.01 | - | - | 3.45 |
| Anthomedusa sp.1 | - | - | 0.1 ± 0.6 | 1.71 - 4.67 | 2.3 |

**Table 1.** Continuation

| Species | Neritic | | Oceanic | | f |
|---|---|---|---|---|---|
| | Mean ± SD | Range of non-zero abundances | Mean ± SD | Range of non-zero abundances | |
| Anthomedusa sp.3 | - | - | 0.1 ± 0.66 | 1.88 - 5.12 | 2.3 |
| *Eucheilota* spp. | 0.03 ± 0.14 | 0.63 - 0.63 | 0.03 ± 0.24 | 1.94 - 1.94 | 2.3 |
| *Eutima marajoara* Tosetto, Neumann-Leitão, Nogueira Junior, 2020 | 13.45 ± 45.49 | 76.39 - 192.62 | - | - | 2.3 |
| Levenellidae sp. | - | - | 0.03 ± 0.21 | 0.46 - 1.7 | 2.3 |
| *Malagazzia carolinae* (Mayer, 1900) | 0.22 ± 0.81 | 0.78 - 3.59 | - | - | 2.3 |
| *Nubiella amazonica* (in press) | 2.9 ± 10.03 | 14.86 - 43.11 | - | - | 2.3 |
| *Obelia* sp. | 3.12 ± 13.81 | 0.63 - 61.78 | - | - | 2.3 |
| *Pegantha martagon* Haeckel, 1879 | - | - | 0.02 ± 0.09 | 0.44 - 0.6 | 2.3 |
| *Aequorea forskalea* Péron & Lesueur, 1810 | - | - | 0.03 ± 0.24 | 1.94 - 1.94 | 1.15 |
| *Amphinema* sp. nov. (in press) | 0.04 ± 0.17 | 0.78 - 0.78 | - | - | 1.15 |
| Anthomedusa sp.2 | - | - | 0.03 ± 0.23 | 1.91 - 1.91 | 1.15 |
| Anthomedusa sp.4 | - | - | 0.03 ± 0.28 | 2.25 - 2.25 | 1.15 |
| *Bougainvillia muscus* (Allman, 1863) | - | - | 0.01 ± 0.06 | 0.47 - 0.47 | 1.15 |
| Campanulariidae sp. | - | - | 0.04 ± 0.3 | 2.46 - 2.46 | 1.15 |
| Corynidae sp. | - | - | 0.01 ± 0.06 | 0.47 - 0.47 | 1.15 |
| *Cytaeis* sp.2 | - | - | 0.01 ± 0.1 | 0.86 - 0.86 | 1.15 |
| *Eirene lactea* (Mayer, 1900) | 0.18 ± 0.79 | 3.51 - 3.51 | - | - | 1.15 |
| Hydromedusae sp. | - | - | 0.01 ± 0.07 | 0.6 - 0.6 | 1.15 |
| *Laodicea undulata* (Forbes & Goodsir, 1853) | 1.14 ± 5.12 | 22.89 - 22.89 | - | - | 1.15 |
| *Mitrocomium cirratum* Haeckel, 1879 | 0.08 ± 0.36 | 1.59 - 1.59 | - | - | 1.15 |
| *Octophialucium bigelowi* Kramp, 1955 | 0.16 ± 0.71 | 3.18 - 3.18 | - | - | 1.15 |
| *Octophialucium haeckeli* (Vannucci & Soares Moreira, 1966) | 0.18 ± 0.79 | 3.51 - 3.51 | - | - | 1.15 |
| *Olindias* sp. | 0.08 ± 0.36 | 1.59 - 1.59 | - | - | 1.15 |

**Table 1.** Continuation

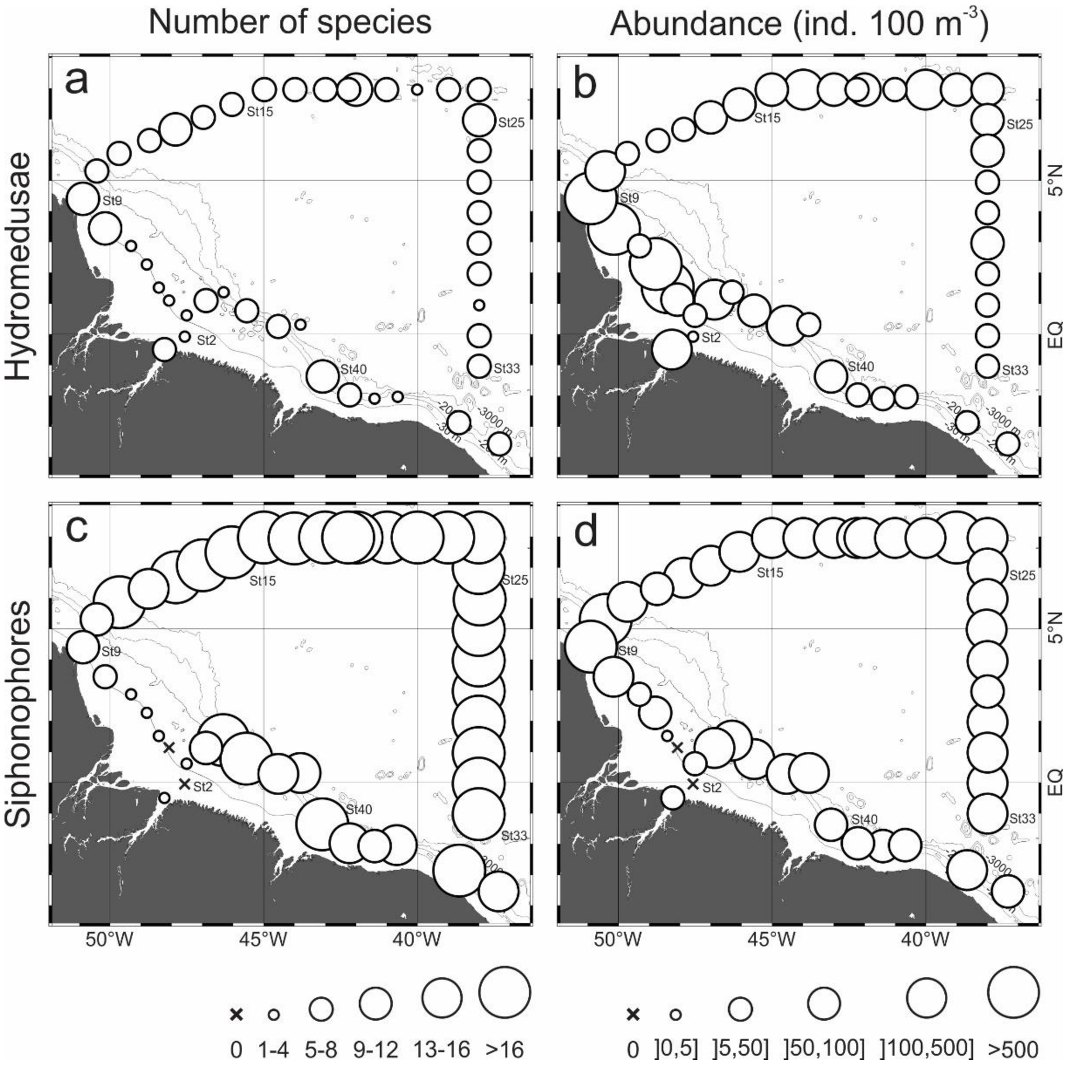
| Species | Neritic | | Oceanic | | f |
|---|---|---|---|---|---|
| | Mean ± SD | Range of non-zero abundances | Mean ± SD | Range of non-zero abundances | |
| *Pegantha triloba* Haeckel, 1879 | - | - | 0.04 ± 0.34 | 2.78 - 2.78 | 1.15 |
| **Scyphomedusae** | | | | | |
| *Nausithoe punctata* Kölliker, 1853 | 0.59 ± 2.3 | 1.49 - 10.28 | 0.33 ± 0.71 | 0.3 - 3.28 | 20.69 |
| *Nausithoe aurea* Da Silveira & Morandini, 1997 * | - | - | 0.03 ± 0.21 | 1.74 - 1.74 | 1.15 |
| **Other** | | | | | |
| Cerinula larvae | 8.94 ± 19.66 | 1.49 - 82.62 | 0.41 ± 0.9 | 0.19 - 4.63 | 29.89 |
| Ephirae larvae | 0.53 ± 1.5 | 1.43 - 6.1 | 0.07 ± 0.32 | 0.44 - 1.85 | 8.05 |
| Athorybia larvae | - | - | 0.08 ± 0.61 | 0.59 - 4.93 | 2.3 |

*Liriope tetraphylla* also dominated in abundance over the area, representing 46% of all medusae. Other representative medusae were *Persa incolorata* (28.8%) and *A. hemistoma* (15.6%). Among siphonophores, *Enneagonum hyalinum* was the most abundant (19.1%), followed by *D. bojani* (18.2%), *C. appendiculata* (12.5%), *Eudoxoides mitra* (10.8%) and *Muggiaea kochii* (10.6%).

*Spatial distribution patterns*

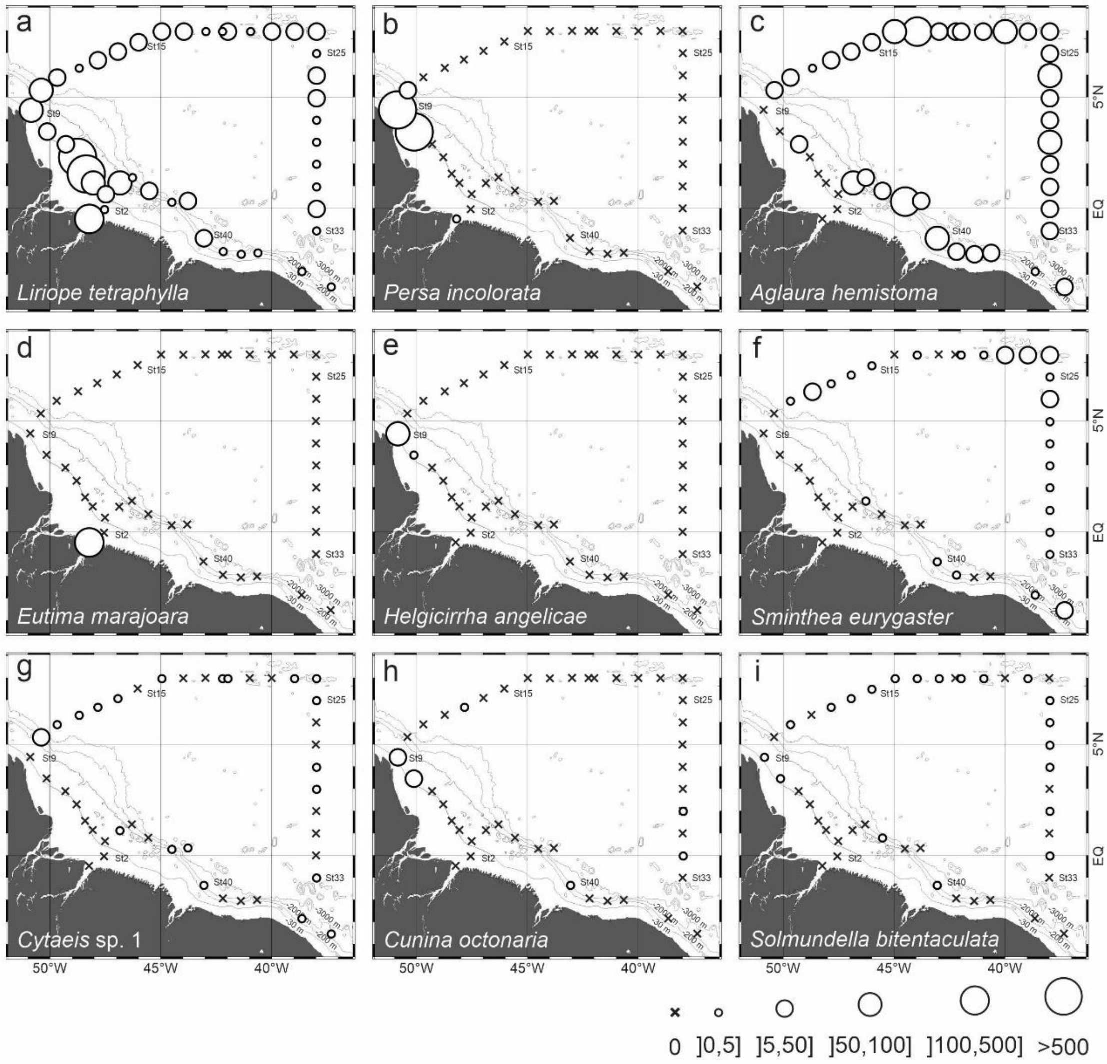
Total medusae abundance data presented highest values and high variability over the continental shelf, ranging from 1.4 to 1710 ind. 100 m$^{-3}$. In this province, while medusae diversity was higher in the stations influenced by the ARP, high abundances occurred in the stations both inside and outside of the ARP. In oceanic waters, highest medusa abundance occurred at stations located in the area influenced by the ARP and diversity was similar in these stations (Fig. 5).

**Figure 5.** Geographic distribution of number of species and total abundance of hydromedusae and siphonophores found in the first 200 m of the water column (mean of 120 and 300 µm meshes) at October 2012.



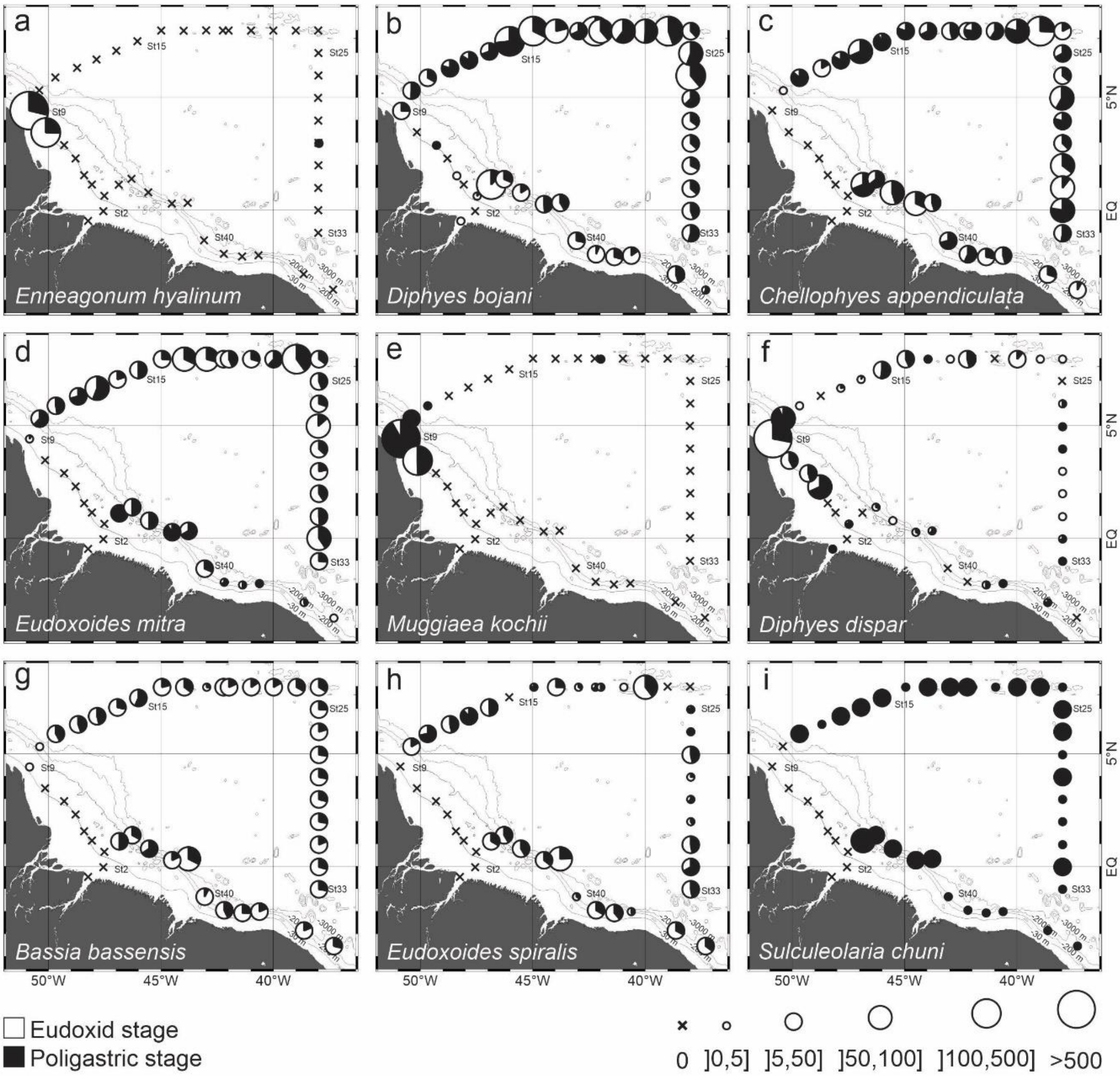
Although widespread all over the sampled site, *L. tetraphylla* dominated neritic stations outside the ARP. Its presence was also constant, although less abundant, in the retroflection area and in the NECC. Lower catches occurred in most oceanic stations under the influence of the NBC. *Persa incolorata*, *Helgicirrha angelicae* and *Cunina octonaria* occurred almost exclusively in neritic stations under influence of the ARP. *Eutima marajoara* occurred in high abundance exclusively at station 1, inside the river estuary. *A. hemistoma* was the dominant medusa through most of the oceanic habitat, *S. eurygaster* was also representative there, usually in lower densities, but nearly disappearing under NBC influence area. *Cytaies* sp. 1 and *Solmundella bitentaculata* occurred scattered in low abundances all over the area (Fig. 6).

**Figure 6.** Geographic distribution and abundance of the dominant hydromedusae found in the first 200 m of the water column (mean of 120 and 300 µm meshes) at October 2012.



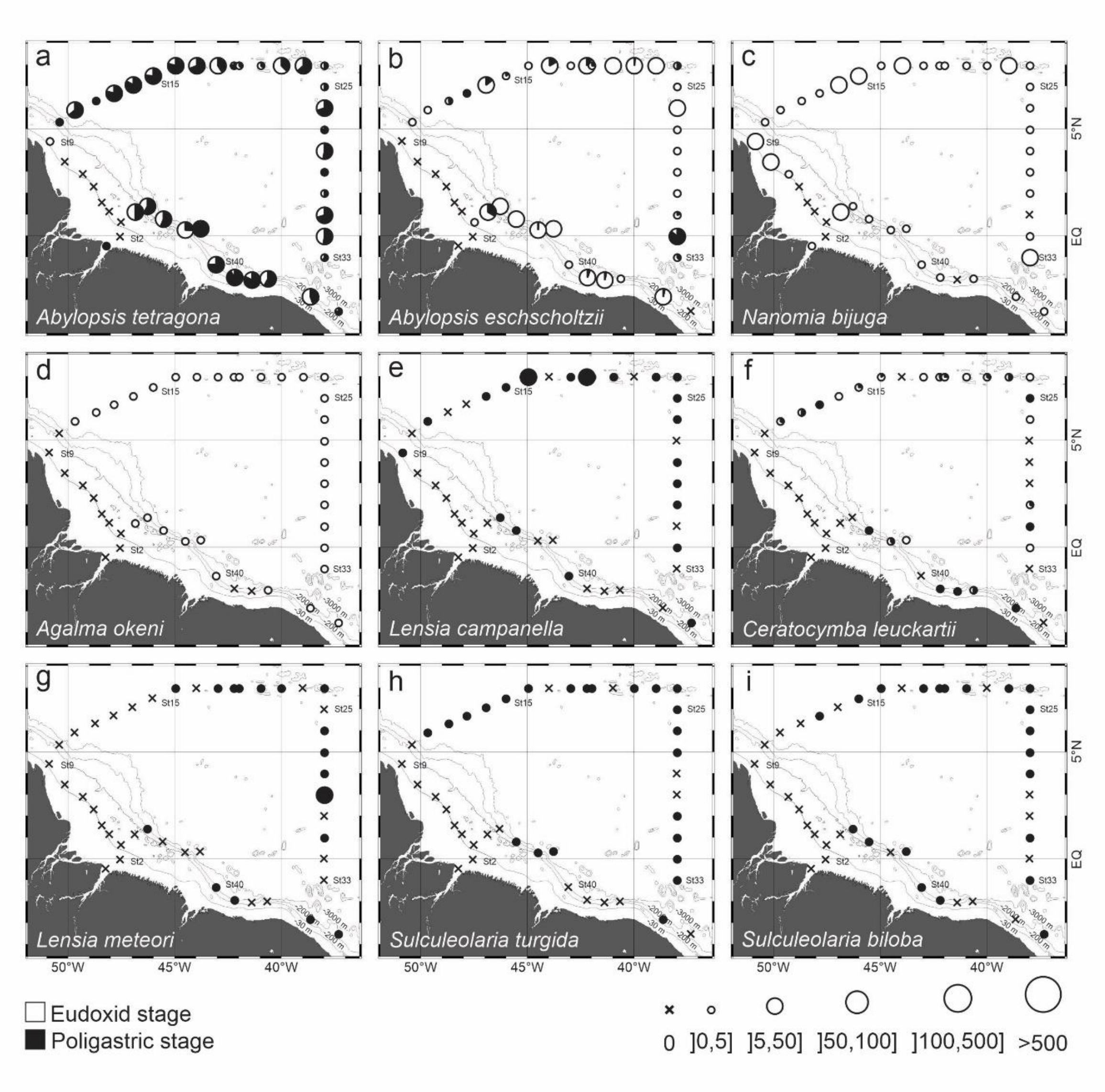
Siphonophores diversity and overall abundance were more constant and typically high in oceanic stations, where it averaged 9.8 species and 197.6 ind. 100 m$^{-3}$ respectivelly. Differently, over the continental shelf siphonophore diversity was considerably lower, typically <5 (mean 2.4), and they even were absent at stations 2 and 4. Abundances in neritic stations also tended to be lower, but very high abundance (3381.3 ind. 100 m$^{-3}$) occurred at station 9 (Fig. 5).

**Figure 7.** Geographic distribution and abundance of the dominant siphonophores found in the first 200 m of the water column (mean of 120 and 300 µm meshes) at October 2012.



*Enneagonum hyalinum* and *M. kochii* occurred in high abundance and almost exclusively in the neritic stations under the influence of the ARP. Although widespread and abundant all over the area, *D. bojani* abundance was markedly higher in the oceanic station under the influence of the ARP. Also widespread, but with lower densities, *Diphyes dispar and N. bijuga* abundance was clearly higher in stations under the influence of the ARP or near its limits both in the neritic and oceanic habitats. All other abundant siphonophores occurred exclusively at oceanic stations and the neritic station 45, located near the shelf break (Fig. 7; 8). Eudoxid and polygastric stages of all calycophoran species presented similar distribution patterns.

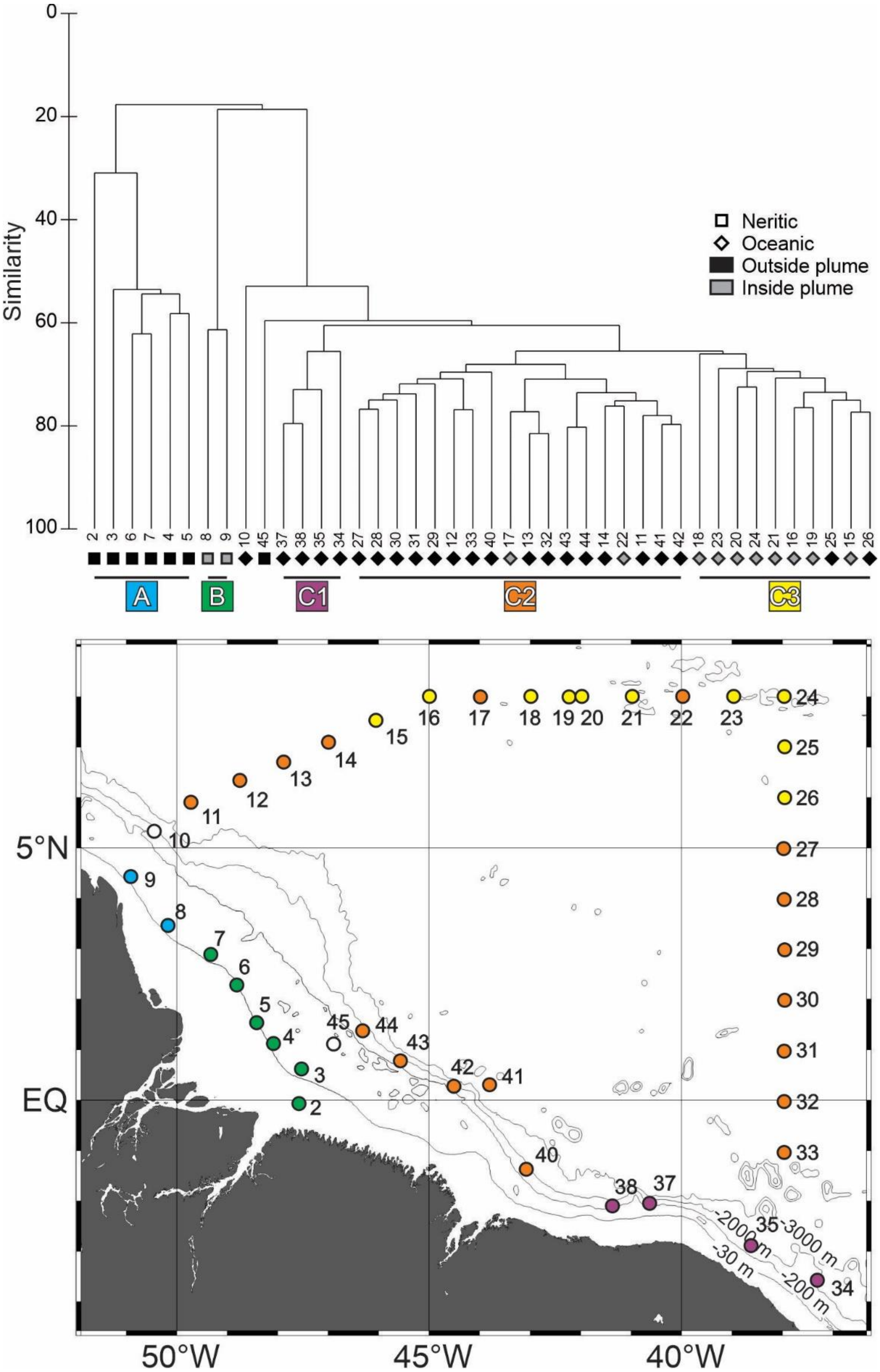
**Figure 8.** Geographic distribution and abundance of other representative siphonophores found in the first 200 m of the water column (mean of 120 and 300 µm meshes) at October 2012.



*Community structure*

Three groups with little resemblance to each other were identified based in the Cluster Analysis dendogram (Fig. 9). Group A was represented by neritic stations without influence of the ARP, except for station 45. Reflecting the high variability in planktonic cnidarian abundance at these stations, the group presented the lowest similarity in SIMPER analysis (39.7%). The group was highly represented by *L. tetraphylla* (Table 2). The two neritic stations under influence of the ARP were placed in Group B. With an average similarity of 69.5%, the group was mainly represented *P. incolorata*, *E. hyalinum*, *M. kochii* and *D. dispar* (Table 2).

**Figure 9.** Cluster analysis dendogram indicating five groups of stations with similar planktonic cnidarian communities in the Western Equatorial Atlantic Ocean.



At group C, represented mainly by oceanic stations, three subgroups and two outliers were delimited. Stations 45 and 10 were located near the shelf break and considered outliers in the group. Group C1 clustered stations 34 to 38, located in the southern portion of the study area (Fig. 9). It was mainly represented by *C. appendiculata*, *B. bassensis* and *A. tetragona* and differed from other oceanic groups by the low occurrences of *E. mitra* and *S. chuni* (Fig. 7, 8; Table 2). The similarity in the group was 69.2 %. Group C2 was represented mainly by the remaining oceanic stations outside the influence of the ARP. With and average similarity of 69.5 %, *C. appendiculata*, *E. mitra* and *B. bassensis* were the main representative of the group (Fig.9; Table2). Except for station 17 and 22 placed in group C2, all oceanic station under the influence of the ARP and station 25 and 26 located near its limit were included at Group C3 (Fig. 9; Table 2), with 69.3 % of similarity. The group was mainly represented by higher abundances of *D. bojani, E. mitra* and *A. hemistoma*.

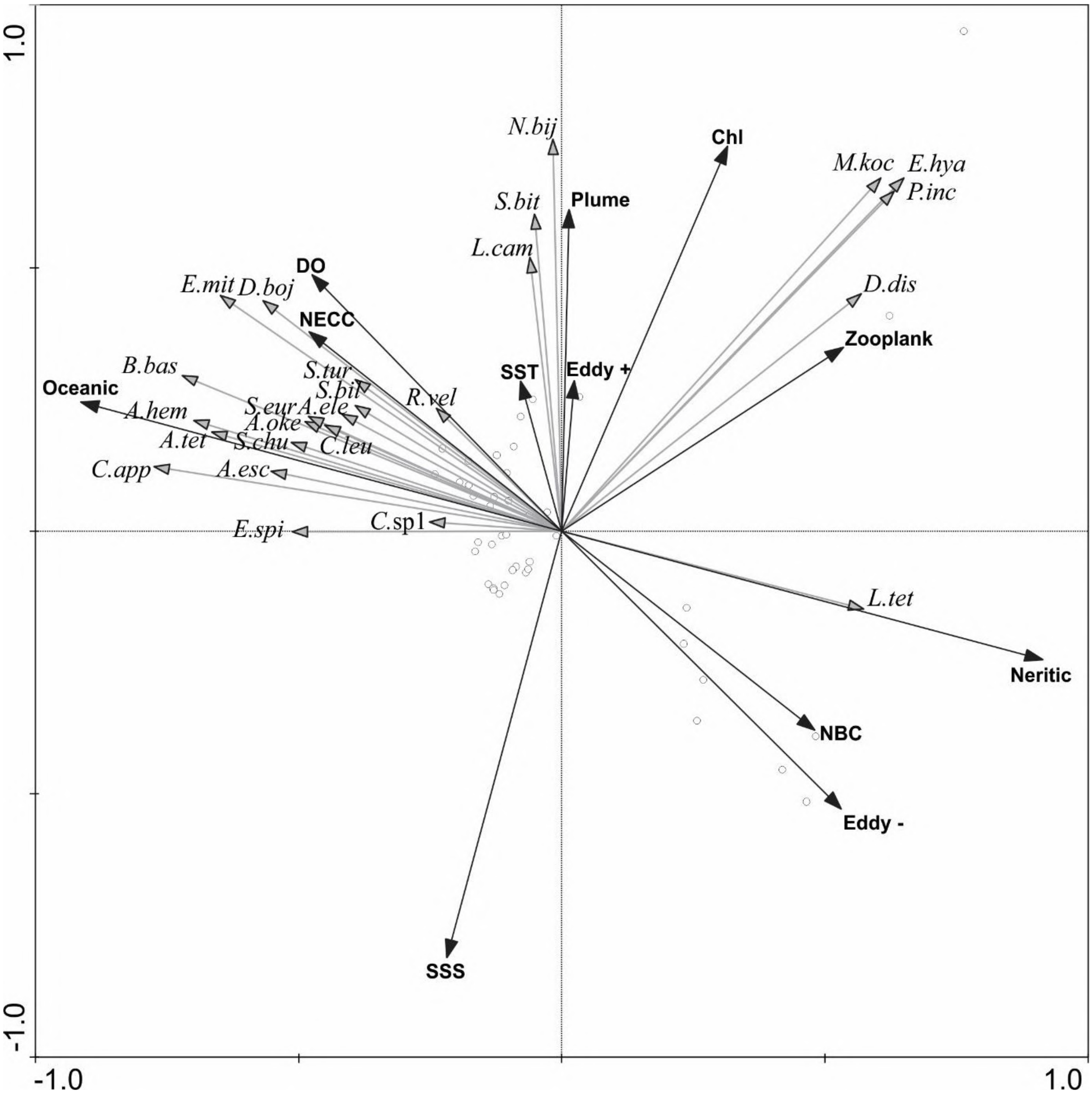
**Table 2.** Results of SIMPER analysis, showing the relative contribution of planktonic cnidarian species in the formation of the groups defined in the Cluster analysis.

| Species | A | B | C1 | C2 | C3 |
|---|---|---|---|---|---|
| *Abylopsis eschscholtzii* | - | - | 5.2 | 4.2 | 4.4 |
| *Abylopsis tetragona* | - | - | 11.9 | 6.9 | 4.6 |
| *Agalma okeni* | - | - | - | 2.1 | 2 |
| *Aglaura hemistoma* | - | - | 11.2 | 9.9 | 10.7 |
| *Bassia Bassensis* | - | - | 17.1 | 10.1 | 7.9 |
| *Ceratocymba leuckartii* | - | - | - | - | 2.1 |
| *Chelophyes Appendiculata* | - | - | 18.8 | 13.4 | 8.2 |
| *Cunina octonaria* | - | 6.8 | - | - | - |
| *Diphyes bojani* | - | - | 10.8 | 9.9 | 13.1 |
| *Diphyes dispar* | 8.1 | 11.5 | - | - | - |
| *Enneagonum hyalinum* | - | 16.3 | - | - | - |
| *Eudoxoides mitra* | - | - | - | 10.8 | 11.2 |
| *Eudoxoides spiralis* | - | - | 11.3 | 7.7 | - |
| *Cerinula larvae* | - | 10.1 | - | - | - |
| *Lensia campanella* | - | - | - | - | 2.7 |
| *Liriope tetraphylla* | 84.1 | 5.7 | 5 | 5.2 | 5.1 |
| *Muggiaea kochii* | - | 14.6 | - | - | - |
| *Nanomia bijuga* | - | 6.7 | - | 2.4 | 3.2 |
| *Persa incolorata* | - | 21.3 | - | - | - |
| *Rhopalonema velatum* | - | - | - | - | 2.1 |
| *Sminthea eurygaster* | - | - | - | 1.8 | 1.9 |
| *Solmundella bitentaculata* | - | - | - | - | 1.6 |
| *Sulculeolaria biloba* | - | - | - | - | 2.6 |
| *Sulculeolaria chuni* | - | - | - | 6.2 | 4.9 |
| *Sulculeolaria turgida* | - | - | - | - | 2.3 |

*Responses to mesoscale processes and environmental gradient*

The first four axes of the RDA explained 62.1% of planktonic cnidarian species variation. Axis 1 explained 36.1% and was mainly negatively related to the oceanic/neritic gradient. Zooplankton biomass and cold-core cyclonic eddies were positively related to this axis. The Second axis explained 16.5% of species variance and was negatively related to surface salinity and cyclonic eddies, and positively related to the ARP, fluorescence  and zooplankton biomass. The third axis explained additional 6.8% of the variance of species and were positively related to surface temperature and the NECC and negatively related to NCB. Axis 4 explained only 2.6% of the variance and was not related to any environmental variable (Fig. 10).

**Figure 10.** Redundancy analysis relating dominant planktonic cnidarian species to environmental gradients and mesoscale processes in the Western Equatorial Atlantic Ocean.



Many oceanic species were closely related to the left portion of the first axis with few relation with axis 2, which represented the salinity gradient of the ARP, reflecting their wide distribution over the oceanic province in the area. Other oceanic species, such as *D. bojani*, *E. mitra* and *R. velatum* correlated also with the positive portion of axis 2, indicating their tolerance and higher abundance in the low salinity oceanic environment induced by the ARP (Fig. 10).

*N. bijuga*, *S. bitentaculata* and *L. campanella* were close related with the positive portion of axis two, indicating their preference for the low salinity environment of the ARP in oceanic and neritic habitats. *Enneagonum hyalinum*, *M. kochii*, *P. incolorata* and *D. dispar* correlated with the positive portions of axis 1 and 2, reflecting their high abundances in neritic stations under the ARP influence, where the higher primary production and food availability occurred. *Liriope tetraphylla* was positively related to the first axis, as a result of its large abundance over the continental shelf both inside and outside the ARP and in the cold-core cyclonic eddy (Fig. 10).

## Discussion

Our results evidenced clearly contrasting planktonic cnidarian assemblages in Western Equatorial Atlantic oceanic and neritic provinces off the Northern Brazilian coast with the Amazon River Plume (ARP) being the main mesoscale physical process shaping the structure of these communities. Differences in the composition of species from continental shelf and oceanic waters were already expected since the coast-ocean gradient is an important driver of planktonic cnidarians and other biological communities distribution observed elsewhere in the world, generally associated with water masses, salinity an temperature gradients, food availability and differences in the basis of food web (Pagès and Gili, 1991b, 1992; Pagès *et al.*, 2001; Nogueira Júnior *et al.*, 2014). This pattern was evidenced by the Cluster and Redundancy Analysis, where stations and species were mainly structured according to the province (neritic or oceanic) and influence of the ARP.

Over the continental shelf, sharp differences were observed in the environments. At stations under the influence of the ARP (Cluster group B), higher diversity and abundance of both hydromedusae and siphonophores were observed. On the other hand, stations outside the ARP (Cluster group A) were dominated by the holoplanktonic hydromedusa *Liriope tetraphylla,* mostly present in high abundance. These constrating characteristics of the assemblage over the continental shelf reflects the unique and complex oceanographic processes occurring simultaneously there, shuch as freshwater runoff, eddies and strong currents.

Although widespread all over the area, *L. tetraphylla* dominated almost alone the neritic province outside the influence of the ARP, where only occasional catches of other species were observed. *L. tetraphylla* is typically abundant in neritic habitats at South, Southeast and Northeast Brazil (Vannucci, 1957; Paranaguá, 1963; Moreira, 1973; Nagata *et al.*, 2014; Nogueira Júnior *et al.*, 2014, 2015), Caribbean Sea (Larson, 1982; Suarez-Morales *et al.*, 1999a, 1999b; Persad *et al.*, 2003) and Gulf of Mexico (Segura-Puertas, 1992; Loman-Ramos *et al.*, 2007; Martell-Hernández *et al.*, 2014; Gutiérrez-Aguirre *et al.*, 2015). Unlike our results, all these studies reported the species co-occurring with other dominant species. Even though, competitive exclusion and segregated distribution was already reported for *L. tetraphylla* and other dominant predatory medusae in the Gulf of Mexico (Flores-Coto *et al.*, 2016), and it could be the mechanism behind our results. Its abundance was particularly high at stations 4, 5 and 6, which were sampled inside a cold-core cyclonic eddy. The surface divergence caused by these eddies may upwell nutrient-rich bottom waters and enhance primary production and consequently benefit the whole food chain by a bottom-up control process, including *L. tetraphylla* population. This event can be noted particularly at station 5 by the increment in fluorescence (Fig. 3D; bellow 10 meter depth) and total zooplankton biomass representing planktonic cnidarians food availability. The relation of *L. tetraphylla* with a cold core cyclonic eddy was also observed in the Gulf of Mexico where the species reached abundances 3 times higher inside it, while other cnidarian species were present only outside (Suarez-Morales *et al.*, 2002). Thereby, an intensive survey, considering also the temporal scale, should be performed to confirm the relation of *L. tetraphylla* with cold core cyclonic eddies in the northern Brazilian continental shelf and other areas as well.

The freshwater input of the ARP over the continental shelf was responsible for intense changes in the environmental background and composition of species inhabiting this environment. Low salinity, more than just acting as a barrier, restricting species sensitive to diluted waters, granted the development of many species that were virtually absent in the remaining habitats. Among these species, the siphonophore *Muggiaea kochii* and the narcomedusa *Cunina octonaria* are typical coastal species with worldwide distribution and may even be found inside estuaries (Vannucci, 1957; Sanvicente-Añorve *et al.*, 2007; Touzri *et al.*, 2012; Andrade, 2014; Nagata *et al.*, 2014; Nogueira Júnior *et al.*, 2014, 2018), thus, with the low salinity their range was expanded in the area reaching the middle continental shelf. Other dominant species found exclusively in this environment were the siphonophore *Enneagonum hyalinum* and the trachyline medusa *Persa incolorata*. Although occasionally associated with coastal and brackish waters (Morales-Ramírez and Nowaczyk, 2006; Sanvicente-Añorve *et al.*, 2007; Li *et al.*, 2012; Gao *et al.*, 2015; Gutiérrez-Aguirre *et al.*, 2015), they also have been reported in open ocean high salinity waters (Gasca and Suárez, 1991; Gasca, 1999; Hosia *et al.*, 2008). The contrasting niches may represent intraspecific variability or even cryptic species; advances on molecular techniques could elucidate this question. The recently described species *Helgicirrha angelicae* until the present is only known from this environment, possibly being an endemic representative. Although not exclusive from this habitat, other remarkable species occurring over the continental shelf under influence of the ARP were the siphonophores *Diphyes dispar* and *Nanomia bijuga*, two cosmopolitan species frequently present in coastal waters and estuaries (Morales-Ramírez and Nowaczyk, 2006; Sanvicente-Añorve *et al.*, 2007; Touzri *et al.*, 2012; Nogueira Júnior *et al.*, 2014, 2018), but also occurring in high saline open waters (Pagès and Gili, 1991b; Batistić *et al.*, 2004; Martell-Hernández *et al.*, 2014).

In addition to the freshwater input lowering salinity, the ARP also discharges a massive amount of nutrients, organic matter and sediments over the continental shelf (Signorini *et al.*, 1999), these increments expressively enhanced the primary production, evidenced by the fluorescence, in the upper layer of the water column, consequently, higher trophic levels are benefited by the large food availability. Under these conditions, associated with the reduced transparency caused by the sediment runoff and suspended particulate matter, cnidarians, which are not visual feeders, may take vantage and proliferate, resulting in large population blooms (Sommer *et al.*, 2002; Condon *et al.*, 2013). Thus, large concentrations were observed for *P. incolarata*, *E. Hyalinum*, *M. kochii* and *D. dispar* populations in the area (up to 2701, 2227, 1185 and 768 ind. 100m³ respectively). This abundance associated with the large sizes of *E. hyallinum* and *D. dispar* expressively contributes to the zooplanktonic biomass of the area (author personal observation), which may have important implications on production of marine snow and sinking of assimilated carbon to deeper layers (Pitt *et al.*, 2009).

Typically, holoplanktonic siphonophores dominate open ocean waters (Lo and Biggs, 1996; Pugh *et al.*, 1997; Lo *et al.*, 2012; Grossmann *et al.*, 2015) while meroplanktonic hydromedusae are abundant in shallow coastal waters (Vannucci, 1957; Bouillon *et al.*, 1986, 2006; Buecher and Gibbons, 2000; Gibbons and Buecher, 2001). In accordance, siphonophores dominated the oceanic assemblage discussed herein (Cluster group C) both in number of species and abundance, however, holoplanktonic hydromedusae such as *Aglaura hemistoma*, *Sminthea eurygaster* and *L. tetraphyla* also were abundant in this habitat, particularly at stations located under influence of the ARP or close to the shelf break. The absence of a benthic polypoid stage in their life cycle allows such animals to be dispersed through large-scale oceanographic processes such as ocean circulation (Boltovskoy *et al.*, 2003; Bouillon *et al.*, 2006).

Unlike the neritic habitat, the ARP did not restrict species distributionin the open ocean, even with surface salinities as low as 32.5. Since oblique zooplankton samples were performed from 200 meters depth to surface, and low salinity ARP waters did not exceeded 50 meters depth, intolerant species may live in deeper high salinity water masses under the ARP. Despite the absence of exclusive species, differences in species abundance were perceptible in the contrasting characteristics of the oceanic habitats. The siphonophores *Chelophyes appendiculata*, *Bassia* *bassensis*, *Eudoxoides spiralis* and *Abylopsis tetragona* were more abundant outside the influence of the ARP. They are typical high salinity oceanic species (Pagès and Gili, 1991b; Lo and Biggs, 1996) that may be restricted to deeper waters under the ARP. A study with stratified samples could elucidate this question.

Otherwise, the siphonophore *Diphyes bojani* was clearly more abundant in the ARP, where in average, it was five times higher than outside the ARP. Other species with a higher probability of occurrence under influence of the ARP were *Eudoxoides mitra*, *D. dispar*, *N. bijuga*, *A. hemistoma*, *S. eurygaster*, *Lensia campanella*, *Sulculeoria turgida*, *Sulculeolaria biloba* and *Ceratocymba leuckartii*. *D. bojani* is a common species from neritic and oceanic habitats all over the world, occurring in a wide range of temperatures and salinities. Its apparently high adaptive capacity may be an advantage in habitat gaps left by other species in these low salinity oceanic waters. The siphonophores *D. dispar* and *N. bijuga* were also abundant in neritic habitats under influence of the ARP, and apparently freshwater inputs benefits then both in neritic and oceanic habitats. Few is known about tolerances and requirements of the other species.

Other oceanographic processes were observed in the oceanic and neritic provinces and may have some influence structuring the planktonic cnidarian communities in the area. Oxygen minimum layers were observed bellow the ARP both in neritic and oceanic provinces, this is a direct consequence of the high rates of organic matter that sinks from the plume and fuel microbial respiration (Diaz and Rosenberg, 2008). Although the hypoxic condition can act as a barrier for many pelagic cnidarians, it also can benefit tolerant species (Purcell *et al.*, 2001; Batistić *et al.*, 2004; Apablaza and Palma, 2006). Intrusions of the South Atlantic Central Water were present in the 200 m sampled of every oceanic station and reached up to 45 m depth at station 21. Cnidarian distribution frequently is close related to water masses (Nogueira Júnior *et al.*, 2014) and distinct communities may have been sampled in our oblique hauls. For both situations, stratified samples would be necessary for a better understanding of how these processes affect the vertical structure of pelagic cnidarians in the area.

Although Alvariño (1968) made some ecological appointments on the cnidarians distribution in the equatorial Atlantic near the area discussed herein, relations with mesoscale oceanographic processes, environmental gradients or with the ARP were not performed to compare with our results. Some species such as *E. mitra*, *D. bojani*, *C. appendiculata*, *E. spiralis* and *L. tetraphyla* were abundant in both works. Taking into account the 47 years between the samples, and recurrent reports of the species in non-ecological studies (Leloup, 1934, 1937, 1955; Leloup and Hentschel, 1938; Alvariño, 1971) we can observe a high persistence on populations of these species through time. On the other hand, other abundant species in our study were not representative or did not even occurred in Alvariño (1968) and other previous studies in the area. Although some of our species were found in very specific habitats that could be out of the spatial range of previous samples, others were widespread and present reports may represent temporal changes and new colonization in this dynamic system.

## Conclusion

This was the first detailed survey on cnidarians community structure from a major river plume reaching mesoscale dimensions in neritic and oceanic provinces. Our data showed that the freshwater runoff of the Amazon River strongly affects the abundance, distribution and taxonomic structure of planktonic cnidarians in neritic and oceanic provinces of the Western Equatorial Atlantic Ocean.

Over the continental shelf, distinctions where sharp and habitats under the influence of the ARP present a diverse community occurring in large abundance. *Enneagonum hyalinum, Muggiaea kochii, Persa incolorata, Cunina octonaria, Diphyes dispar* and *Nanomia bijuga* were representive species in these productive, low saline and turbid waters. Outside the ARP influence *Liriope tetraphylla* dominated almost alone the neritic habitat, with a cold core cyclonic eddy shaping its distribution in the area. Divergences in the oceanic province were less pronounced but still expressive, occurring mainly in the dominant species abundance. *Chelophyes appendiculata*, *Bassia bassensis*, *Eudoxoides spiralis* and *Abylopsis tetragona* occurred in larger abundances in oceanic areas outside the ARP influence and *Diphyes bojani, Diphyes dispar* and *Nanomia bijuga* were more abundant under its influence.

As expected, the Western Equatorial Atlantic Ocean under the influence of the ARP revealed a complex system, with many physical and biogeochemical processes occurring simultaneously and its complexity reflected in the structure of cnidarian community. Our survey took the first steps in the understanding of ecosystem interactions and functioning in the area, for now on, other spatial and temporal scales, as well as stratified samples and other perspectives should be performed for the complete understanding of this complex environment.

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# 6 ARTIGO 3 - INFLUENCE OF THE AMAZON RIVER PLUME IN THE SPATIAL DISTRIBUTION OF NEUSTONIC CNIDARIANS IN THE WESTERN EQUATORIAL ATLANTIC OCEAN

## Abstract

The neuston layer is a complex environment where oceanographic and atmospheric processes interact. Marine organism, such as cnidarians, inhabiting the layer are exposed to these conditions. In the Western Equatorial Atlantic, the large freshwater discharge of the Amazon River spreads a surface plume of low salinity and high nutrients that can be traced hundreds of kilometers in the neutons. Thus, in this study we investigated the spatial distribution and abundance of neustonic cnidarian species from the Western Equatorial Atlantic to evaluate the effects of the Amazon River Plume and other characteristics of the environment in the structure of the community. The area over the continental shelf under influence of the plume presented a diverse community with many relevant species such as Enneagonun hyalinun, D. dispar, N. bijuga, L. tetraphylla and M. kochii, while outside its influence the hydromedusae Liriope tetraphylla dominated almost alone. In the open ocean holoplanktonic siphonophores dominated and differences is species composition among areas inside and outside the influence of the plume were less pronounced. Results indicated that the neustonic cnidarian community presented a spatial structure similar to epipelagic waters, where the inshore-offshore gradient and the dynamics of the Amazon River Plume are the main mesoscale drivers of species distribution and abundance.

**Keywords:** Medusae. Siphonophores. Gelatinous zooplankton. Amazonian Coast. Pleuston.

## Introduction

The neuston comprises the biological community inhabiting the not well-structured surface layer of the water column in the interface with the atmosphere (Zaitsev 1971, Hardy 1982). It is a critical zone for marine biota, where in addition to physical oceanographic processes and surface water conditions such as temperature and salinity, the system is affected by atmospheric variability. Thus, aspects as light intensity, wind stress, turbulence and air temperature contribute in shaping the distribution of organisms (Zaitsev 1971). The surface layer is also an accumulation zone of terrestrial debris, pollutants, micro and macro plastics and river freshwater run-off, spreading for hundreds of kilometers such in the case of the Amazon River plume (ARP) in the Western Equatorial Atlantic (Hellweger & Gordon 2002, Ryan et al. 2009, Molleri et al. 2010). All these features increase the complexity of the neustonic habitat.

Despite the thickness of the neustonic layer, it covers 71% of the surface of the planet, being one of the most ubiquitous ecological communities (Hardy 1991). It plays a major role in global biogeochemical processes such as $CO_2$ assimilation and production of marine snow, sinking carbon to deeper layers (Hays et al. 2005, Engel et al. 2017). It is also a key environment in the complex processes involved in the life cycle and reproduction of many marine organisms with high abundance and diversity of larvae and juvenile stages (Abelló & Frankland 1997, Gallardo et al. 2012, Sabatés et al. 2015). In addition, the neustonic assemblage is an important food source for fish and other pelagic groups (Cardinale 2003, Pusineri et al. 2005).

While fish and other organisms sporadically visit the neuston to feed (Cardinale 2003, Pusineri et al. 2005), species with less mobility such as small cnidarians may permanently inhabit it, probably presenting more specific responses to the extreme condition of this environment. Cnidarians play a significant role in the food web, occasionally controlling the pelagic community and collapsing fisheries and other human activities(Pitt et al. 2009, Purcell 2012). However, studies subjecting zooneuston tend to focus on general taxa (Lira et al. 2014, Liparoto et al. 2017, Collard et al. 2020) or dominant groups such as copepods (Cañete et al. 2016), and the cnidarian community is set aside. Therefore, there is very sparse knowledge on the distribution of neustonic cnidarians and the main processes associated to it.

In the Western Equatorial Atlantic Ocean, the massive discharge of the Amazon River creates a surface plume of low-salinity, high nutrients, and suspended and dissolved materials which spreads through the surface layer reaching the Caribbean Sea and North Atlantic (Molleri et al. 2010). The reach of the ARP is mainly affected by its discharge, the North Brazilian Current (NBC) and wind fields (Geyer 1995, Lentz 1995, Lentz & Limeburner 1995, Geyer et al. 1996, Nittrouer & DeMaster 1996, Molleri et al. 2010). Three general patterns occur throughout the year. Between January and April, the ARP flow continuously northwest along the Brazilian coast carried mainly by NE winds. From April to July the ARP reaches the Caribbean region due to the higher discharge, NBC transport and SE winds. From August to December, the retroflection of the NBC, around 5°N and 10°N, disperses the ARP to the east feeding the North Equatorial Counter Current (NECC; Molleri et al. 2010, Coles et al. 2013)

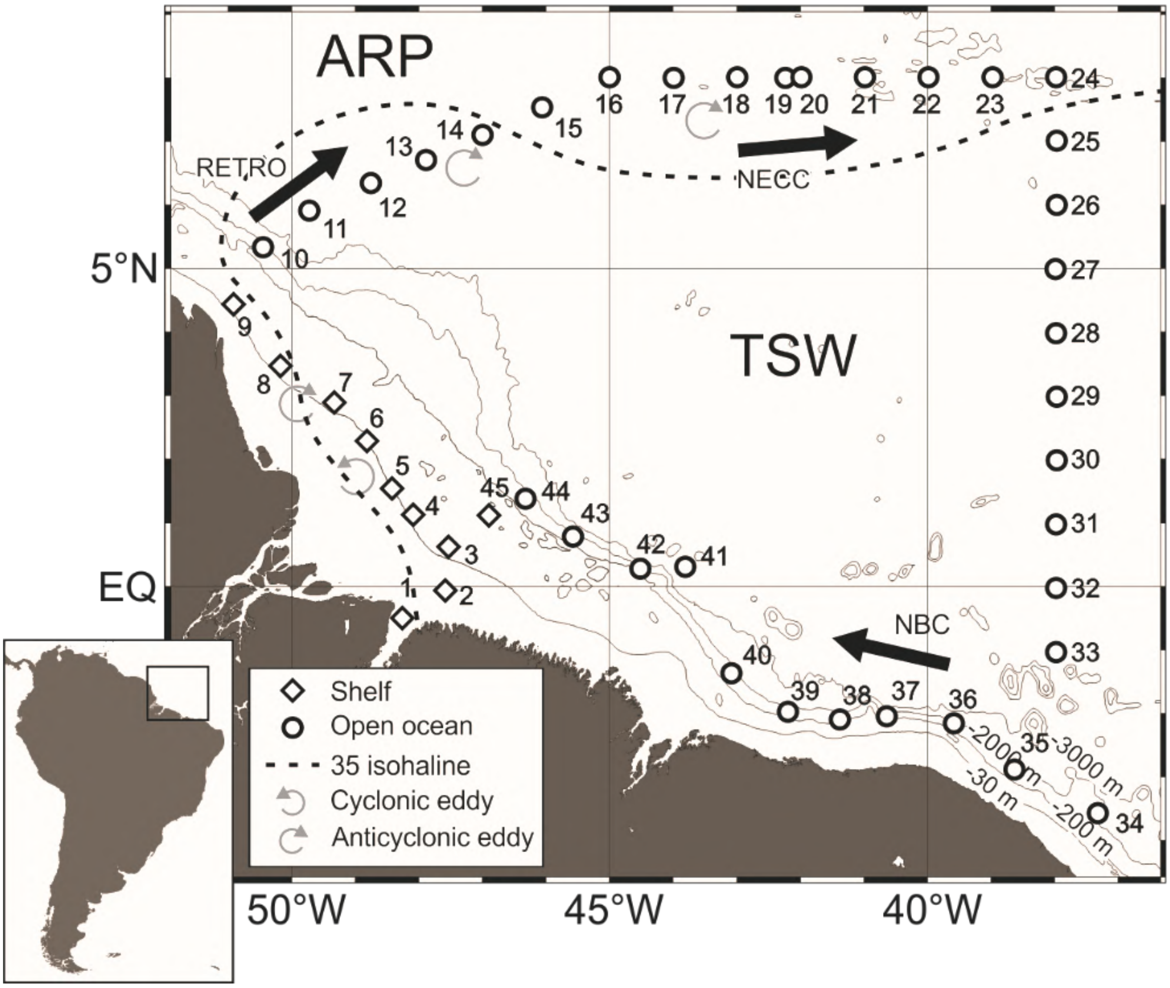
The plume is one of the main forces shaping planktonic cnidarian distribution in epipelagic waters over the continental shelf and open ocean in the area, along with other mesoscale precesses, such as eddies, current field and the inshore-offshore gradient (Section 4.2). These processes may be particularly more pronounced to organisms in the neuston due to the instability of the environment; however, they were never tested on neustonic cnidarians. Thus, in this study we evaluated the spatial structure of the neustonic cnidarian community from the continental shelf and adjacent oceanic waters of northern Brazil in the equatorial Atlantic and its relation with physical environment. The study was based on the hypothesis that mesoscale processes such as the ARP and cross-shelf characteristics of the environment are the main factors shaping species distribution.

## Materials and Methods

*Sampling*

Data and samples were obtained during the oceanographic cruise Camadas Finas III, aboard the research vessel NHo. Cruzeiro do Sul - H38 (DHN/Brazilian Navy) along the north Brazilian continental shelf (bottom depth <130 m) between the Amazon and Oyapok river mouths and in equatorial Atlantic oceanic waters (bottom depth >130 m) between 8°N, 51°W and 3.5°S, 37°W (Fig.1). It was performed during October 9-31, 2012, corresponding to the period when the retroflection of the NBC disperses the plume to the east feeding the NECC (Molleri et al. 2010).

**Figure 1.** Geographic location of the study area in the North Brazilian continental shelf and adjacent Western Equatorial Atlantic Ocean, showing the sampled stations and mesocale processes occurring in October 2012. ARP = Amazon River plume; TSW = Tropical Surface Water; NBC = North Brazilian Current; RETRO = North Brazilian Current retroflection; NECC=North Equatorial Counter Current. The 35 isohaline indicate surface limits of the ARP.



Zooneuston samples were obtained at 45 stations along the track of the cruise with a David-Hempel aluminum catamaran (Hydro-Bios, Kiel, Germany) equipped with two superposed nets with rectangular mouth (30x15 cm each one) and a 500 µm mesh. The upper net was adjusted exactly centered at the air-water interface, sampling the epineuston layer from the surface to 7.5 cm depth, while the lower net sampled the hyponeuston layer from 7.5 cm to 22.5 cm depth. The catamaran was hauled during 20 minutes at a speed of 2-3 knots each station. The lower net was fitted with a flowmeter (Hydro-Bios) to estimate the volume filtered during each trawl. The zooneuston samples were fixed with 4% formaldehyde buffered with sodium tetraborate (0.5 g.$l^{-1}$).

In laboratory, whole samples were analyzed under stereomicroscope and specimens were identified (mainly following Bouillon 1999, Pugh 1999, Bouillon et al. 2006) and counted. Abundances were standardized as number of individuals per 100 $m^{-3}$ for medusae and number of colonies per 100 $m^{-3}$ for siphonophores. For calycophorans, the number of anterior nectophores was used for estimating the polygastric stage abundance, and eudoxid bracts for the eudoxid stage abundance (e.g. Hosia & Båmstedt 2007, Hosia et al. 2008). For physonects and the calycophora *Hippopodius hippopus*, number of colonies were roughly estimated by dividing the number of nectophores by 10 (Pugh 1984).

Salinity, temperature (°C), density ($\sigma_t$), dissolved oxygen (mg$L^{-1}$) and fluorescence vertical profiles, characterization of water masses, current speed and directions and presence of cyclonic and antyciclonic eddies were obtained for the sampling period. Methods and results were described in Tosetto et al. (Section 4.2). Main mesoscale processes observed in the area are shown in figure 1.

*Data analysis*

To dampen effects of dominant species, in all analyses abundance data was transformed by log (x + 1). Station 1 was excluded from all analysis since it was the only station sampled inside the estuary. A Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson et al. 2008) was used to test for differences in the cnidarian community structure between epineuston and hiponeuston. Since no significant difference were observed (PseudoF = 1.594, P = 0.107) we considered both samples from each station as replicates.

Spatial patterns in neustonic cnidarian community abundance were identified by hierarchical cluster analysis using Bray–Curtis similarity matrix. The validity of the groups defined by the cluster analysis was tested though SIMPROF test (5% significance level). A Similarity Percentage (SIMPER) analysis was performed to identify representative species and their contribution to similarity within the groups defined by the cluster analysis.

To identify associations between representative neustonic cnidarian taxa (species occurring in more than 21 stations and species with high abundance in few stations) and the environment, a constrained ordination analysis was performed. Detrended Canonical Correspondence Analysis (DCCA) revealed a small length of variable gradients (< 3), indicating that a linear method was appropriate to use on this occasion, and thus Redundancy Analysis (RDA) was selected (Lepš & Šmilauer 2003). Predominant current was included as dummy categorical explanatory variable. Bottom depth, max value of fluorescence (as an indirect measure of biological productivity) in the first 200 m of the water column, and surface temperature and salinity were included as continuous explanatory variables.

Distribution maps were produced in Ocean Data View 5.0 (Schlitzer 2020) and QGIS 3.10 (QGIS Development Team 2021). Cluster, SIMPROF, SIMPER and PERMANOVA analysis were performed in Primer v.6+PERMANOVA (Clarke & Gorley 2006). DCCA and RDA were performed in CANOCO 4.5 (Lepš & Šmilauer 2003).

## Results

### *Species composition*

A total of 55 taxa of cnidarians were observed in the neustonic layer of the study area, corresponding to one scyphomedusae, 23 hydromedusae (hereafter pelagic hydroids of Anthoathecate are included in this category for convenience) and 31 siphonophores (table 1). Furthermore, unidentifiable cerinula, ephyrae and athorybia larval forms were found. *Liriope tetraphylla* was the most frequent hydromedusae, present in 55.6% of the samples, followed by *Porpita porpita* (26.7%), *Aglaura hemistoma* (24.4%) and *Cytaeis* sp.3 (22.2%, table 1). *L. tetraphylla* also dominated in abundance, representing 56.1% of all hydromedusae. Other representative hydomedusae were *Cytaeis* sp.3 (17.8%) and *Cunina octonaria* (11.5%). Among Siphonophores, the most frequent were *Chelophyes appendiculata* (67.8%), *Diphyes bojani* (61.1%), *Bassia bassensis* (57.8%), *Abylopsis eschscholtzii* (56.7%) and *Diphyes dispar* (50%; Table 1). When considering abundance, *C. appendiculata* also dominated (32%), followed by *D. bojani* (19.6%), *D. dispar* (12.1 %), *B. bassensis* (9%) and *A. eschscholtzii* (7.2%).

### *Spatial distribution patterns*

Hydromedusae diversity was generally low both over the continental shelf (1.8 ± 2.3) and in the open ocean (1.8 ± 1.5). However, some samples under the influence of the ARP in both environments presented slight higher diversity, reaching 9 species in station 8 (Fig. 2a). Otherwise, hydromedusae total abundance over the continental shelf peaked outside the ARP. In the open ocean, stations under influence of the ARP and in the retroflection area (particularly station 10) presented higher abundances, which were generally lower in the remaining open ocean (Fig. 2b).

**Table 1.** Basic statistics of neustonic cnidarian species from neritic and oceanic provinces in the Western Equatorial Atlantic Ocean. Mean abundance (ind. 100 m$^{-3}$) and standard deviation, range of abundance, frequency of occurrence (f; considering both provinces) and temperature and salinity ranges.

| Species | Neritic | | Oceanic | | f | Temperature | Salinity |
|---|---|---|---|---|---|---|---|
| | Mean ± SD | Range of non-zero abundances | Mean ± SD | Range of non-zero abundances | | | |
| **“Hydromedusae”** | | | | | | | |
| *Liriope tetraphylla* (Chamisso & Eysenhardt, 1821) | 106.52 ± 228.22 | 3.09 - 810.1 | 29.1 ± 129.86 | 1.62 - 855.85 | 55.56 | 26.26 - 29.69 | 18.18 - 36.64 |
| *Porpita porpita* (Linnaeus, 1758) | 0.39 ± 1.72 | 7.71 - 7.71 | 6.42 ± 19.18 | 1.67 - 130.14 | 26.67 | 26.26 - 29.78 | 32.78 - 36.35 |
| *Aglaura hemistoma* Péron & Lesueur, 1810 | 5.21 ± 12.91 | 2.39 - 46.26 | 1.31 ± 3.31 | 1.36 - 16.69 | 24.44 | 26.38 - 29.69 | 31.58 - 37.06 |
| *Cytaeis* sp.3 | - | - | 18.89 ± 65.36 | 1.76 - 344.86 | 22.22 | 26.65 - 29.69 | 32.78 - 36.3 |
| *Cunina octonaria* McCrady, 1859 | 0.17 ± 0.69 | 0.38 - 3.09 | 12.21 ± 92.87 | 2.82 - 776.07 | 8.89 | 27.81 - 29.6 | 31.58 - 36.48 |
| *Annatiara affinis* (Hartlaub, 1914) | - | - | 0.47 ± 1.89 | 2.29 - 13.24 | 6.67 | 27.63 - 29.55 | 32.55 - 36.29 |
| *Rhopalonema velatum* Gegenbaur, 1857 | 0.19 ± 0.86 | 3.86 - 3.86 | 0.14 ± 0.89 | 3.34 - 6.68 | 3.33 | 26.61 - 27.99 | 36.08 - 36.26 |
| *Clytia* spp. | 0.35 ± 1.08 | 3.09 - 3.86 | 0.02 ± 0.16 | 1.36 - 1.36 | 3.33 | 26.61 - 29.04 | 31.58 - 36.26 |
| *Aequorea macrodactyla* (Brandt, 1835) | 0.96 ± 3.51 | 3.86 - 15.42 | 0.01 ± 0.12 | 0.99 - 0.99 | 3.33 | 26.52 - 26.61 | 36.26 - 36.27 |
| *Corymorpha gracilis* (Brooks, 1883) | - | - | 0.09 ± 0.56 | 1.81 - 4.32 | 2.22 | 27.89 - 28.4 | 35.94 - 36.12 |
| *Laodicea undulata* (Forbes & Goodsir, 1853) | - | - | 0.05 ± 0.32 | 1.19 - 2.39 | 2.22 | 26.5 - 26.5 | 36.31 - 36.31 |
| *Pegantha triloba* Haeckel, 1879 | - | - | 0.52 ± 3.86 | 4.63 - 32 | 2.22 | 27.63 - 28.07 | 36 - 36.29 |
| *Malagazzia carolinae* (Mayer, 1900) | 0.31 ± 1.38 | 6.18 - 6.18 | 0.02 ± 0.14 | 1.21 - 1.21 | 2.22 | 27.81 - 29.55 | 31.58 - 32.55 |
| *Persa incolorata* McCrady, 1859 | 1.39 ± 4.96 | 6.18 - 21.62 | - | - | 2.22 | 27.81 - 27.81 | 31.58 - 31.58 |
| *Eirene viridula* (Péron & Lesueur, 1810) | 4.1 ± 15.12 | 15.44 - 66.63 | - | - | 2.22 | 27.81 - 28.23 | 18.18 - 31.58 |
| Eirenidae sp. | - | - | 0.04 ± 0.3 | 2.52 - 2.52 | 1.11 | 26.38 - 26.38 | 36.3 - 36.3 |
| *Mitrocomella* sp. | - | - | 0.1 ± 0.82 | 6.86 - 6.86 | 1.11 | 27.63 - 27.63 | 36.29 - 36.29 |
| *Pegantha laevis* H.B. Bigelow, 1909 | - | - | 0.03 ± 0.29 | 2.4 - 2.4 | 1.11 | 27.91 - 27.91 | 36.17 - 36.17 |
| *Stauridiosarsia producta* (Wright, 1858) | - | - | 0.04 ± 0.36 | 3.03 - 3.03 | 1.11 | 26.95 - 26.95 | 36.3 - 36.3 |
| *Velella velella* (Linnaeus, 1758) | - | - | 0.02 ± 0.21 | 1.75 - 1.75 | 1.11 | 26.65 - 26.65 | 36.3 - 36.3 |
| *Cytaeis* sp.4 | 0.15 ± 0.69 | 3.09 - 3.09 | - | - | 1.11 | 27.81 - 27.81 | 31.58 - 31.58 |

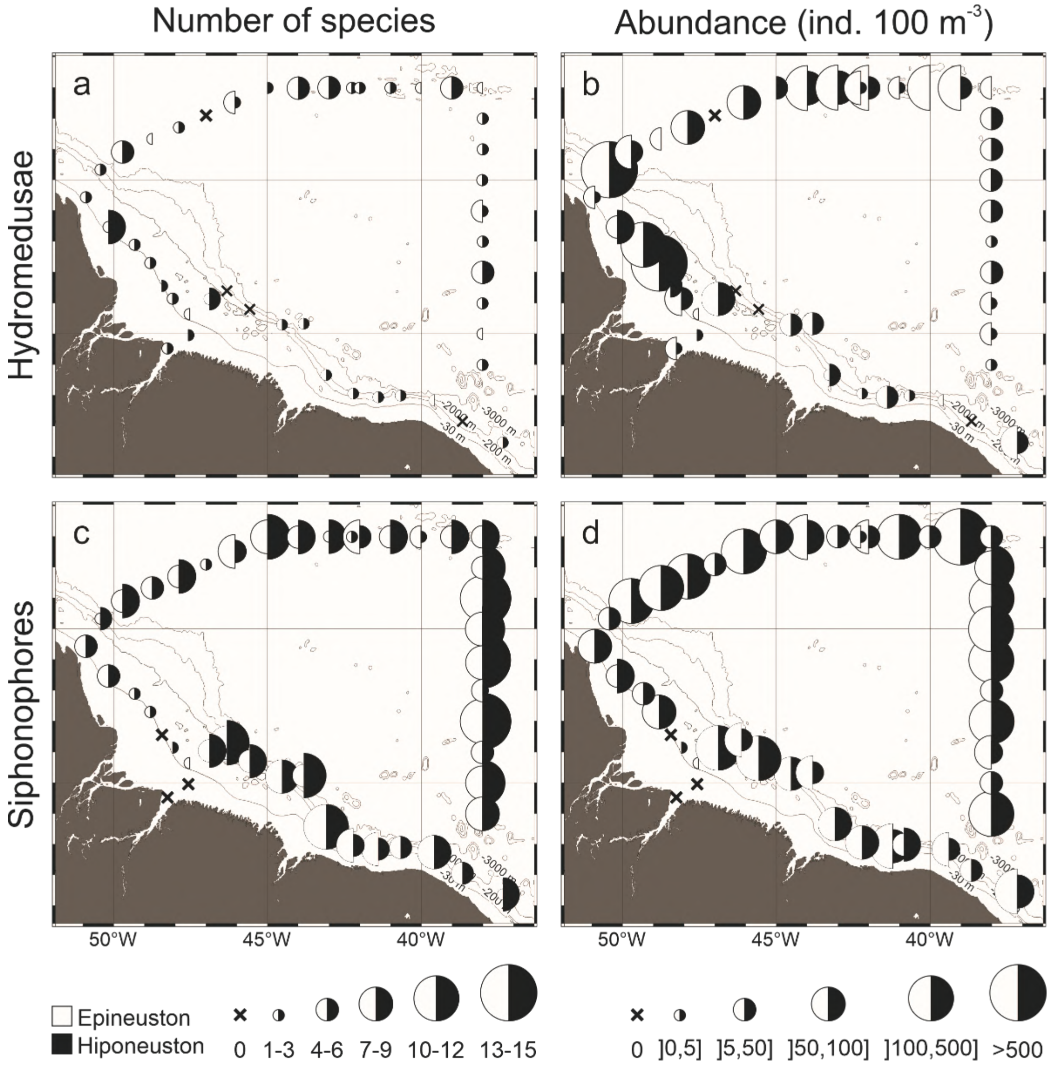
**Table 1.** Continuation.

| Species | Neritic | | Oceanic | | f | Temperature | Salinity |
|---|---|---|---|---|---|---|---|
| | Mean ± SD | Range of non-zero abundances | Mean ± SD | Range of non-zero abundances | | | |
| *Octophialucium haeckeli* (Vannucci & Soares Moreira, 1966) | 0.15 ± 0.69 | 3.09 - 3.09 | - | - | 1.11 | 27.81 - 27.81 | 31.58 - 31.58 |
| *Eucheilota* sp. | 0.31 ± 1.38 | 6.18 - 6.18 | - | - | 1.11 | 27.81 - 27.81 | 31.58 - 31.58 |
| **Scyphomedusae** | | | | | | | |
| *Nausithoe aurea* Silveira & Morandini, 1997 | - | - | 0.05 ± 0.4 | 3.35 - 3.35 | 1.11 | 29.69 - 29.69 | 34.4 - 34.4 |
| Ephyrae | 0.25 ± 1.11 | 4.95 - 4.95 | 1.79 ± 11.74 | 1.36 - 97.01 | 7.78 | 28.05 - 29.69 | 34 - 36.51 |
| **Siphonophorae** | | | | | | | |
| *Chelophyes appendiculata* (Eschscholtz, 1829) | 4.55 ± 13.08 | 6.18 - 46.26 | 38.41 ± 71.15 | 1.07 - 391.37 | 67.78 | 26.21 - 29.78 | 31.58 - 36.35 |
| *Diphyes bojani* (Eschscholtz, 1825) | 5.42 ± 15.78 | 1.56 - 61.69 | 22.74 ± 40.83 | 0.64 - 179.61 | 61.11 | 26.21 - 29.69 | 31.05 - 36.51 |
| *Bassia bassensis* (Quoy & Gaimard, 1833) | 0.31 ± 1.38 | 6.18 - 6.18 | 11.04 ± 19.15 | 0.64 - 120.39 | 57.78 | 26.21 - 29.69 | 31.58 - 36.35 |
| *Abylopsis eschscholtzii* (Huxley, 1859) | 0.4 ± 1.72 | 0.38 - 7.71 | 8.76 ± 11.7 | 1.67 - 55.27 | 56.67 | 26.21 - 29.69 | 32.55 - 36.48 |
| *Diphyes dispar* Chamisso & Eysenhardt, 1821 | 12.8 ± 24.31 | 6.24 - 81.75 | 11.37 ± 31.7 | 0.87 - 203.34 | 50 | 26.61 - 29.78 | 31.05 - 36.51 |
| *Sulculeolaria chuni* (Lens & van Riemsdijk, 1908) | 2.12 ± 6.56 | 19.28 - 23.13 | 4.2 ± 12.09 | 0.64 - 79.44 | 42.22 | 26.38 - 29.78 | 32.55 - 36.31 |
| *Abylopsis tetragona* (Otto, 1823) | 0.39 ± 1.72 | 7.71 - 7.71 | 3.48 ± 5.8 | 1.28 - 30.27 | 40 | 26.21 - 29.69 | 34 - 36.35 |
| *Agalma okenii* Eschscholtz, 1825 | - | - | 2.24 ± 4.73 | 0.64 - 30.98 | 37.78 | 26.26 - 29.69 | 32.55 - 36.35 |
| *Nanomia bijuga* (Delle Chiaje, 1844) | 1.21 ± 2.32 | 2.48 - 6.24 | 1.18 ± 2.38 | 1.41 - 11.03 | 28.89 | 27.81 - 29.78 | 31.05 - 36.51 |
| *Eudoxoides spiralis* (Bigelow, 1911) | - | - | 2.14 ± 4.86 | 0.66 - 22.62 | 22.22 | 26.21 - 28.26 | 36 - 36.35 |
| *Muggiaea kochii* (Will, 1844) | 1.79 ± 5.04 | 3.09 - 17.16 | 0.87 ± 1.91 | 0.66 - 8.73 | 22.22 | 26.21 - 28.45 | 31.05 - 36.35 |
| *Lensia campanella* (Moser, 1917) | 0.19 ± 0.86 | 3.86 - 3.86 | 0.37 ± 1.08 | 1.21 - 4.63 | 11.11 | 26.49 - 29.55 | 32.55 - 36.3 |
| *Eudoxoides mitra* (Huxley, 1859) | 0.39 ± 1.72 | 7.71 - 7.71 | 0.33 ± 1.01 | 1.2 - 6.03 | 11.11 | 26.61 - 29.6 | 32.55 - 36.26 |
| *Ceratocymba leuckartii* (Huxley, 1859 | - | - | 0.46 ± 1.49 | 1.07 - 8.17 | 10 | 26.95 - 29.6 | 32.78 - 36.3 |
| *Sulculeolaria turgida* (Gegenbaur, 1854) | - | - | 0.37 ± 1.09 | 0.64 - 5.18 | 10 | 26.92 - 29.55 | 32.55 - 36.29 |
| *Cordagalma ordinatum* (Haeckel, 1888) | 0.19 ± 0.86 | 3.86 - 3.86 | 0.43 ± 1.49 | 1.67 - 9.05 | 10 | 26.61 - 29.52 | 34.23 - 36.3 |

**Table 1.** Continuation.

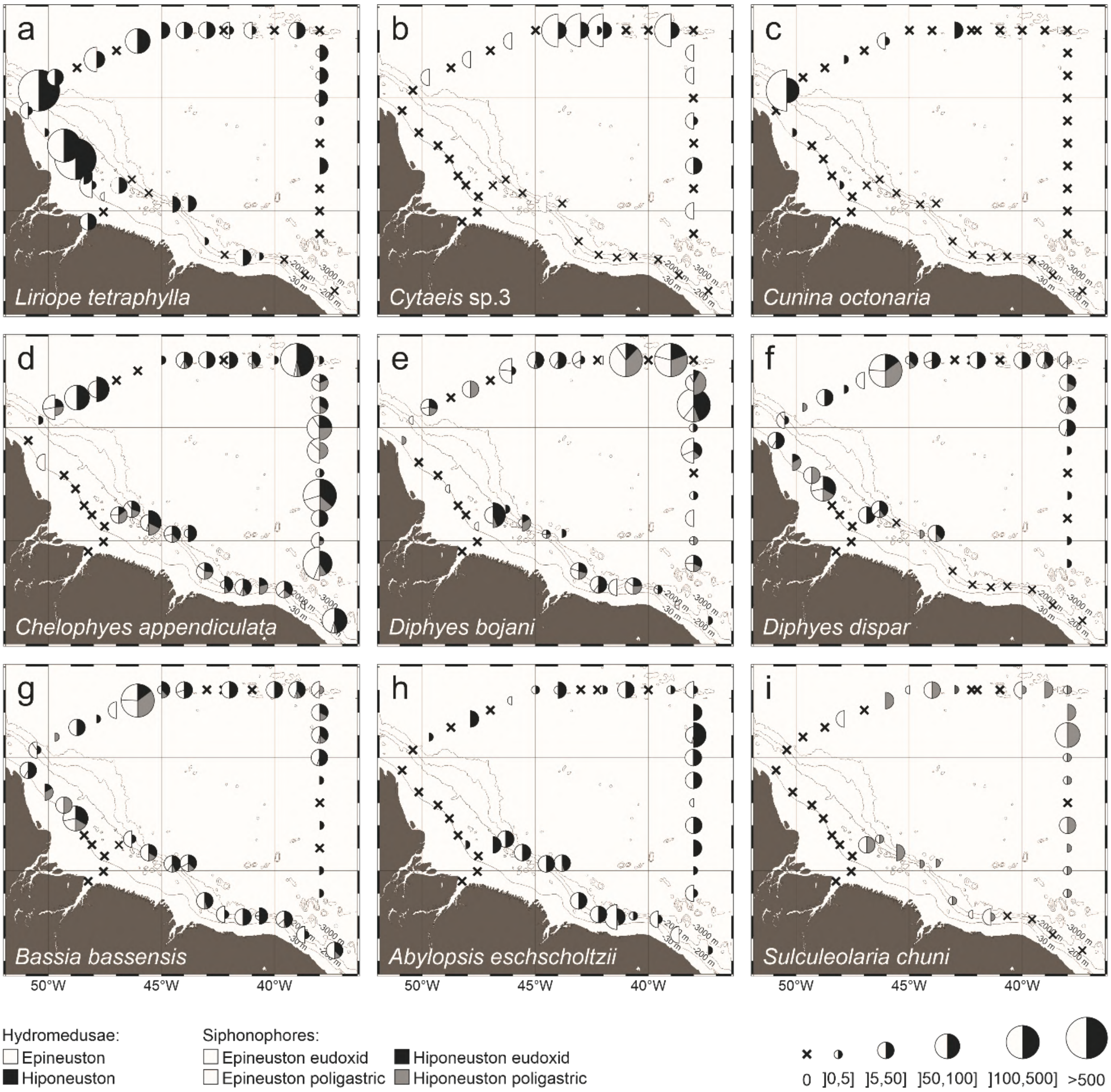
| Species | Neritic | | Oceanic | | f | Temperature | Salinity |
|---|---|---|---|---|---|---|---|
| | Mean ± SD | Range of non-zero abundances | Mean ± SD | Range of non-zero abundances | | | |
| *Agalma elegans* (Sars, 1846) | - | - | 0.4 ± 1.39 | 0.99 - 9.14 | 8.89 | 26.52 - 27.99 | 36.08 - 36.3 |
| *Sulculeolaria monoica* (Chun, 1888) | - | - | 1.92 ± 11.34 | 1.36 - 88.5 | 6.67 | 28.26 - 29.55 | 32.55 - 36.29 |
| *Solmundella bitentaculata* (Quoy & Gaimard, 1833) | 0.19 ± 0.86 | 3.86 - 3.86 | 0.66 ± 2.82 | 3.23 - 18.54 | 6.67 | 26.61 - 29.48 | 33.51 - 36.29 |
| *Physophora hydrostatica* Forsskål, 1775 | - | - | 0.19 ± 0.84 | 1.2 - 4.57 | 4.44 | 27.63 - 29.38 | 34 - 36.29 |
| *Enneagonum hyalinum* Quoy & Gaimard, 1827 | 5.27 ± 12.46 | 15.6 - 49.41 | - | - | 4.44 | 27.81 - 27.88 | 31.05 - 31.58 |
| *Physalia physalis* (Linnaeus, 1758) | - | - | 0.13 ± 0.64 | 1.98 - 3.68 | 3.33 | 26.52 - 29.78 | 34.23 - 36.27 |
| *Abyla* sp. | - | - | 0.05 ± 0.33 | 1.36 - 2.4 | 2.22 | 27.91 - 29.04 | 35.45 - 36.17 |
| *Athorybia rosacea* (Forsskål, 1775) | - | - | 0.12 ± 0.7 | 3.68 - 4.63 | 2.22 | 28.07 - 29.52 | 34.23 - 36 |
| *Halistemma rubrum* (Vogt, 1852) | - | - | 0.1 ± 0.61 | 2.29 - 4.63 | 2.22 | 27.63 - 28.07 | 36 - 36.29 |
| *Lensia conoidea* (Keferstein & Ehlers, 1860) | - | - | 0.12 ± 0.8 | 1.73 - 6.47 | 2.22 | 27.89 - 28.45 | 35.58 - 36.12 |
| *Lensia cossack* Totton, 1941 | - | - | 0.05 ± 0.31 | 1.21 - 2.29 | 2.22 | 27.63 - 29.55 | 32.55 - 36.29 |
| *Sulculeolaria biloba* (Sars, 1846) | - | - | 0.05 ± 0.3 | 0.99 - 2.32 | 2.22 | 26.52 - 28.07 | 36 - 36.27 |
| *Lensia subtilis* (Chun, 1886) | 0.25 ± 1.11 | 4.95 - 4.95 | 0.04 ± 0.36 | 3.03 - 3.03 | 2.22 | 26.95 - 28.05 | 36.3 - 36.51 |
| *Hippopodius hippopus* (Forsskål, 1776) | - | - | 0.02 ± 0.14 | 1.21 - 1.21 | 1.11 | 29.55 - 29.55 | 32.55 - 32.55 |
| *Lensia subtiloides* (Lens & van Riemsdijk, 1908) | - | - | 0.01 ± 0.08 | 0.64 - 0.64 | 1.11 | 26.92 - 26.92 | 36.28 - 36.28 |
| Athorybia larvae | - | - | 0.05 ± 0.4 | 3.35 - 3.35 | 1.11 | 29.69 - 29.69 | 34.4 - 34.4 |
| **Anthozoa** | | | | | | | |
| Cerinula | - | - | 0.54 ± 2.7 | 0.66 - 20.18 | 5.56 | 26.21 - 26.5 | 36.3 - 36.33 |

**Figure 2.** Geographic distribution of number of species and total abundance of hydromedusae and siphonophores found in the epi- and hiponeuston layers at October 2012.



*Liriope tetraphylla* was the main responsible for hydromedusae abundance pattern over the continental shelf, where the species was quite more abundant outside the ARP, particularly at stations were cyclonic and anti-cyclonic eddies were present, reaching 810.1 ind. 100 m$^{-3}$ at station 6 (Fig. 3a). In the open ocean *L. tetraphylla* was widespread over the area, however higher abundances were observed in the retroflection region, where the species peaked in station 10 (855.9 ind. 100 m$^{-3}$; Fig. 3a). Otherwise, *Cytaeis* sp.3, was absent over the continental shelf. In the open ocean the species was scattered distributed through the area, however its abundance was quite higher in stations under influence of the ARP were it reached 344.9 ind. 100 m$^{-3}$ (Fig 3b). *C. octonaria* occurred in high abundance exclusively at station 10 where it reached 776.1 ind. 100 m$^{-3}$, only occasional catches of the species occurred in other stations (Fig. 3c).

**Figure 3.** Geographic distribution and abundance of representative cnidarian species found in the epi- and hiponeuston layers at October 2012.

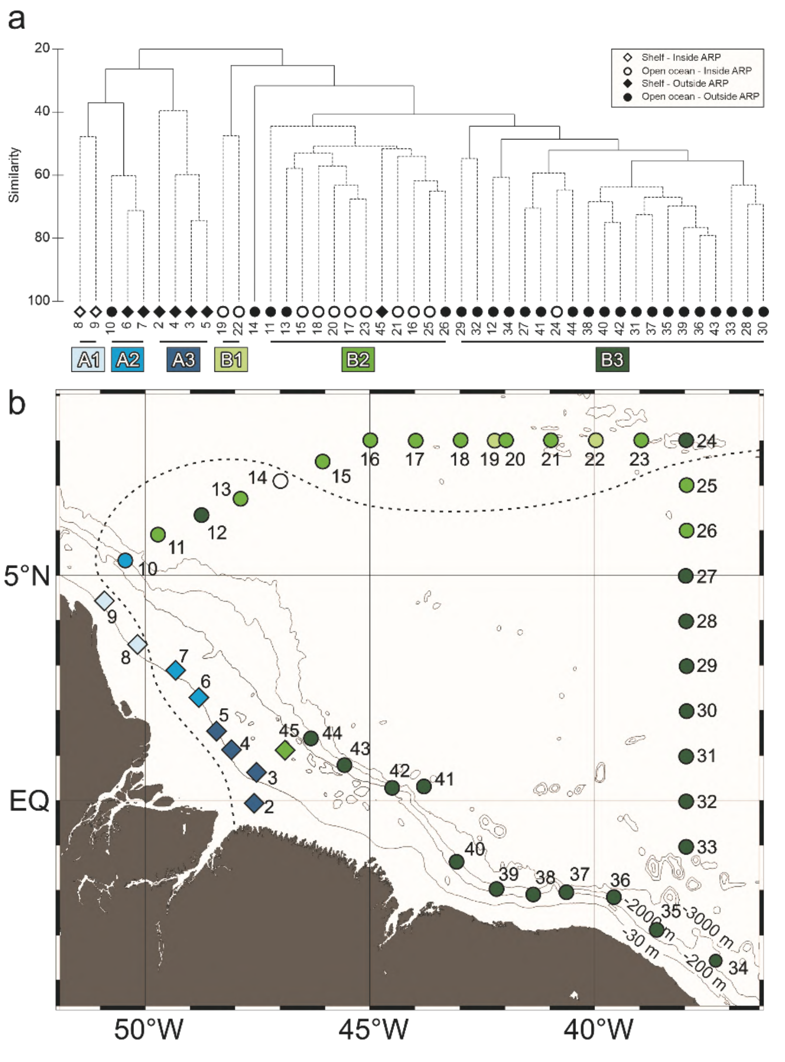


Number of siphonophore species was generally high all over the oceanic province (Fig. 2c), averaging 6.8 ± 3 species per sample. Over the continental shelf, stations under influence of the ARP and station 45, near the shelf break, presented slight higher siphonophore species (Fig. 2c). Siphonophere total abundance was high throughout the oceanic province as well (Fig. 2d). Over the continental shelf no clear pattern was observed, with stations inside and outside the ARP presenting high abundances (Fig. 2d). Among representative siphonophores, *C. appendiculata*, *D. bojani*, *A. eschscholtzii* and *Sulculeolaria chuni* were virtually absent over the continental shelf while *D. dispar* and *B. basensis* were present in stations 8 and 9, under influence of the ARP and 6 and 7, outside its influence (Fig 3d-i). In the open ocean the six species were widespread over the area with no clear pattern between stations inside and outside the influence of the ARP (Fig 3d-i).

*Community structure*

The cluster analysis depicted two main groups (A and B) with less than 30 % similarity between each other (Fig. 4a). Group A was composed by stations over the continental shelf and group B by oceanic stations. Exceptions were two stations located near the shelf break; station 10 is an oceanic station placed in group A and station 45 a neritic station placed in group B (Fig. 4). The SIMPROF analysis indicated statistical significance for several subgroups in both main groups (Fig. 4 a). For practical purpose, the five small subgroups in the right branch of groups B were considered a single subgroup (B3).

**Figure 4.** (a) Cluster analysis dendogram indicating two main groups and subgroups of stations with similar neustonic cnidarian communities in the Western Equatorial Atlantic Ocean. (b) Geographic distribution of cluster groups.



Subgroup A1 was formed by the stations over the continental shelf under influence of the ARP (Fig. 4). With 45.2% similarity, the group was represented by the siphonophores *Enneagonun hyalinum*, *D. dispar*, *Nanomia bijuga*, *Muggiaea kochii* and the hydromedusae *L. tetraphylla* (table 2). Group A2 (61.4% similarity), was represented by stations 6, 7 and 10 were *L. tetrephylla* occurred in high abundance. *D. dispar* also was representative in the group (Fig. 4, table 2). Group A3 (25.1% similarity) included the remaining station over the continental shelf (Fig. 4), where *L. tetraphylla* occurred almost alone (table 2), and only occasional catches of other species occurred.

In the open ocean, subgroup B1 (41.3% similarity) was represented by two stations under influence of the ARP where *Porpita porpita* occurred in high abundance (Fig. 4, table 2). Subgroup B2 (50% similarity) included remaining stations under influence of the ARP (except for station 24), some stations near the plume borders and station 45, over the continental shelf (Fig. 4). These stations presented higher abundances of *D. bojani*, *L. tetraphylla*, *D. dispar* and *Cytaeis* sp.3 than the remaining oceanic stations (included in B3). Other species representative in the group were *C. appendiculata*, *A. eschscholtzii* and *S. chuni* (table 2). Subgroup B3 (51.4% similarity) was mainly represented by oceanic stations outside the ARP with higher abundances of *C. appendiculata*, *B. bassensis*, *A. eschscholtzii* and *Abylopsis tetragona* (Fig. 4, table 2).

**Table 2.** Results of SIMPER analysis, showing the relative contribution of neustonic cnidarian species in the formation of the groups defined in the Cluster analysis.

| Species | A1 | A2 | A3 | B1 | B2 | B3 |
|---|---|---|---|---|---|---|
| *Abylopsis eschscholtzii* | | | | | 7.59 | 16.36 |
| *Abylopsis tetragona* | | | | | | 9.6 |
| *Agalma okeni* | | | | | 3.48 | 3.77 |
| *Aglaura hemistoma* | | | | | 2.05 | |
| *Bassia bassensis* | | | | | | 19.81 |
| *Chelophyes appendiculata* | | | | | 13.39 | 21.7 |
| *Cytaeis* sp.1 | | | | | 8.39 | |
| *Diphyes bojani* | | | | | 20.01 | 9.11 |
| *Diphyes dispar* | 26.12 | 29.46 | | | 9.1 | |
| *Enneagonum hyalinum* | 33.44 | | | | | |
| *Eudoxoides mitra* | | | | | 1.78 | |
| *Liriope tetraphylla* | 10.47 | 64.95 | 100 | | 14.98 | |
| *Muggiaea kochii* | 10.47 | | | | | |
| *Nanomia bijuga* | 19.48 | | | | 3.63 | |
| *Porpita porpita* | | | | 100 | 2.66 | 3.95 |
| *Sulculeolaria chuni* | | | | | 4.35 | 3.93 |

*Responses to mesoscale processes and environmental gradient*

The four canonical axes of the RDA explained 32.6% of species variance (Table 3). Monte Carlo test showed that the first (F-ratio = 9.2, P-value = 0.002) and all four canonical axes together (F-ratio = 3.183, P-value = 0.002) were significant. Bottom depth was negatively related to axis 1 and positively related to axis 2. Bottom depth was negatively related to both axes. Salinity and NBC were negatively related to axis 2. Temperature was positively related to both axes. Fluorescence was positively related to axis 1 and negatively related to axis 2. NECC was positively related to axis 1.

*Abylopsis eschscholtzii*, *Agalma okeni*, *C. appendiculata*, *Cytaeis* sp.3, *D. bojani*, *S. chuni* and *P. porpita* were related to bottom depth. *Cytaeis* sp.3 and *P. porpita* were also related to NECC. *A. tetragona*, *B. bassensis* and *Eudoxoides spiralis* were slightly related to salinity.

*Diphyes dispar* and *N. bijuga* were negatively related to salinity and positively with temperature with little relation to bottom depth. *L tetraplyla* was slightly related to temperature and florescence and *A. hemistoma* was neither related to salinity or bottom depth.

**Figure 5.** Redundancy analysis relating representative neustonic cnidarian species to environmental gradients and mesoscale processes in the Western Equatorial Atlantic Ocean. NBC = North Brazilian Current; NECC=North Equatorial Counter Current.

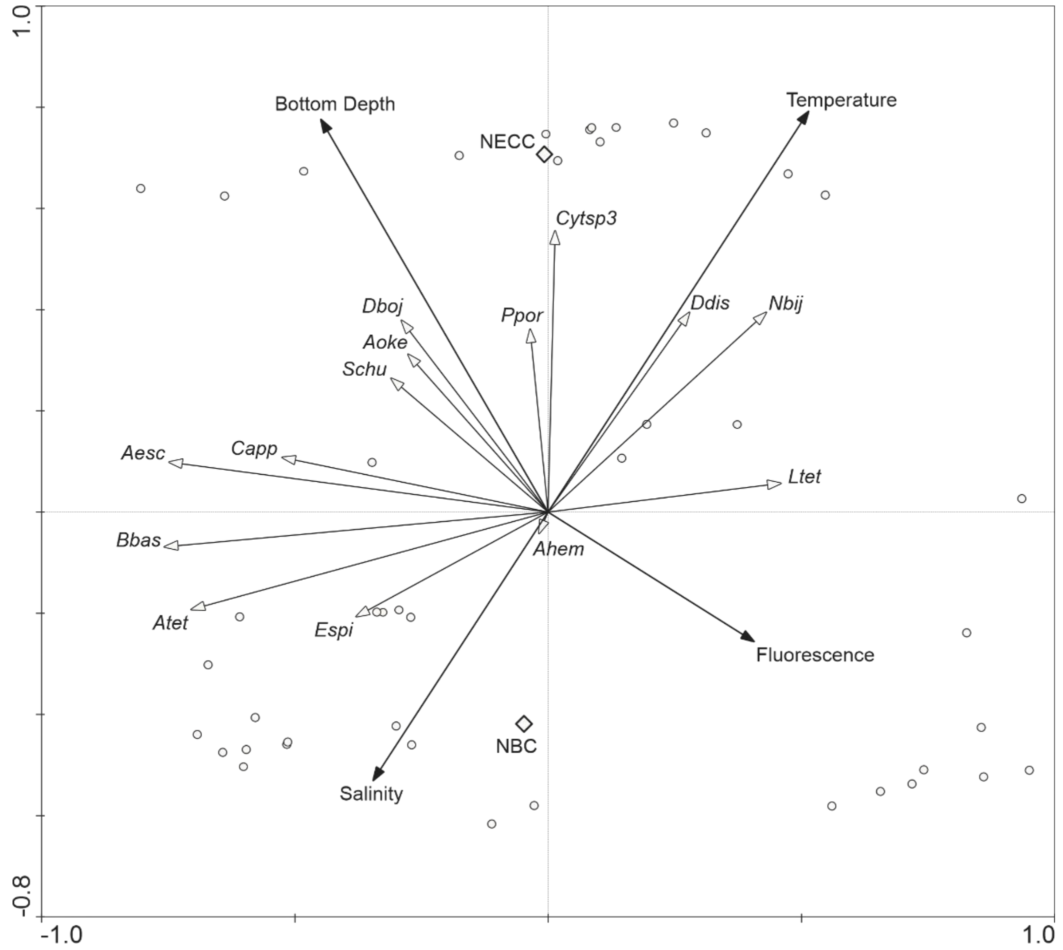


**Table 3.** Summary of the Redundancy Analysis performed between neustonic cnidarian species to environmental gradients and mesoscale processes in the Equatorial Atlantic Ocean.

| | **Axis 1** | **Axis 2** | **Axis 3** | **Axis 4** |
|---|---|---|---|---|
| Eigenvalues | 0.199 | 0.087 | 0.024 | 0.016 |
| Species-environment correlations | 0.851 | 0.668 | 0.663 | 0.386 |
| **Cumulative variance (%):** | | | | |
| Of species data | 19.9 | 28.7 | 31 | 32.7 |
| Of species-environment relation | 58.5 | 84.2 | 91.2 | 96 |
| **Correlations of explanatory variables:** | | | | |
| Bottom depth | -0.4482 | 0.7753 | 0.4079 | -0.1676 |
| Surface temperature | 0.5137 | 0.7917 | 0.0211 | -0.2514 |
| Surface salinity | -0.3457 | -0.5303 | 0.2381 | 0.4036 |
| Fluorescence | 0.4066 | -0.2563 | -0.2494 | -0.0206 |
| NBC | -0.1054 | -0.922 | -0.124 | -0.3258 |
| NECC | -0.0096 | 0.9265 | -0.3458 | -0.0861 |

## Discussion

This was the first study characterizing the distribution and abundance of pelagic cnidarians in the neustonic layer and its relation to physical environment. The neustonic layer of the continental shelf and adjacent oceanic waters of northern Brazil in the equatorial Atlantic presented an unexpected diverse cnidarian community comprising 55 taxa. Although it may seem low when compared to the 91 taxa observed in epipelagic plankton samples from the same area (Section 4.2), it is still remarkable since the neuston is a very thin portion of the water column, representing less than 0.2% of the depth sampled in the planktonic hauls. In addition, many species from the neuston were absent in deeper layers. Some of them are characteristic from the environment and were already expected, such as the floating species *P. porpita*, *Physalia physalis* and *Velella velella* (Iosilevskii & Weihs 2009, Purcell et al. 2015). Others were rare such as *Stauridiosarsia producta* and *Pegantha laevis* and its presence in the neuston may represent occasional catches. Differently, *Cytaeis* sp.3 occurred in high abundance exclusively in the neuston. This species do not have any apparent morphological adaptation for floating, such as pneumatophores or oil sacs, and its presence in the layer may be due to active behavior.

Despite the differences in species composition, the general pattern in the structure of cnidarian community was similar in epipelagic plankton (Section 4.2) and neuston. In both, the coast-ocean gradient was the main force shaping species distribution. A common pattern in marine communities, since beyond the two provinces presenting significant differences in water conditions and food web structure and energy availability, the shallow seabed in the continental shelf provides suitable habitat for polyps of meroplanktonic medusae (Pagès et al. 1991, Pagès & Gili 1992, Nogueira Júnior et al. 2014). However, this pattern was less pronounced in other western boundary systems with narrower continental shelves, where strong currents transported oceanic water and it associated species over the continental shelf, as observed in the northeast coast of Brazil and east coast of Africa (Thibault-Botha et al. 2004, Tosetto et al. 2021). The larger continental shelf of Northern Brazil and seasonal dynamics of the ARP may prevent these oceanic species to settle down in this neritic environment.

The two stations under influence of the ARP over the continental shelf (subgroup A1), were quite distinct both in epipelagic plankton and neuston. *Enneagonun hyalinun*, *D. dispar*, *N. bijuga*, *L. tetraphylla* and *M. kochii* were relevant clustering the group in both strata. Although some of these species were present in the oceanic environment, they are frequently found in coastal and/or estuarine waters ( Morales-Ramírez and Nowaczyk 2006; Sanvicente-Añorve et al. 2007; Touzri et al. 2012; Nogueira Júnior et al. 2014, 2018; Nagata et al. 2014). The low salinity caused by the APR may have granted them to reach the middle continental shelf since they were almost absent in the neritic stations outside the influence of the plume. Otherwise, *Persa incolorata*, which was one of the dominant species in the stations in epipelagic plankton samples (Section 4.2), was almost absent in neuston. Although it may indicate the preference of this species for deeper layers, selectivity of mesh used here cannot be ignored, since these are very small organisms known to be underestimated in larger meshes (Appendix 4; Tosetto et al. 2019). *C. octonaria*, also abundant and almost exclusive in the neritic ARP in these plankton samples (Section 4.2), in neuston was quite more abundant in the neighboring station 10, which may be caused by current advection and/or other unevaluated processes.

The stations over the continental shelf outside influence of the ARP (except station 45) were dominated by *L. tetraphylla* almost alone both in plankton (Section 4.2) and neuston and distinction among subgroups B2 and B3 were based in differences in its abundance and in the presence of *D. dispar* in B2. *L. tetraphylla* is typically abundant in neritic environments of the tropical and subtropical western side of Atlantic Ocean, however, unlike our results, the species typically/usually co-occurr with other dominant species (e.g. Vannucci 1957, Persad et al. 2003, Nogueira Júnior et al. 2014, 2015, Nagata et al. 2014, Martell-Hernández et al. 2014, Gutiérrez-Aguirre et al. 2015, Tosetto et al. 2021). The neritic cnidarian community of the East China Sea, other western boundary system with large continental shelf presented more dominant species co-occurring as well. The reasons behind the solitary dominance of *L. tetraphyla* in eastern equatorial Atlantic may be related to the presence of eddies and its high competitive capacity (Suarez-Morales et al. 2002, Flores-Coto et al. 2016; Section 4.2), however, an intensive survey, considering fine temporal scale and vertical distribution, should be performed to confirm it.

As in epipelagic plankton samples, holoplanktonic siphonophores dominated the neustonic layer in the open ocean waters (group B) in number of species and abundance. An expected result since the non-dependence on rigid substrates for polyp settlement allows these organisms to survive and disperse offshore (Mapstone 2014). Beyond the siphonophores, the hydromedusae *L. tetraphylla*, *A. hemistoma*, *P. porpita* and *Cytaeis* sp.3 were representative in the open ocean as well. The two former species have no polypoid stage in their life cycle and *P. porpita* is a pelagic hydroid stage, thus these organisms are free to disperse offshore. However, anthoathecate hydrozoans such as *Cytaeis* sp.3 generally are meroplanktonic and its polyps require rigid substrates (Bouillon et al. 2006). Some factors may help explaining its distribution and high abundance in open waters: (i) The species was highly related to NECC, flowing eastward, thus this strong current may be carrying the medusae from shallow waters to the west, outside the range of our study area, such as Caribbean Sea, where *Cytaeis* spp. are common (Larson 1982, Suarez-Morales et al. 1999). (ii) Most individuals collected presented medusae budding directly in their gonads, what is common in the genus (Bouillon 1999), this kind of asexual reproduction unbinds the species from the benthic stage and its demand for shallow substrates. (iii) the North Brazilian ridge is present in the area (Hayes & Ewing 1970) thus, many seamounts could supply the dependence on shallow substrates for hydroids.

In the open ocean, similarly to epipelagic plankton (Section 4.2), the ARP (surface salinity as low as 32.5) did not caused significant changes in the species composition of neustonic cnidarian community and main divergences occurred in species abundance. However, unlike epipelagic plankton, these differences were less prominent, more variable and did not follow the 35 isohaline that characterize the ARP (Fig. 4; Silva et al. 2005). Regardless, *D. bojani*, *D. dispar*, *P. porpita* and *Cytaeis* sp.3 were more abundant in oceanic stations under influence of the ARP (subgroups B1 and B2). *D. bojani* and *D. dispar* were also the dominant siphonophores in epipelagic plankton of oceanic waters under influence of the ARP (Section 4.2). These species have high niche plasticity, being present in neritic and oceanic habitats in a wide salinity range all over the world (Sanvicente-Añorve et al. 2009, Nogueira Júnior et al. 2014, Grossmann et al. 2015, Uribe-Palomino et al. 2019, Tosetto et al. 2021) and succeeded in the low salinity and nutrient rich environment of the ARP. *Eudoxoides mitra* and *Sminthea eurygaster* were dominant in the epipelagic plankton of oceanic waters under influence of the ARP (Section 4.2), but were almost absent in the neuston. These species are considerably larger than *P. incolarata*, and therefore mesh selectivity is unlikely to have significantly affected the current estimated densities. Thus, we can infer that they preferentially inhabit deeper layers. Other siphonophore species typically present in offshore waters, such as *C. appendiculata*, *B. bassensis* and *A. escscholtzii* (Pagès & Gili 1991, Lo & Biggs 1996, Lo et al. 2012, Lüskow et al. 2019) did not presented remarkable changes in abundance inside and outside the ARP, being widespread all over the oceanic waters of the study area indicating these species tolerate low salinity at least to some extent. Otherwise*, A. tetragona* and *E. spiralis* were more abundant outside the influence of the ARP indicating their preference for high salinity waters in the area.

Although general patterns in the neustonic and epipelagic planktonic cnidarian community were similar, the differences observed are noteworthy. While the cluster analysis on epipelagic plankton data revealed a robust structure almost following the isohaline characterizing the ARP and the inshore-offshore gradient (Section 4.2), in the neuston, oceanic stations located outside the influence of the ARP were included in subgroup B2. Remaining stations outside the ARP, instead forming a single group, were subdivided in several valid subgroups (which we grouped together in subgroup B3). This arrangement reflected the high variability in species abundance observed in the layer. Several factors may be behind this variability. First, the neuston is sensitive to many oceanographic and atmospheric processes occurring in smaller scales than the ones evaluate in this study. Turbulence, submesocale eddies, waves, wind and variations in solar radiation caused by cloud cover and dial cycle may significantly contribute to plankton patchiness in sea surface (Hardy 1982, Zaitsev 2005). In addition, the volume of seawater filtered in neuston hauls is quite lower than in large bongo nets used to sample epipelagic plankton, reducing chances of capturing patches of organisms and increasing variability.

In conclusion, we observed a similar pattern between neustonic and epipelagic planktonic cnidarian community in the Western Equatorial Atlantic Ocean, where the inshore-offshore gradient and the dynamics of the ARP are the main mesoscale drivers of species distribution and abundance. However, the neustonic layer presented particularities, and the community influenced by the ARP did not follow exactly its limits reflecting the variability in species abundance, which is at least in part due to the oceanographic and climatic instability occurring in the interface between ocean and atmosphere. We also observed divergences in species composition, with the presence of not only floating species such as *P. physalis*, *P. porpita* and *V. velella* but also *Cytaeis* sp.3 in the neustonic community.

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# 7 CONCLUSÃO GERAL

O oceano Atlântico equatorial sob influência da pluma do rio Amazonas apresentou uma alta biodiversidade na comunidade de cnidários pelágicos representada por 93 espécies. A alta biodiversidade observada é explicada pela grande extensão da área de estudo e variedade de ecossistemas e habitats ocorrendo simultaneamente, incluindo diferentes estratos da coluna d’água, águas estuarinas, águas costeiras, águas da plataforma continental com um complexo sistema recifal, águas oceânicas com uma grande amplitude salina causada pela pluma do rio Amazonas, vórtices ciclônicos e anticiclônicos e correntes fluindo em direções opostas. Entre as 93 espécies foram encontradas duas novas espécies de hidromedusas da família Eirenidae, *Eutima marajoara* e *Helgicirrha angelicae*, as primeiras ocorrências para o Brasil das espécies *Cirrholovenia polynema*, *Pegantha laevis* e *Forskalia tholoides*, além de várias outras primeiras ocorrências em nível regional e local.

A pluma do rio Amazonas se mostrou o principal processo oceanográfico em mesoescala moldando a distribuição da comunidade de cnidários planctônicos e neustônicos tanto na plataforma continental, onde as diferenças mais marcadas foram observadas, quanto no oceano aberto. Na plataforma continental, espécies como *Persa incolorata*, *Enneagonun hyalinun*, *Muggiaea kochii* e *Diphyes dispar*, foram restritas, ou ocorreram em abundâncias bem mais altas na região sob influência da pluma. Já no oceano aberto as diferenças foram relacionadas a abundância da espécies: enquanto as áreas fora da influência da pluma foram marcadas por abundancias maiores das espécies *Chelophyes appendiculata*, *Bassia bassensis*, *Eudoxoides spiralis* e *Abylopsis tetragona*, a área sob influência da pluma apresentou maior abundância das espécies *Diphyes bojani*, *D. dispar* e *Cytaeis* sp.1. Embora os resultados no plâncton epipelágico e neustôn tenham sido semelhantes, diferenças também foram observadas tanto na composição taxonômica, com ambos os ambientes apresentando espécies exclusivas quanto nos padrões de distribuição espacial na região oceânica, que foram menos marcados na comunidade neustônica.

Como esperado, o oceano Atlântico equatorial sob influência da pluma do rio Amazonas se mostrou um sistema complexo, com muitos processos físicos e biogeoquímicos ocorrendo simultaneamente, e essa complexidade refletiu na estrutura da comunidade de cnidários pelágicos. Esse estudo deu os primeiros passos buscando o entendimento das interações e funcionamento dos ecossistemas na área, adiante, novas pesquisas, considerando outras escalas espaciais e temporais, bem como outros estrados da coluna d’água e outras perspectivas devem ser realizadas para uma compreensão adequada desse sistema complexo.

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# APÊNDICE A – NEW RECORDS OF *PEGANTHA* SPP. (HYDROZOA: NARCOMEDUSAE) OFF NORTHERN BRAZIL

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# New records of *Pegantha* spp. (Hydrozoa: Narcomedusae) off Northern Brazil

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**Abstract.** Specimens of *Pegantha laevis* H.B. Bigelow, 1909 and *Pegantha triloba* Haeckel, 1879 were found in oceanic waters off the northern Brazilian coast. The former species is clearly distinct due to the thickness and shape of peripheral channels, while the latter is recognized mainly due to the exumbrellar furrows and long otoporpae. This study represents the first actual record of *P. laevis* inside the Brazilian Economic Exclusive zone, since previous reports were far away from the coast, and clarifies the presence of *P. triloba* off Brazil.

**Key-Words.** Jellyfish; Cnidaria; Hydrozoa; Taxonomy; Biodiversity; South Atlantic.

## INTRODUCTION

Holoplanktonic hydromedusae of the family Solmarisidae Haeckel, 1879 is distinguished from other Narcomedusae mainly by the absence of manubrial pouches, thus the periphery of manubrium is circular and unbroken at the same level as the tentacles rise. Two genera are recognized in the family: i) *Pegantha* Haeckel, 1879, with a peripheral canal system and otoporpae, and gonads forming lobes on the margin of manubrium wall; and ii) *Solmaris* Haeckel, 1879, without peripheral canal system and otoporpae and with simple annular gonads (Bouillon & Boero, 2000; Bouillon, *et al.* 2004, 2006).

Currently there are five valid species of *Pegantha,* in addition to many doubtful names regarded as *"taxon inquirendum"* or possible synonymies (Schuchert, 2015). All valid species are widely distributed, mostly in epipelagic oceanic waters (Kramp, 1957, 1961; Bouillon, 1999). At southwestern Atlantic all the five species have been found (Bouillon, 1999), among which *Pegantha laevis* H.B. Bigelow, 1909 was recorded off Argentina and in oceanic waters > 1,300 km offshore the Brazilian coast (Kramp, 1957; Genzano *et al.,* 2008). *Pegantha triloba* Haeckel, 1879 was recorded at Fernando de Noronha archipelago (Vanhöffen, 1913) and offshore North of Brazil (Ranson, 1949; Kramp, 1959b), but its occurrence has been overlooked by Oliveira *et al.* (2016) in the census of Cnidaria from South America, and thus its distribution became uncertain. Hydromedusae are important predators in marine zooplankton and information on its distribution is essential for understanding species diversity, biogeographic patterns and marine ecosystem functioning. In this study, we report the occurrence of both species on North Brazilian shelf and offshore waters, extending northwards the known distribution of *P. laevis* in the western Atlantic and clarifying the presence of *P. triloba* in Brazilian waters.

## MATERIALS AND METHODS

One specimen of *Pegantha laevis* and eight specimens of *Pegantha triloba* were found in superficial plankton samples collected in oceanic waters off the northern coast of Brazil (Table 1) with a David-Hempel catamaran (Hydro-Bios, Kiel, Germany) equipped with two superposed nets, each with a rectangular mouth and 500 µm mesh size. Sub-superficial temperature and salinity was measured with a Seabird SBE 25 Sealogger CTD profiler. Specimens were depos-

**Table 1.** *Pegantha laevis* and *Pegantha triloba* occurrences off northern Brazil. T = temperature; S = salinity.

| | Location | Number of specimens | T(°C) | S | Bottom depth (m) |
|---|---|---|---|---|---|
| *P. laevis* | 0.0013°N, 38.0073°W | 1 | 27.9 | 36.2 | 4,426 |
| *P. triloba* | 3.9963°N, 38.0042°W | 7 | 28.1 | 36 | 4,208 |
| | 5.9126°N, 49.7035°W | 1 | 27.6 | 36.2 | 3,592 |

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ited in the *Museu de Oceanografia Prof. Petrônio Alves Coelho* from *Universidade Federal de Pernambuco*. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

## RESULTS AND DISCUSSION

The single *Pegantha laevis* medusa found was 9 mm in bell diameter. Umbrella flattened with completely smooth surface (Fig. 1A). The specimen was damaged

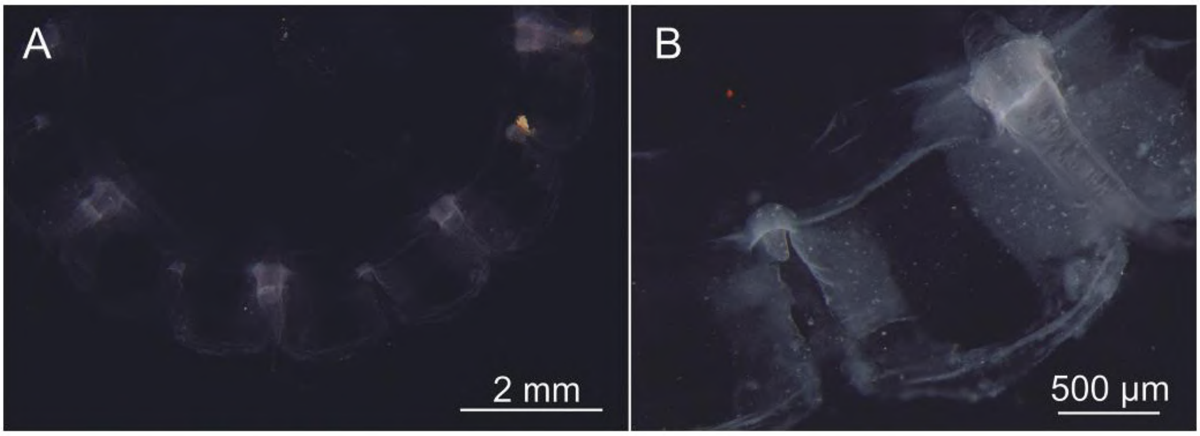

**Figure 1.** *Pegantha laevis* medusa from North Brazil. (A) Aboral view. (B) Detail of marginal lappet and peripheral channel.

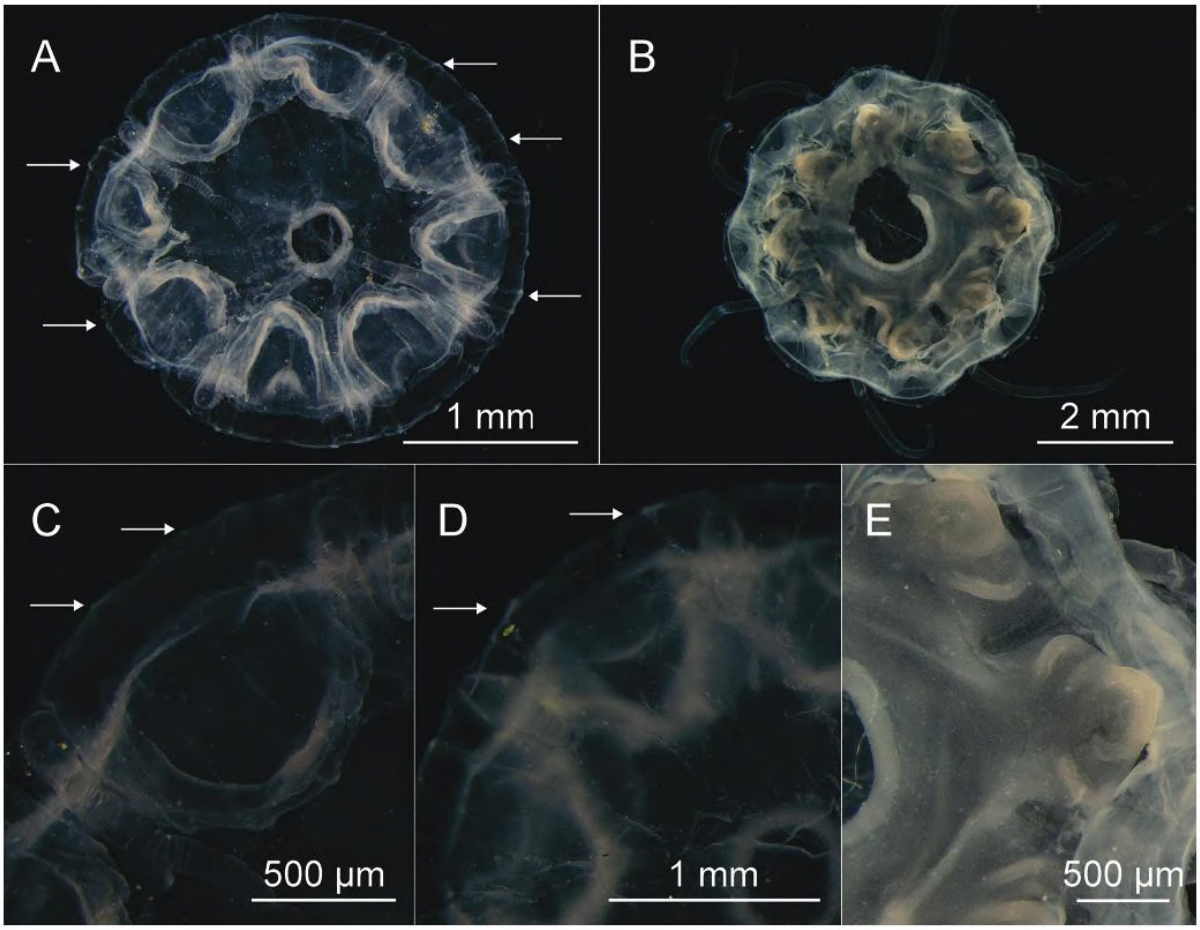

**Figure 2.** *Pegantha triloba* medusae from North Brazil. (A and B) Oral view. (C) Detail of marginal lappet and otoporpae. (D) Aboral view showing furrows and ridges on exumbrella. (E) Detail of tri-lobed gonads. Arrows indicate some otoporpae.

and *ca.* 1/5 of the margin was missing, and about 16 square marginal lappets were estimated. Peripheral canals quadrate, very broad mainly in the sides which represent 1/3-1/4 of the total lappet width and do not tapering (Fig. 1B). Only remnants of short otoporpae present, with nearly the same length of the peripheral canal width. Gonads absent.

A total of eight individuals of *Pegantha triloba* were analyzed, ranging from 1.5 to 4.6 mm in bell diameter (Fig. 2A). Seven medusae presented eight marginal lappets and one medusa had nine lappets. Peripheral canals thin, more or less triangular with rounded or pointed margins (Fig. 2B). Typically, three long otoporpae in the smaller medusae and five in the two larger ones, reaching almost the middle of the central disk and tapering upwards; exumbrella with furrows from the base of the tentacles to almost the apex, leaving the central disk smooth (Figs. 2A, B). The largest specimen presented gonads with three lobes (Figs. 2B, D), except one of the gonads with a single lobe.

Species of the genus *Pegantha* are mostly characterized by the width and/or shape of the peripheral canals, the size of the otoporpae and the presence/absence of exumbrellar furrows (Kramp, 1957, 1959b, 1961, 1965, 1968; Pagès *et al.,* 1992; Bouillon, 1999; Bouillon *et al.,* 2004). The number of gonadal lobes has also been used by earlier researchers (*e.g.,* Haeckel 1879), but this has been long shown to be highly variable and not accurate to distinguish species (*e.g.,* Bigelow, 1909; Kramp, 1961).

*Pegantha triloba* is easily distinguished from the remaining species by the exumbrella with furrows. This character, along with the long otoporpae and relatively thin peripheral canal system (Fig. 2B), confirm the present identification (*e.g.,* Bigelow, 1909; Kramp, 1957, 1959b, 1961; Bouillon, 1999). Bigelow (1909) described the otoporpae reaching the level of the base of the tentacles, however latter authors indicate the otoporpae may be considerably longer than the lappet, reaching the apex of the exumbrella (Kramp, 1957) likewise the present material (Fig. 2D). The observed medusae have 8-9 marginal lappets and tentacles, less than the 12-16 typically reported for this species. This may be attributed to the small size of our specimens (Xu & Wu, 1998), in spite the fact that one of them already had gonads. Although medusae as small as 5-7 mm have 12-14 lappets (Kramp, 1957), our specimens are smaller (1.5 to 4.6 mm) and in accordance with the medusa reported by Bigelow (1909) (with 2.5 mm in diameter and 7 lappets). The smaller number of otoporpae (3-5 per lappet) observed in the present specimens is also probably related to the small size of the medusae sampled here (see Bigelow, 1909: 88).

Among *Pegantha* species with smooth exumbrella, *P. laevis* differs from *Pegantha clara* R.P. Bigelow, 1909 and *Pegantha rubiginosa* (Kölliker, 1853) in the thickness of the peripheral canals. *Pegantha martagon* Haeckel, 1879 has also thick peripheral canals, however those from *P. laevis* are even thicker, being almost as wide as the space between them (Kramp, 1957; Fig. 1B). Also, the peripheral canals of *P. martagon* taper towards the margin (Bigelow, 1909; Kramp, 1957, 1961), while the same is not true for *P. laevis* (Fig. 1B). These differences in the

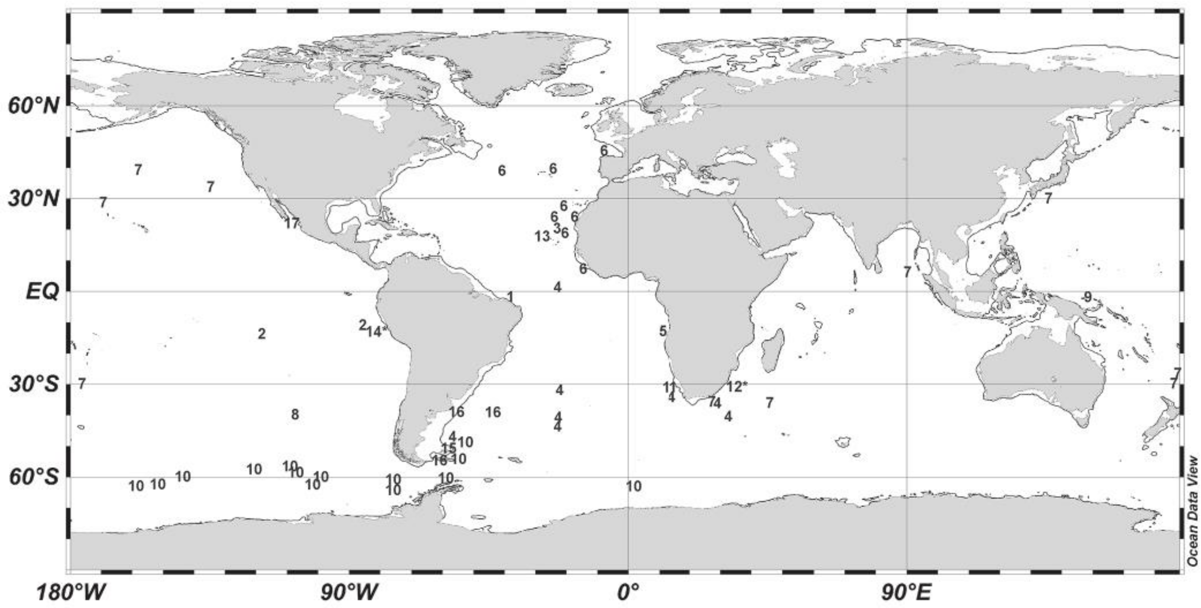

**Figure 3.** Global distribution of the narcomedusa *Pegantha laevis* based on this study and literature records. The dashed line shows the 250 m isobath, roughly corresponding to the shelf break (generated using Ocean Data View software; Schlitzer, 2007). Data Source: 1 = this study; 2 = Bigelow, 1909; 3 = Kramp, 1955; 4 = Kramp, 1957; 5 = Kramp, 1959a; 6 = Kramp, 1959b; 7 = Kramp, 1965; 8 = Fagetti, 1973; 9 = Bouillon *et al.,* 1986; Bouillon, 1978; 10 = Navas-Pereira & Vannucci, 1990; 11 = Pagès *et al.,* 1992; 12 = Buecher *et al.,* 2005; 13 = León *et al.,* 2005; 14 = Ayón *et al.,* 2008; 15 = Genzano *et al.,* 2008; 16 = Rodriguez, 2012; 17 = Gasca & Browne, 2017.

peripheral canal system are robust and may help even the identification of badly preserved specimens (Kramp, 1957). In addition, *P. martagon* has a vaulted umbrella, while in *P. laevis* the umbrella is flatter and lenticular (Bouillon, 1999).

Although *P. laevis* is not a common species (Kramp, 1959b, 1968), it is widely distributed in tropical, temperate and even Antarctic (temperatures down to 0.2°C; Navas-Pereira & Vannucci, 1990) regions of the three large oceans, but mostly in the Atlantic and Pacific (Fig. 3). Its known distribution is somewhat skewed southwards, with current records not surpassing 50°N, but reaching nearly 70°S (Fig. 3). In South Atlantic waters, the occurrence of this species was recorded off the African and Argentinean coast and in the center of the Atlantic at tropical, temperate and polar latitudes (Fig. 3). Recently, Oliveira *et al.* (2016) considered this medusa as integrating the Brazilian fauna based on Kramp's (1957) record at 31.27°S, 29.94°W (number 4 in Fig. 3). However, this location is > 1,300 km offshore, in the center of Atlantic Ocean (Fig. 3), and far outside the economic exclusive zone and Brazilian waters. Thus, the present study represents the first actual record of this species off Brazil.

*Pegantha triloba* is widely distributed in oceanic waters of the Atlantic, Indian and Pacific Oceans, mainly in warm latitudes between *ca.* 30°N and 30°S (Fig. 4). Outside this latitudinal range, *P. triloba* has been recorded at northwest of South Georgia (48°S), in the Mediterranean and in the Southern Ocean, a single record on each locality (respectively numbers 5, 4 and 35 in Fig. 4). The two latter records may be misidentifications (Kramp, 1959b, 1965). In the South Atlantic, the species was recorded off the African coast and in several oceanic localities between Africa and South America (Fig. 4). Although there were some previous records of this species on Brazilian waters (Ranson, 1949; Kramp, 1959b), these occurrences were overlooked in a recent review (Oliveira *et al.*, 2016), perhaps because they were reported only as "Atlantic" or "Equatorial Atlantic". Thus, this study highlights the presence of *P. triloba* in oceanic waters offshore northern Brazilian coast. While specimens collected in this study were in the subsurface, this species has extensive vertical distribution from surface to strata as deep as 5,000 m (Bigelow, 1909; Kramp, 1959b, 1965).

Holoplanktonic animals such as *Pegantha* species usually present a wide distribution in the oceans, being dispersed by large-scale processes such as global circulation (Boltovskoy *et al.*, 2003). Furthermore, many Narcomedusae early life stages are parasitic (Xu & Wu, 1998; Osborn, 2000), and movement and migration of their hosts can also contribute to the wide distribution of *P. laevis* and *P. triloba* (Figs. 3, 4).

The waters off the northern Brazilian coast are amongst the least studied regarding zooplankton in general (Lopes, 2007) and medusae in particular (Oliveira *et al.*, 2016), leaving a gap in the understanding of spe-

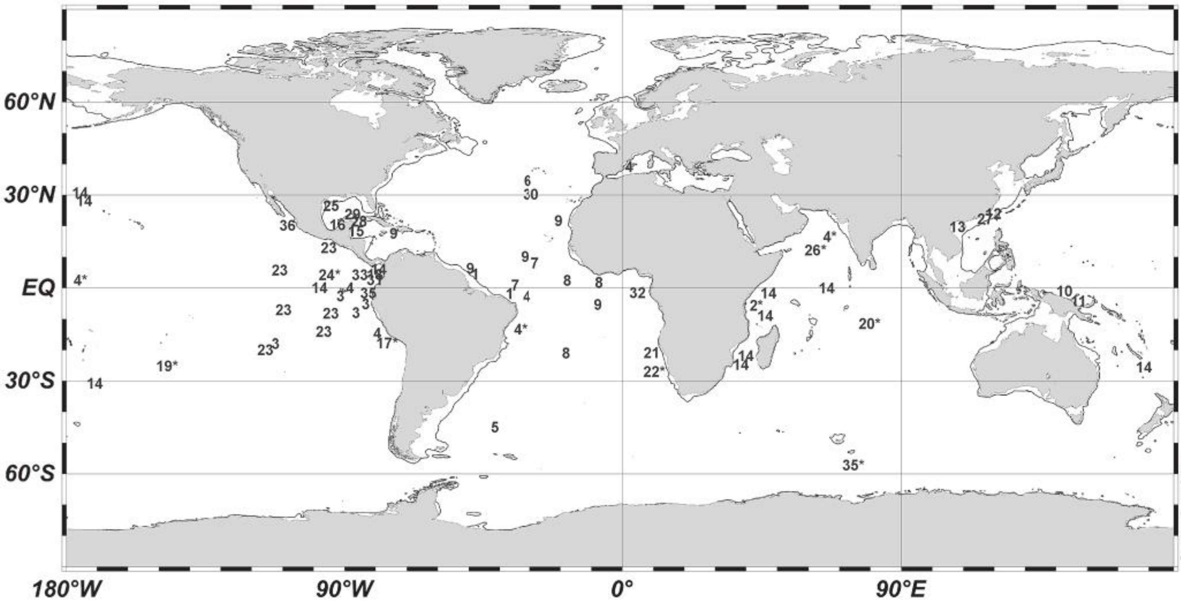

**Figure 4.** Global distribution of the narcomedusa *Pegantha triloba* based on this study and literature records. The dashed line shows the 250 m isobath, roughly corresponding to the shelf break (generated using Ocean Data View software; Schlitzer, 2007). Data Source: 1 = this study; 2 = Haeckel, 1879; 3 = Bigelow, 1909; 4 = Vanhöffen, 1913; 5 = Kramp, 1948a; 6 = Kramp, 1948b *apud* Kramp, 1961; 7 = Ranson, 1949; 8 = Kramp, 1957; 9 = Kramp, 1959b; 10 = Bouillon *et al.*, 1988; 11 = Bouillon *et al.*, 1986; 12 = Chang, 2008; 13 = Du *et al.*, 2012; 14 = Kramp, 1965; 15 = Larson, 1982; 16 = Loman-Ramos *et al.*, 2007; 17 = Ayón *et al.*, 2008; 18 = Baldrich & López, 2010; 19 = Navas-Pereira & Vannucci, 1990; 20 = Navas-Pereira & Vannucci, 1991; 21 = Pagès, 1992; 22 = Pagès *et al.*, 1992; 23 = Segura-Puertas, 1984; 24 = Segura-Puertas, 1991; 25 = Suárez-Morales *et al.*, 2002; 26 = Vannucci & Navas, 1973; 27 = Xu & Wu, 1998; 28 = Suárez-Morales *et al.*, 1999; 29 = Segura-Puertas, 1992; 30 = Bleeker & Van Der Spoel, 1988; 31 = Chaparro & Peralta, 2013; 32 = Repelin, 1965; 33 = Chaparro, 2007; 34 = Muñoz-Pozo, 2015; 35 = Vanhöffen, 1912 *apud* Kramp, 1961; 36 = Fernández-Álamo, 2002.

cies diversity and biogeographical patterns. Particularly considering the Amazon River plume as a potential barrier for marine organisms (*e.g.*, Rocha, 2003), and the potential high diversity of this understudied tropical and highly productive ecosystem. These aspects emphasize the need of comprehensive surveys in the area and faunistic studies such as the present one.

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# APÊNDICE B – FIRST RECORD OF *CIRRHOLOVENIA POLYNEMA* (HYDROZOA: LEPTOTHECATA) IN THE WESTERN ATLANTIC OCEAN

Periódico: Ocean and Coastal Research

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OCEAN AND COASTAL RESEARCH

# First record of *Cirrholovenia polynema* (Hydrozoa: Leptothecata) in the Western Atlantic Ocean

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Meroplanktonic hydromedusae of the family Cirrholoveniidae Bouillon, 1984 are distinguished from other Leptothecata medusae mainly by the presence of four simple radial canals, marginal cirri, at least four closed statocysts and absence of a gastric peduncle (Bouillon 1999, Bouillon et al. 2006). The genus *Cirrholovenia* Kramp, 1959 is to date the sole representative of Cirrholoveniidae, presenting characteristics of the family (Bouillon and Boero 2000, Bouillon et al. 2006, Schuchert 2020).

*Cirrholovenia* was described with the species *Cirrholovenia polynema* Kramp, 1959 and *Cirrholovenia tetranema* Kramp, 1959 collected in the Indo-Pacific. The genus was first included in the family Lovenellidae Russell, 1953 (Kramp 1959) and later classified as a new family by Bouillon (1984). Two additional species were described in the genus, *Cirrholovenia reticulata* Xu & Huang, 2004 and *Cirrholovenia violacea* Gershwin, Zeidler & Davie, 2010, both in the Western Pacific Ocean (Xu and Huang 2004, Gershwin et al. 2010), resulting in four valid species to date (Schuchert 2020).

Hydromedusae are diversified, important predators in marine habitats; information on their distribution is essential for understanding species diversity, biogeographic patterns and marine ecosystem functioning (Tewksbury et al. 2014, Hays et al. 2018). During two cruises characterizing the zooplanktonic communities from the tropical and equatorial Western Atlantic Ocean (Bertrand 2015, Neumann-Leitão et al. 2018, Tosetto et al. 2019) specimens of *C. polynema* were observed for the first time on the Western side of the Atlantic Ocean. In the present study, we report these occurrences and provide a detailed review of the global distribution of the species along with some insights into the taxonomy of the group.

Specimens were obtained during the "Camadas Finas III" survey conducted in October, 2012, aboard the research vessel NHo. Cruzeiro do Sul - H38 (DHN/Brazilian Navy) off North Brazil and the "Acoustics along the Brazilian coast (ABRACOS 1)" survey conducted in October 2015, aboard the French R/V ANTEA off Northeast Brazil (Coordinates: 7.5°N, 46.0°W; 8.0°N, 42.0°W; 7.0°N, 38.0°W; 2.0°N, 38.0°W; 3.93°S, 32.52°W). Samples were collected in oblique hauls, using a bongo plankton net with 300 µm mesh and 0.6 m opening, from near bottom to surface over the continental shelf, and 200 m depth to surface in open waters. Material was fixed with 4% formaldehyde buffered with sodium tetraborate (0.5 g $L^{-1}$). Specimens were deposited in the *Museu de Invertebrados Paulo Young* from *Universidade Federal da Paraíba* (CIPY1121, CIPY 1124, CIPY 1125).

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The seven specimens sampled presented a lenticular umbrella ranging from 2.4 to 6 mm wide (Fig. 1 a; b), with thin mesoglea. The velum is broad. Manubrium were large with crenulated lips (Fig. 1 a; b). Only one of the specimens presented gonads, which were still developing along the middle of the four radial canals (Fig. 1 b). The two largest species presented 12 fully developed tentacles with heart-shaped bulbs and about two or three rudimentary bulbs between them (Fig. 1 a; b). Up to eight marginal cirri and one or two closed statocysts distributed between successive tentacles (Fig. 1 c).

The four radial canals, presence of closed statocysts and marginal cirri, and absence of a gastric peduncle assigned the specimens to the family Cirrholovenidae and genus *Cirrholovenia* (Bouillon et al. 2006). Among the four currently described species in the genus, *C. tetranema* differs from present specimens by always having four marginal tentacles and no rudimentary bulbs. Its umbrella typically higher than flatter and cylindrical gonads, occupying almost the whole length of the radial canals, also differ in shape and position from our specimens (Kramp 1959, Bouillon et al. 2004; Table 1). *C. reticulata* also was described with only four marginal tentacles. However, this species was described based on a single small specimen (0.8 mm) presenting rudimentary bulbs and reticular papillae on the exumbrella (Xu and Huang 2004; Table 1), typically present in recently released medusae (Bouillon et al. 2006). Moreover, considering that only a single small medusa of *C. reticulata* has been described, it is not known whether the rudimentary bulbs will develop tentacles or remain rudimentary as the medusa grows. Thus, *C. reticulata* may be a juvenile of another species, a hypothesis that should be tested pending more specimens to be found and/or molecular analyses performed. In any case, the present specimens match with *C. polynema*, which may have up to 20 marginal tentacles, linear gonads along the middle portion of radial canals and up to eight marginal cirri and two statocysts between adjacent tentacles (Kramp 1959; Table 1).

The remaining species of the genus, *C. violacea*, was described with a short and broad gastric peduncle (Gershwin et al. 2010). However, the absence of gastric peduncle is a remarkable characteristic distinguishing Cirrholovenidae from other Leptothecata medusae with closed statocysts such as Lovenellidae, where the genus *Cirrholovenia*

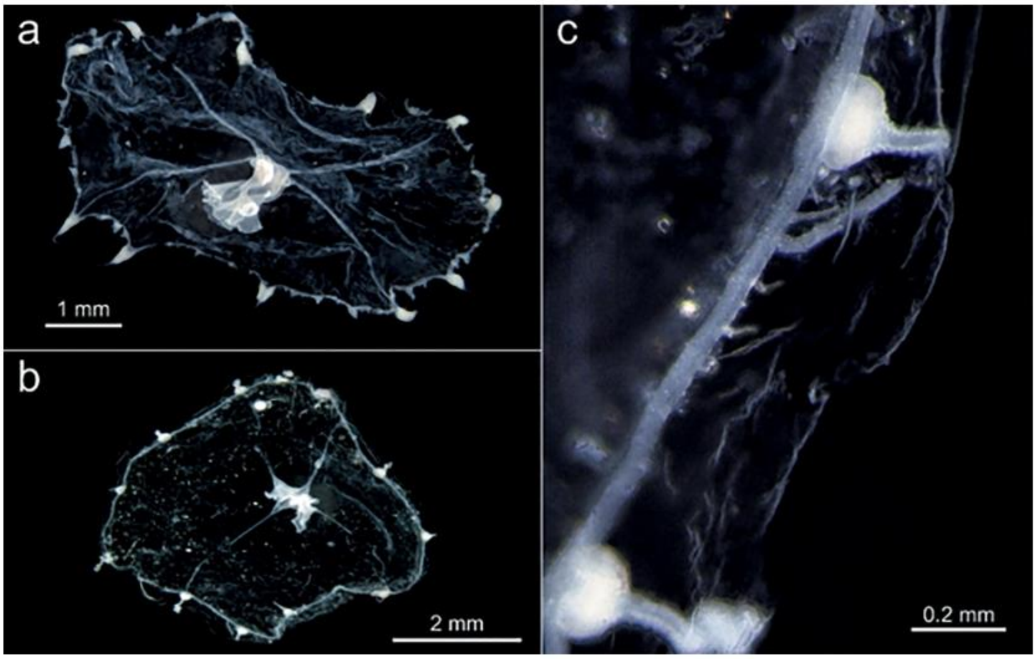

**Figure 1.** *Cirrholovenia polynema* medusae from North Brazil. (a and b) Oral view. (c) Detail of bell margin showing statocysts and marginal cirri.

was previously included, and Eirenidae Haeckel, 1879 medusae (Kramp 1959, Bouillon 1984, Bouillon et al. 2006). This issue was apparently overlooked in the *C. violacea* description; it seems likely that the species has been included in the wrong family and genus. Among Eirenidae, the genus *Phialopsis* Torrey, 1909 include species with a short and broad gastric peduncle, more than 8 statocysts and marginal cirri, matching with the description of the specimen classified as *C. violacea*. Although it differed in the number of marginal structures and shape of the gonads from the other two known species of *Phialopsis* (Table 1), the description was based on a small and immature individual that could develop into one of these two species. Further analysis of the material is necessary to elucidate this question.

*C. polynema* was first described from the Java Sea (Kramp 1959), and is widely distributed in tropical and subtropical areas from the Indo-Pacific, mainly between 30°N and 30°S (Kramp 1959, 1962, 1965, Bouillon et al. 1986, Du et al. 2012; Fig. 2). Occurrences outside this range also were recorded in temperate areas off New Zealand and Chile (Kramp 1965, Fagetti 1973; Fig. 2). In the Atlantic Ocean the species was only recorded in St.

**Table 1.** Comparison of main characteristics of the valid medusae species from the genus *Cirrholovenia* and *Phialopsis* NI = Not informed.

| Species | Bell diameter | Tentacles | Rudimentary bulbs | Marginal cirri | Statocysts | Gonads | Reference |
|---|---|---|---|---|---|---|---|
| Present specimens | 2.4 to 6 mm | Up to 12 | Up to 3 between successive tentacles | Up to 8 between successive tentacles | 1 or 2 between successive tentacles | Linear, along the middle of radial canals | This study |
| *Cirrholovenia polynema* Kramp, 1959 | Up to 8 mm | Up to 20 | Few | Up to 8 between successive tentacles | Twice as numerous as tentacles | Linear, along the middle of radial canals | Kramp, 1959 |
| *Cirrholovenia tetranema* Kramp, 1959 | Up to 1.5 mm | 4 | None | Up to 8 between successive tentacles | 1 or 2 between successive tentacles | Thick and cylindrical, occupying almost the whole length of the radial canals | Kramp, 1959 |
| *Cirrholovenia reticulate* Xu & Huang, 2004 | Up to 0.8 | 4 | 1 between successive tentacles | 5 between successive tentacles | 1 between successive tentacles | Cylindrical, occupying almost the whole length of the radial canals | Xu & Huang, 2004 |
| *Cirrholovenia* (?) *violacea* Gershwin, Zeidler & Davie, 2010 | 1.34 mm | 12 | Apparently absent | Same number as statocysts | 3 - 5 between successive tentacles | On the middle of radial canals | Gershwin et al, 2010 |
| *Phialopsis diegensis* Torrey, 1909 | NI | 16-28 | 8-9 between successive tentacles | More numerous than marginal papillae | 2 - 5 between successive tentacles | Linear, occupying 3/4 of the distal portion of radial canals | Torrey, 1909 |
| *Phialopsis averruciformis* Huang, Xu & Lin, 2013 | 32 mm | 52 | Absent | 3 - 5 between successive tentacles | 1 or 2 between successive tentacles | Linear, extending from the basal part of peduncle to almost to the bell margin | Wang et al, 2013 |

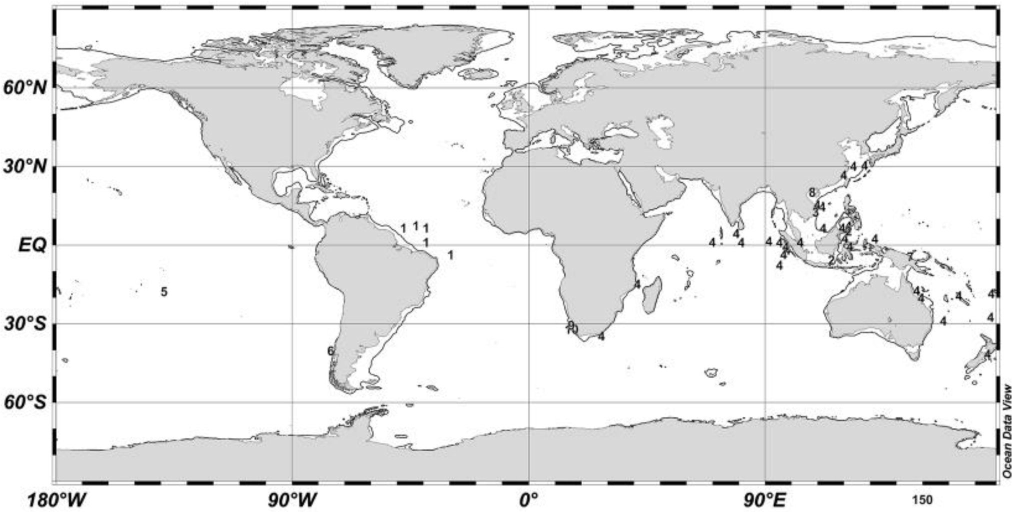

**Figure 2.** Global distribution of *Cirrholovenia polynema* based on this study and published records. The continuous line shows the 250-m isobath, roughly corresponding to the shelf break (generated using Ocean Data View software; Schlitzer, 2007). Data Source: 1 = This study; 2 = (Kramp 1959); 3 = (Kramp 1962); 4 = (Kramp 1965); 5 = (Michel 1969); 6 = (Fagetti 1973); 7 = (Bouillon et al. 1986); 8 = (Du et al. 2012); 9 = (Buecher and Gibbons 2000); 10 = (Gibbons and Buecher 2001).

Helena Bay, South Africa (Buecher and Gibbons 2000, Gibbons and Buecher 2001; Fig. 2), this area is under influence of the Benguela Current, which is partially fed by the Agulhas Current (Pagès and Gili 1992), coming from the Indian Ocean, thus the presence of the species could be expected there. In this study, we observed *C. polynema* in several locations of the tropical western border of the Atlantic Ocean for the first time, confirming the species is present in the Atlantic far beyond the influence of Agulhas Current in South Africa and ubiquitous to all ocean basins.

Four of the five specimens were collected in tropical open ocean up to 1000 km away from the coast (surface temperature ranging from 28 to 29.6°C and surface salinity ranging from 32.78 to 36.08) and one around the Fernando de Noronha Archipelago (26.6°C surface temperature and 36.2 surface salinity). As a meroplanktonic species, many occurrences of *C. polynema* were over the continental shelf (Kramp 1962, 1965, Gibbons and Buecher 2001), where benthic hydroids may easily find substrates for their development. Yet, its presence in offshore areas slightly away from the shelf break and around oceanic islands is not unusual (Kramp 1965, Michel 1969), suggesting the species can potentially inhabit this environment (probably driven by currents) reaching new areas for polyp settlement, and it would justify its wide distribution in tropical and subtropical areas around the world.

Knowledge regarding zooplankton biodiversity in general and cnidarians in particular from the waters off North and Northeast Brazil is scarce (Oliveira et al. 2016, Boltovskoy and Valentin 2018). Thus, the current report contributes not only to the understanding of local biodiversity, but also for and adequate comprehension of global biogeographic and diversity patterns.

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**Ethical approval:** The authors followed all applicable international, national, and/or institutional guidelines for animal testing, animal care and use of animals.

**Sampling and field studies:** The authors have obtained all necessary permits for sampling and observational field studies from the competent authorities.

## AUTHOR CONTRIBUTIONS

Experiment design: S.N.L. and A.B. Sampling: A.B. Sorting of Material: E.G.T. Species identification: E.G.T. and M.N.J. Manuscript writing: E.G.T., M.N.J., S.N.L. and A.B. Manuscript review: E.G.T., M.N.J., S.N.L. and A.B.

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# APÊNDICE C – APÊNDICE C. NEW SPECIES OF EIRENIDAE (HYDROZOA: LEPTOTHECATA) FROM THE AMAZONIAN COAST (NORTHERN BRAZIL)

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# New species of Eirenidae (Hydrozoa: Leptothecata) from the Amazonian coast (northern Brazil)

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**Summary:** Two new Eirenidae medusae species were collected on the Amazonian coast, *Eutima marajoara* n. sp. and *Helgicirrha angelicae* n. sp. The former differs from other species of the genus by the gonads extending along almost the entire length of the subumbrellar portion of the radial canals but not connected to the ring canal, up to 40 marginal tentacles with conical bulbs and 48 marginal warts, lateral cirri and adaxial papillae on some marginal warts and tentacular bulbs. *Helgicirrha angelicae* n. sp. differs from other species of the genus by the gonads on the middle portion of the radial canals with medusa buds, the short gastric peduncle, up to 20 marginal tentacles, some with adaxial papillae, up to three marginal warts and two statocysts between successive tentacles, and lateral cirri both on tentacle bulbs and marginal warts.

**Keywords:** jellyfish; Cnidaria; Hydrozoa; taxonomy; biodiversity; Atlantic Ocean; new species.

**Nuevas especies de Eirenidae (Hydrozoa: Leptothecata) de la costa amazónica (norte de Brasil)**

**Resumen:** En la costa amazónica se recolectaron dos nuevas especies de medusas Eirenidae, *Eutima marajoara* n. sp. y *Helgicirrha angelicae* n. sp. La primera se diferencia de otras especies del género por las gónadas que se extienden a lo largo de casi toda la longitud de la porción subumbrellar de los canales radiales, pero no conectados al canal circular, hasta 40 tentáculos marginales con bulbos cónicos y 48 verrugas marginales, cirros laterales y papilas adaxiales en algunas verrugas marginales y bulbos tentaculares. *Helgicirrha angelicae* n. sp. se diferencia de otras especies del género por las gónadas en la porción media de los canales radiales con yemas de medusa, pedúnculo gástrico corto, hasta 20 tentáculos marginales, algunos con papilas adaxiales, hasta tres verrugas marginales y dos estatocistos entre tentáculos sucesivos, lateral cirros tanto en bulbos de tentáculos como en verrugas marginales.

**Palabras clave:** medusa; Cnidaria; hidrozoos; taxonomia; biodiversidad; océano Atlántico; especies nuevas.

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## INTRODUCTION

Hydromedusae from the family Eirenidae Haeckel, 1879 are easily distinguished from other Leptothecata by the presence of a distinct gastric peduncle and closed statocysts (Bouillon et al. 2006). In some Eirenidae genera there are eight statocysts (rarely 12) while in others there are an indefinite number, but always more than eight in adult medusae (Bouillon 1984, 1999, Bouillon et al. 2006). Among those with eight statocysts, *Eutima* McCrady, 1859 differs from *Eugymnanthea* Palombi, 1936 by the adult medusae

Table 1. – Comparison of main characters of the valid medusae species of the genus *Eutima*. ND, no data.

| Species | Umbrella | Tentacles | Warts | Gonads | Papillae | Peduncle | Distribution | Reference |
|---|---|---|---|---|---|---|---|---|
| *Eutima marajoara* n. sp. | Up to 9.5 mm with thin mesoglea | Up to 40 | Up to 48 | Subumbrella | Present | 1/4 of umbrella diameter | North Brazil | This study |
| *Eutima cirrhifera* (Kakinuma, 1964) | Up to 9.8 mm | 8 | 24-49 | Subumbrella | Absent | Small | Japan | Kakinuma, 1964, Bouillon 1984 |
| *Eutima coerulea* (Agassiz, 1862) | Up to 10 mm, mesoglea thick at apex | 32 | 96 | Restricted to peduncle | Absent | 1/2 of umbrella diameter, tapering | Bahamas, Florida, Tortuga | Kramp 1961, Bouillon 1999 |
| *Eutima commensalis* Santhakumari, 1970 | Up to 5.9 mm | 8 | 48-80 | Subumbrella | Absent | Small | Indian, Arabian Sea | Santhakumari 1970, Bouillon 1984 |
| *Eutima curva* Browne, 1905 | Up to 25 mm, with thick mesoglea | 4 | 120-140 | Restricted to peduncle | Absent | Long, pyramidal above | Indo-Pacific, China Sea | Kramp 1961, Bouillon and Barnett 1999 |
| *Eutima diademata* (Kramp, 1959) | Up to 15 mm, almost hemispherical | 8 | 50-80 | 8: 4 on radial canals, 4 on peduncle | Absent | Long | Indo-Pacific | Kramp 1959, Guo et al. 2008 |
| *Eutima gegenbauri* (Haeckel, 1864) | Up to 20 mm, hemispherical | 8 to 16 | 60-80 | 8: 4 on radial canals, 4 on peduncle | Present | Very long | Mediterranean, European Atlantic, Australia, China Sea | Kramp 1961, Bouillon 1984 |
| *Eutima gentiana* (Haeckel, 1879) | Up to 8 mm, higher than wide | 8 | 16 | Restricted to peduncle | Absent | Very long | Canary Islands, China Sea | Kramp 1961, Bouillon 1984 |
| *Eutima gracilis* (Forbes and Goodsir, 1853) | Up to 13 mm, with thick mesoglea | 2 or 4 | 40-80 | Restricted to peduncle | Absent | Long and narrow, with conical base | Mediterranean, European Atlantic, West Africa | Kramp 1961, Bouillon 1999 |
| *Eutima hartlaubi* Kramp, 1958 | Up to 15 mm, flatter than hemispherical | 12 to 14 | 32 | 8: 4 on radial canals, 4 on peduncle | Absent | 1/2 of umbrella diameter | Djibouti, Nicobar, Aden Gulf, Indian | Kramp 1958, Bouillon 1984 |
| *Eutima japonica* Uchida, 1925 | Hemispherical | 8 | 16 | Subumbrella, part of peduncle | Absent | Small | Japan, North Pacific | Kramp 1961, Bouillon 1984 |
| *Eutima levuka* (Agassiz and Mayer, 1899) | Up to 15 mm | 8 | 100 | 8: 4 on radial canals, 4 on peduncle | Absent | 1 1/2 of umbrella diameter | Indo-Pacific, China Sea | Kramp 1961, Bouillon 1984 |
| *Eutima longigonia* Bouillon, 1984 | Up to 88 mm, flatter than hemispherical | 8 | 64-80 | Restricted to peduncle | Absent | = umbrella diameter | Papua New Guinea | Bouillon 1984 |
| *Eutima mira* McCrady, 1859 | Up to 30 mm, as broad as wide | 4 | ~100 | 8: 4 on radial canals, 4 on peduncle | Absent | Long, tapering | Indo-Pacific, Brazil, Northeast Atlantic, China Sea | Kramp 1961, Bouillon 1999 |
| *Eutima modesta* (Hartlaub, 1909) | Up to 8 mm, flat | 16 | 16+ | Subumbrella | Absent | 1/2 of umbrella diameter | Djibouti, Aden Gulf | Kramp 1961, Bouillon 1984 |
| *Eutima mucosa* Bouillon, 1984 | Up to 15 mm, flat | 8 | 56-80 | Subumbrella | Absent | 1/2 of umbrella diameter | Papua New Guinea | Bouillon 1984 |
| *Eutima neucaledonia* Uchida, 1964 | Up to 9 mm, flat | 8 | 48-56 | Subumbrella | Absent | = umbrella diameter | New Caledonia | Uchida 1964, Bouillon 1984 |
| *Eutima orientalis* (Browne, 1905) | Up to 6 mm | 4 | 60-80 | 8: 4 on radial canals, 4 on peduncle | Absent | 2x umbrella diameter | Sri Lanka | Kramp 1968 |
| *Eutima sapinhoa* Narchi and Hebling, 1975 | Up to 4 mm, slightly higher than wide | 4 | 28 | Subumbrella | Absent | = umbrella diameter | Brazil | Narchi and Hebling 1975, Bouillon 1984 |
| *Eutima suzannae* Allwein, 1967 | 5.7 mm, wider than high | 8 | 32 | Subumbrella | Present | 1/2 of umbrella diameter | North Carolina | Allwein 1967, Bouillon 1984 |
| *Eutima variabilis* McCrady, 1859 | ND | 20 (4 longer) | 36 | 8: 4 on radial canals, 4 on peduncle | Absent | 1-1.5 of umbrella height | East USA, China Sea | Kramp 1961, Bouillon 1984 |
| *Eutima taiwanensis* Xu, Huang and Guo, 2019 | Up to 12 mm, hemispherical | 12-16 | 80-120 | 8: 4 on radial canals, 4 on peduncle | Absent | Long | Taiwan Strait | Guo et al. 2019 |

with tentacles and from *Eutimalphes* Haeckel, 1879, *Eutonina* Hartlaub, 1897 and *Neotima* Petersen, 1962 by the presence of lateral cirri on marginal warts and/or tentacles (Bouillon 1999, Bouillon et al. 2006). In the second case, *Helgicirrha* Hartlaub, 1909 differs from *Eirene* Eschscholtz, 1829, *Tima* Eschscholtz, 1829 and *Phialopsis* Torrey, 1909 by the presence of lateral cirri on tentacular bulbs and from *Irenium* Haeckel, 1879 by the gonads restricted to the subumbrellar part of the radial canals (Bouillon 1999, Bouillon et al. 2006).

Currently there are 22 valid species described in the genus *Eutima* and 11 (one with a temporary name) in *Helgicirrha* in the World Register of Marine Species (Schuchert 2020). Although the general shape of the umbrella, gastric peduncle and manubrium may help with identification, species in the two genera are mainly distinguished by the shape and position of the gonads, the number of marginal structures and presence/absence of adaxial papillae or excretory pores (Kramp 1961, Bouillon 1984). This is not an easy assignment since most species show a high level of intraspecific variability (Tables 1, 2), which has not been described in detail, particularly when in juvenile and/or not fully developed specimens.

Specimens from two Eirenidae species were found in a scientific expedition along the Amazonian coast of northern Brazil (Araujo et al. 2017, Tosetto et al. 2019). Species of the family are typically coastal and/or estuarine, often occurring in high abundance (Canché-Canché and Castellanos-Osorio 2005, Morales-Ramírez and Nowaczyk 2006, Mediseh et al. 2017). This aspect, associated with the high feeding rates of pelagic cnidarians (Hays et al. 2018), may place them as significant predators in these environments. The specimens found clearly belonged to the genera *Eutima* and *Helgicirrha* because of the characteristics explained above, but did not fit in any of the currently known species. Thus, the objective of this work is to describe *Eutima marajoara* n. sp. and *Helgicirrha angelicae* n. sp. In addition, the main characteristics of all species described in both genera are compiled and compared (Tables 1, 2).

## MATERIALS AND METHODS

Specimens were obtained from samples collected in October 2012 at Marajó Bay and along the Amazonian coast, northern Brazil (Fig. 1), with oblique hauls from near bottom to the surface, using a Bongo net with 120 and 300 μm mesh and 0.3 and 0.6 m mouth opening, respectively. The material was fixed with 4% formaldehyde buffered with sodium tetraborate (0.5 g $l^{-1}$). The type material was deposited at the cnidarian collection of the *Museu de Zoologia da Universidade de São Paulo* (MZUSP), with additional paratypes deposited at the *Coleção de Invertabrados Paulo Young* from *Universidade Federal da Paraíba* (CIPY). All applicable international, national and institutional guidelines for the care and use of animals were followed.

In the laboratory, specimens were measured and the number of marginal structures per quadrant was counted under an optical microscope. We considered each quadrant separately in order to test for individual variability and to alleviate the problem that some specimens had quadrants with parts of the margin damaged and structures missing. Relationships between umbrella diameter and number and ratio of marginal structures were modelled with linear regressions with Statsoft Statistica 10 software.

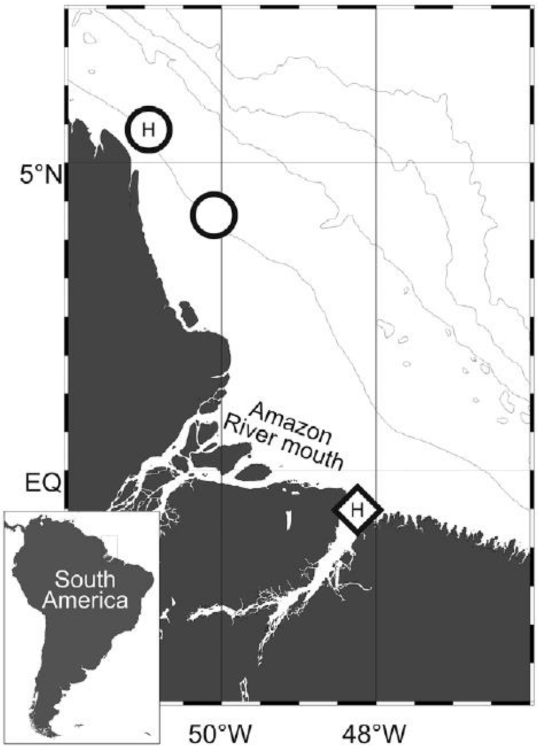

Fig. 1. – Sample sites for *Eutima marajoara* n. sp. (circles) and *Helgicirrha angelicae* n. sp. (diamond) along the Amazonian coast. “H” indicates holotype locality.

## RESULTS

Class Hydrozoa Owen, 1843
Subclass Hydroidolina Collins, 2000
Order Leptothecata Cornelius, 1992
Family Eirenidae Haeckel, 1879
Genus *Eutima* McCrady, 1859
***Eutima marajoara*** n. sp.
(Fig. 2)

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*Material examined.* 0.034383°S, 47.57213°W: 175 specimens (10/14/2012). Holotype: MZUSP 8516 (Umbrella diameter: 8 mm, male, Fig. 2A). Paratypes: MZUSP 8517 (75 specimens), MZUSP 8518 (42 specimens), CIPY 1122 (57 specimens).

*Etymology.* Specimens were collected in the waters of Marajó Bay in northern Brazil. Marajoara refers to the native society that inhabited the area before European occupation and gave name to the bay.

Table 2. – Comparison of main characters of the valid medusae species of the genus *Helgicirrha*. ND, no data.

| Species | Width | Umbrella | Tentacles | Marginal warts | Statocysts |
|---|---|---|---|---|---|
| *Helgicirrha angelicae* n. sp. | Up to 8.5 mm | Flatter than hemispherical, with thin mesoglea | Up to 20 | 1-3 between successive tentacles | Generally 1 between successive tentacles |
| *Helgicirrha brevistyla* Xu and Huang, 1983 | Up to 16 mm | Higher than hemispherical | 28-54 | 0-2 between successive tentacles | 1-2 between successive tentacles |
| *Helgicirrha cari* (Haeckel, 1864) | Up to 50 mm | Flatter than hemispherical, with thin mesoglea | Up to 60 | Up to 100 | Up to 100 |
| *Helgicirrha cornelii* Bouillon, 1984 | Up to 9 mm | Flatter than hemispherical, with thick mesoglea in centre | 16 | 16 small rudimentary bulbs and 32 small protuberances | 16 |
| *Helgicirrha danduensis* (Bigelow, 1904) | Up to 25 mm | Flatter than hemispherical, somewhat conical | 32 | About 17 | 32 |
| *Helgicirrha gemmifera* Bouillon, 1984 | Up to 5 mm | Almost flat, with thin mesoglea | 4 | 11-15 | 8-16 |
| *Helgicirrha irregularis* Bouillon, Boero and Seghers, 1988 | Up to 20 mm | Flatter than hemispherical, with thin mesoglea | 16-180 | Up to 80, 0-8 between successive tentacles | 18 |
| *Helgicirrha malayensis* (Stiasny, 1928) | Up to 20 mm | With thin mesoglea | 30-140 | Variable | 1- between tentacles |
| *Helgicirrha medusifera* (Bigelow, 1909) | Up to 8 mm | Moderately high | Up to 21 | As numerous as the tentacles in small medusae, fewer in larger specimens | 1 between successive tentacles |
| *Helgicirrha ovalis* Huang, Xu, Lin and Guo, 2010 | Up to 6.5 mm | Flatter than hemispherical, with thin mesoglea | 8 | 1-2 between successive tentacles | 2-3 between successive tentacles |
| *Helgicirrha weaveri* Allwein, 1967 | Up to 25 mm | Almost hemispherical, with moderately thick mesoglea | Up to 14 | 4-6 between successive tentacles | 1 between successive tentacles |
| *Helgicirrha sinuatus* Xu, Huang and Du, 2012 | 12-22 mm | Flatter than hemispherical | 16-24 | 3-5 between successive tentacles | 3-4 between successive tentacles |

| Species | Adaxial papillae and/or excretory pores | Gonads |
|---|---|---|
| *Helgicirrha angelicae* n. sp. | Some bulbs and warts with papillae | Linear, in the middle portion of radial canals, with medusa buds |
| *Helgicirrha brevistyla* Xu and Huang, 1983 | ND | Elongated, from near the base of peduncle to near the umbrella margin |
| *Helgicirrha cari* (Haeckel, 1864) | Pores present | Linear, from near the base of peduncle to near the umbrella margin |
| *Helgicirrha cornelii* Bouillon, 1984 | Absent | Linear, beginning in the middle part of the canal and posteriorly extending distally, but never reaching the margin |
| *Helgicirrha danduensis* (Bigelow, 1904) | ND | Spindle-shaped, occupying the distal 2/3 of the canals |
| *Helgicirrha gemmifera* Bouillon, 1984 | Absent | In the middle portion of radial canals, with medusa buds |
| *Helgicirrha irregularis* Bouillon, Boero and Seghers, 1988 | Absent | Sinuous, extending from the base of the peduncle to the distal quarter or radial canals |
| *Helgicirrha malayensis* (Stiasny, 1928) | ND | Long, extending from inwards, sometimes continuing along upper part of peduncle |
| *Helgicirrha medusifera* (Bigelow, 1909) | Pores on papillae | Cylindrical, on distal third of the radial canals (not reaching the umbrella margin), with medusa buds |
| *Helgicirrha ovalis* Huang, Xu, Lin and Guo, 2010 | ND | Oval, in the middle of radial canals |
| *Helgicirrha weaveri* Allwein, 1967 | Pores on tentacle bulbs and marginal warts | Narrow, from near the base of peduncle to near the umbrella margin |
| *Helgicirrha sinuatus* Xu, Huang and Du, 2012 | Pores on tentacle bulbs and marginal warts | Sinuous, occupying the distal 2/3 or 1/3 of the canals |

Table 2 (cont.). – Comparison of main characters of the valid medusae species of the genus *Helgicirrha*. ND, no data.

| Species | Peduncle | Manubrium | Distribution | Reference |
|---|---|---|---|---|
| *Helgicirrha angelicae* n. sp. | Prismatic, about 1/4 of umbrella diameter | Small, with 4 lips | North Brazil | This study |
| *Helgicirrha brevistyla* Xu and Huang, 1983 | About 1/6 of umbrella diameter | Quadratic with four slightly folded lips | China | Xu and Huang 1983 |
| *Helgicirrha cari* (Haeckel, 1864) | Variable | Variable | North Sea, Adriatic, Mediterranean, Benguela Current, Mexican Caribbean | Kramp 1961, Pagès et al. 1992, Bouillon 1999 |
| *Helgicirrha cornelii* Bouillon, 1984 | Less than 11/5 of umbrella diameter | With evident lips | Papua New Guinea | Bouillon 1984 |
| *Helgicirrha danduensis* (Bigelow, 1904) | Long, reaching well beyond umbrella margin | 1/2 as long as the peduncle, with evident lips | Maldive islands | Bigelow 1904 |
| *Helgicirrha gemmifera* Bouillon, 1984 | About 1/4 of umbrella diameter | Long, without apparent lips | Papua New Guinea | Bouillon 1984 |
| *Helgicirrha irregularis* Bouillon, Boero and Seghers, 1988 | Cylindrical, about 3/4 of umbrella diameter | Short, with developed and scalloped lips | Papua New Guinea | Bouillon et al. 1988 |
| *Helgicirrha malayensis* (Stiasny, 1928) | Conical | Short | Papua New Guinea, Java Sea, Madras, India, China | Kramp 1961, Bouillon et al. 1988 |
| *Helgicirrha medusifera* (Bigelow, 1909) | Conical, about 1/4 of umbrella diameter | Short with 4 simple lips | Pacific coast of Mexico, Arabian Sea, Bay of Bengal, Taiwan strait | Bigelow 1909, Vannucci and Santhakumari 1969, Wang et al. 2013 |
| *Helgicirrha ovalis* Huang, Xu, Lin and Guo, 2010 | Short | Prismatic with four lips | Taiwan Strait | Huang et al. 2010 |
| *Helgicirrha weaveri* Allwein, 1967 | About 1/4 of umbrella diameter | Small with curved lips | North Carolina, USA | Allwein 1967 |
| *Helgicirrha sinuatus* Xu, Huang and Du, 2012 | Very long | Small and square | Beibu Gulf (China) | Du et al. 2012 |

*Diagnosis*. *Eutima* medusa with gonads restricted to subumbrella, extending along almost entire length of subumbrellar portion of radial canals. Approximately 32 (up to 40) marginal tentacles with conical bulbs and 32 (up to 48) marginal warts. Some marginal warts and tentacular bulbs with lateral cirri and a few with adaxial papillae.

*Description* (based on several specimens). Umbrella flat, ranging from 1.5 to 9.2 mm wide, with thin mesoglea. Manubrium tubular with folded lips. Narrow prismatic gastric peduncle, about 1/4 of umbrella diameter in length. Gonads restricted to subumbrella, linear, extending along almost entire length of subumbrellar portion of radial canals but not connected to ring canal and gastric peduncle (Fig. 2A, B). Approximately 32 (up to 40) marginal tentacles with conical bulbs in adult medusae. Up to 48 marginal warts in different sizes, usually two or three between successive tentacles in small medusae, fewer in larger specimens (as shown by the increase in the ratio between tentacles and warts, Fig. 3). Up to eight statocysts. Some warts and bulbs with lateral cirri (Fig 2C) and a few with adaxial papillae (Fig. 2D). Velum narrow.

*Development*. Positive significant ($p<0.05$) relationships were observed between umbrella diameter and mean number of marginal tentacles, warts, ratio between tentacles and warts and statocysts per umbrella quadrant (Table 3, Fig. 3). Positive values of b coefficient indicate the number of tentacles and warts increases with medusa development (Table 3). While smaller specimens (1.5~2 mm) had one or two tentacles and two to four warts on each quadrant, individuals of intermediate sizes around 5 mm had approximately four tentacles and six warts per quadrant (note some individuals had up two 11 warts per quadrant in this stage) and bigger ones (~9 mm) had up to 10 tentacles and 12 warts per quadrant (Fig. 3). Positive values of b coefficient of tentacles/warts ratio also indicate that warts are relatively more abundant in juveniles (Fig. 3). Although the relationship between umbrella diameter and statocyst number was significant (*p* value almost 0.05, very close to the threshold limit of significance), the low value of the b coefficient indicates that the number of statocysts does not increase with medusa development, as was expected because species of *Eutima* are considered to have a fixed number of statocysts (Table 3, Fig. 3).

*Ecological notes*. Specimens were found in estuarine waters (8 m bottom depth) of the Marajó Bay, mouth of Pará and Amazon Rivers, at 28.3°C temperature and 18.2 salinity throughout the water column.

### Genus *Helgicirrha* Hartlaub, 1909
### ***Helgicirrha angelicae*** n. sp.
(Fig. 4)

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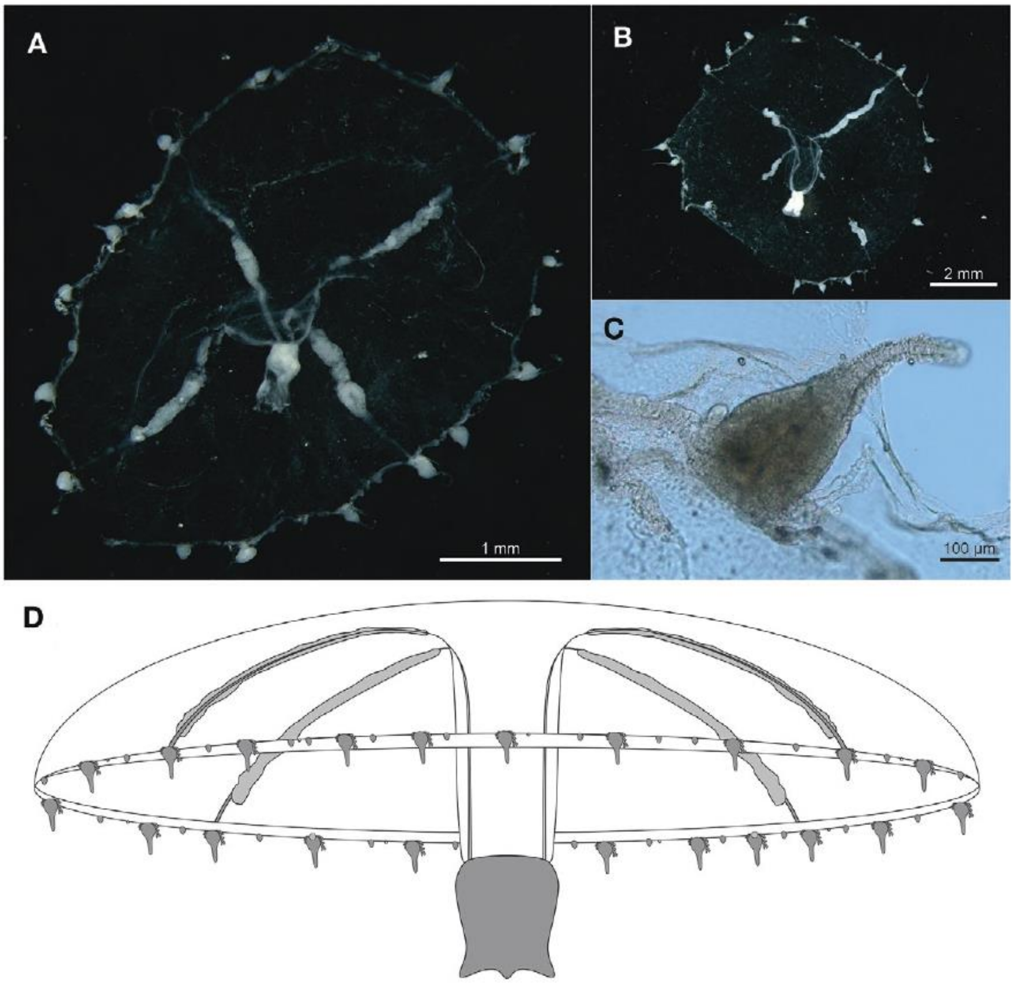

Fig. 2. – *Eutima marajoara* n. sp. A, oral view of the holotype; B, paratype; C, detail of a tentacular bulb with lateral cirri; D, schematic representation of adult specimen.

*Material examined*. 4.44°N, 50.896°W: 64 specimens (10/21/2012). Holotype: MZUSP 8519 (Umbrella diameter: 6 mm, male, Fig. 4A). Paratypes: MZUSP 8520 (42 specimens), CIPY 1123 (18 specimens). 3.47516°N, 50.16°W: 3 specimens (10/21/2012).

*Etymology*. This species is named after Professor Maria Angélica Haddad, one of the pioneers of hydrozoan studies in Brazil whose passion encouraged generations of students.

Diagnosis. *Helgicirrha* medusa with gonads on middle portion of radial canals, with medusa buds. Short gastric peduncle. Up to 20 marginal tentacles, some with adaxial papillae. Generally one to three marginal warts and one statocyst between successive tentacles. Lateral cirri on tentacle bulbs and some marginal warts.

*Description* (based on several specimens). Umbrella flatter than a hemisphere, ranging from 0.8 to 8.5 mm wide, with thin mesoglea. Small manubrium, mouth with four short simple lips. Short and narrow prismatic gastric peduncle, about 1/4 of umbrella width in length. Linear gonads on middle portion of radial canals, with developing medusa buds (Fig. 4A, C). Up to 20 marginal tentacles with conical bulbs. Up to 28 marginal warts in different sizes, usually one to three between successive tentacles. Lateral cirri on tentacle

Table 3. – Summary and coefficients (a, b) of linear regression relating umbrella diameter and mean number of marginal structures per umbrella quadrant (number of structures = a + b * umbrella diameter) in *Eutima marajoara* n. sp. and *Helgicirrha angelicae* n. sp. (n, number of specimens analysed; a, intercept; b, inclination; p values <0.05 are considered significant).

| | n | F | p | a | b |
|---|---|---|---|---|---|
| *Eutima marajoara* | | | | | |
| Tentacles | 49 | 197.21 | <0.0001 | 0.5 | 0.87 |
| Marginal warts | 49 | 56.14 | <0.0001 | 2.62 | 0.76 |
| Tentacles/warts ratio | 49 | 13.03 | <0.0001 | 0.51 | 0.05 |
| Statocysts | 47 | 4.07 | 0.0496 | 1.11 | 0.06 |
| *Helgicirrha angelicae* | | | | | |
| Tentacles | 18 | 152.39 | <0.0001 | 0.33 | 0.56 |
| Marginal warts | 17 | 25.69 | <0.0001 | -0.1 | 0.87 |
| Tentacles/warts ratio | 17 | 1.76 | 0.21 | 1.08 | -0.05 |
| Statocysts | 15 | 24.77 | <0.0001 | 0.3 | 0.45 |

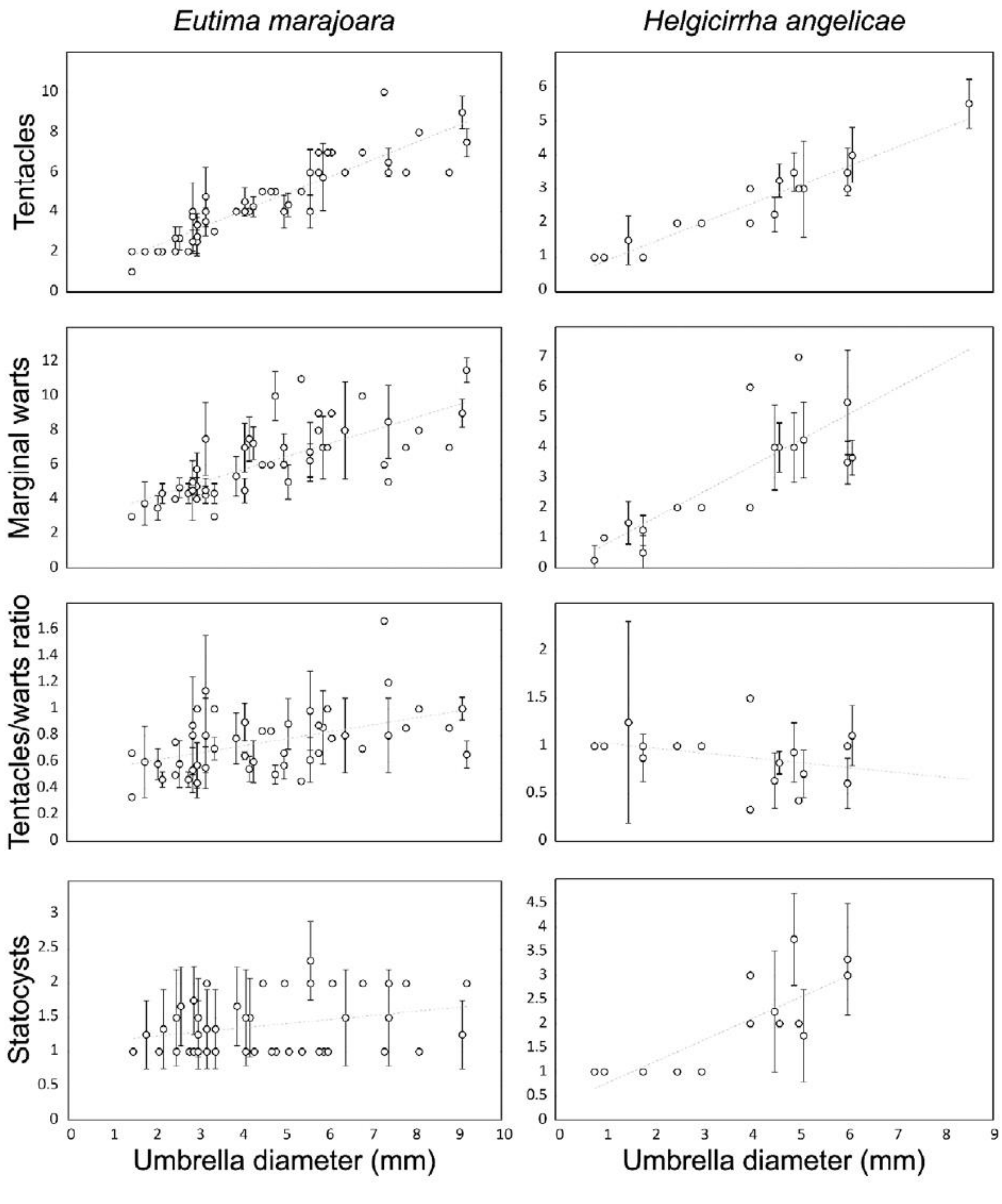

Fig. 3. – *Eutima marajoara* n. sp. and *Helgicirrha angelicae* n. sp. relationship between mean number of marginal structures per umbrella quadrant and umbrella diameter. Symbols are mean+SD for each individual; symbols without error bars indicate that data from a single quadrant were available; dotted lines are the result of linear regressions (Table 3).

bulbs and some marginal warts (Fig. 4B). Generally one statocyst between successive tentacles. Some bulbs with adaxial papillae. Velum narrow.

*Development*. Positive significant ($p<0.05$) relationships were observed between umbrella diameter and mean number of marginal tentacles, warts, and statocysts per umbrella quadrant (Table 3, Fig. 3). Positive values of b coefficient indicate that the number of tentacles, warts and statocysts increase with medusa development (Table 3). Smaller specimens (~1 mm) had one perradial tentacle, one or no interradial warts and one statocyst in each quadrant. Intermediate stages (~4.5 mm) had around three tentacles, four warts and 2.5 statocysts per quadrant and bigger specimens (6~8 mm) had up to six tentacles, seven warts and five statocysts per quadrant (Table 3, Fig. 3). Ratios between tentacles and warts were not significantly correlated with umbrella diameter.

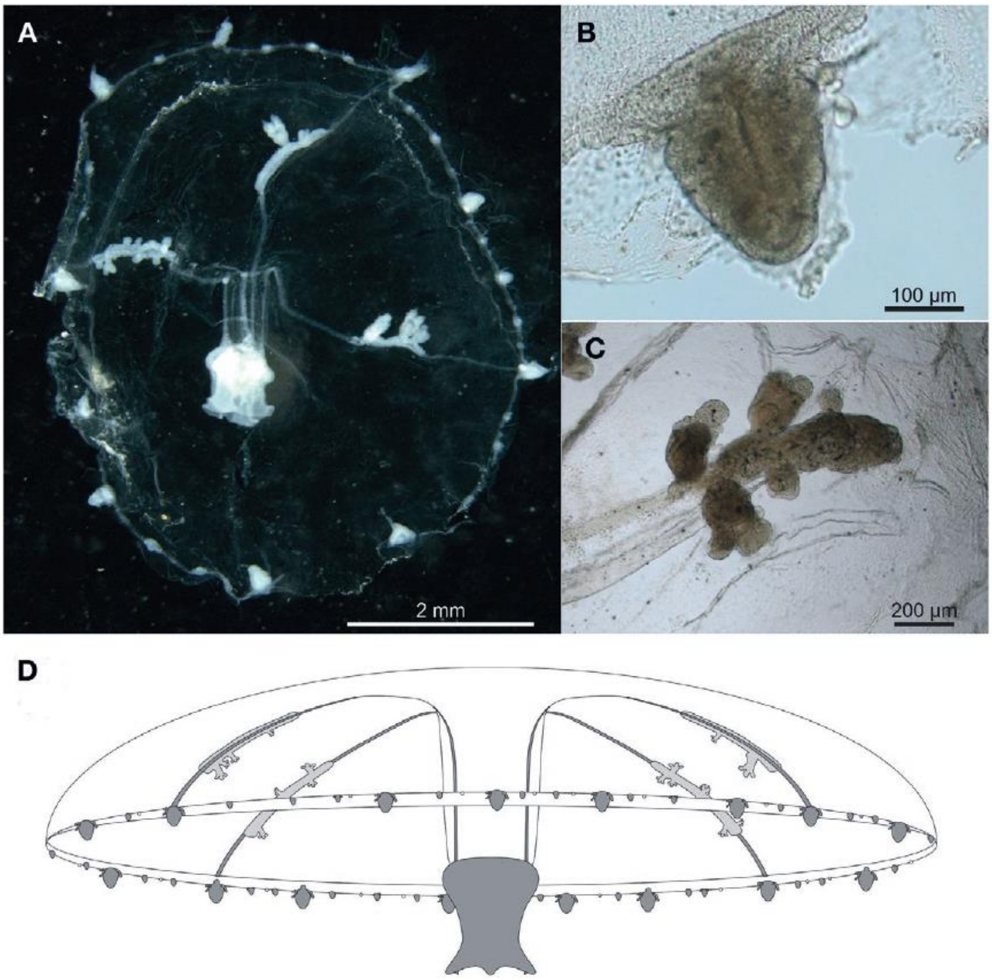

Fig. 4. – *Helgicirrha angelicae* n. sp. A, oral view of the holotype; B, detail of the tentacular bulb with lateral cirri; C, detail of a gonad with medusa buds; D, schematic representation of adult specimen.

*Ecological notes*. Specimens were found in neritic waters over a reef system (30-65 m bottom depth) under the influence of the Amazon River plume with water column temperature ranging from 24.9°C to 27.9°C and salinity from 31.1 to 36.3.

## DISCUSSION

Genera of the family Eirenidae are mainly distinguished by the number of statocysts, the position of the gonads and the presence of marginal structures such as, cirri, warts and adaxial papillae (Bouillon et al. 2006). *Eutima* and *Helgicirrha* species always have lateral cirri on the tentacle bulbs and/or marginal warts, and some species of both genera have adaxial papillae and gonads restricted to the subumbrella (Bouillon 1984, Bouillon et al. 2006, Schuchert 2017), as do the specimens found in this study. However, *Eutima* species have eight statocysts (rarely 12) in adult medusae and *Helgicirrha* always has more than eight and up to an indefinite number (Bouillon 1984, Bouillon et al. 2006). The number of statocysts is the main character distinguishing the two genera (the absence of excretory pores in *Eutima* is controversial and will be discussed later) and was used to assign the genera of the two species discussed herein. However, when the medusae development was observed, smaller specimens of both had fewer statocysts (Fig. 3C, G), and observations based on these individuals, associated with the fragility of these organisms (marginal structures are frequently lost in net trawls and/or formalin fixation), could lead to misidentification. These observations reinforce the need to examine fully developed specimens and to characterize their ontogenetic development for accurate identification and to elucidate the taxonomy of complex families such as Eirenidae.

Distinctive characters of *Eutima marajoara* n. sp. are the gonads restricted to the subumbrella, the adaxial papillae on few marginal warts and/or tentacle bulbs and the large number of marginal tentacles. Among the other seven species described in the genus with gonads restricted to the subumbrella, only *Eutima* *suzannae* Allwein, 1967 also have adaxial papillae (Table 1). However, unlike in *E. marajoara* n. sp., in *E. suzannae* papillae are restricted to the marginal warts. Other differences are the longer gastric peduncle in *E. suzannae* and the number of tentacles and marginal warts. While *E. marajoara* have up to 40 (usually 32 in adults) tentacles and 1 to 3 warts between successive tentacles, *E. suzannae* have only eight tentacles and four warts between them (Allwein 1967). Moreover, the high number of tentacles in *E. marajoara* n. sp. is noteworthy. While most species in the genus have eight or four tentacles, only *E. marajoara* n. sp. and *Eutima coerulea* (Agassiz, 1862) have more than 20. However, in *E. coerulea* the gonads are restricted to the peduncle, unlike in our specimens (Table 1).

The original description of *Eutima* included species without papillae (McCrady 1859). A few years later *Octorchis* Haeckel, 1864 was described (Haeckel 1864), differing from *Eutima* mainly in the presence of adaxial papillae in *Octorchis* and their absence in *Eutima* (e.g. Russell 1953). Subsequent studies considered both as subgenera within the genus *Eutima* (Kramp 1961, Bouillon 1984). Currently the subgenus rank fell out of use and all species previously considered *Octorchis* are included within *Eutima* (Schuchert 2020), which now encompasses eirenids with eight statocysts and lateral cirri, with or without papillae (Kramp 1961, Bouillon 1984, Schuchert 2020; Table 1). One open question is whether these papillae do possess an excretory pore, which would be necessary to regard them as excretory papillae (as mentioned in recent diagnoses, e.g. Bouillon and Boero 2000, Bouillon et al. 2006), because this is hard to verify and requires detailed histological observations (Schuchert 2017).

Only the hydroid stage and newly released medusa are known in *Eutima ostrearum* (Mattox and Crowell, 1951). Hydroids of this species were found inhabiting the mantle cavity of oysters in an estuarine system in Puerto Rico (Mattox and Crowell 1951). Due to the close geographic location and similar habitat (e.g. estuarine waters), *E. marajoara* n. sp. could be the adult medusa of *E. ostrearum*. Future studies based on molecular data from both localities and on hydroids inhabiting the Marajó Bay are necessary to answer this question. However, newly released *E. ostrearum* of up to 3 mm displayed no lateral cirri and had no sign of a gastric peduncle (Mattox and Crowell 1951). Although these characters may develop later in the medusa ontogeny, they differ from our smaller specimens within the same size range (1.5-3 mm), which already had lateral cirri and a small but clearly visible peduncle. These differences suggest they are different species.

Specimens of *Helgicirrha angelicae* n. sp. have linear gonads located in the middle portion of the radial canals. Shape and position of gonads are important characters for the taxonomy of *Helgicirrha* and other Eirenidae medusae (e.g. Bouillon 1984, Bouillon et al. 1988, Huang et al. 2010). Indeed, the gonadal position was helpful to distinguish the present specimens from *Helgicirrha brevistyla* Xu and Huang, 1983, *Helgicirrha cari* (Haeckel, 1864), *Helgicirrha danduensis* (Bigelow, 1904), *Helgicirrha irregularis* Bouillon, Boero and Seghers, 1988, *Helgicirrha malayensis* (Stiasny, 1928), *Helgicirrha medusifera* (Bigelow, 1909), *Helgicirrha weaveri* Allwein, 1967 and *Helgicirrha sinuatus* Xu, Huang and Du, 2012, which have gonads in other positions than the middle portion of the radial canals (see Table 2 and reference therein). Among the remaining species, *Helgicirrha cornelii* Bouillon, 1984, *Helgicirrha gemmifera* Bouillon, 1984 and *Helgicirrha ovalis* Huang, Xu, Lin and Guo, 2010, unlike our specimens, do not have adaxial papillae either on the tentacular bulbs or on the marginal warts. In addition, they are distinct from the current specimens in the lower number of tentacles and shape of the gonads in the case of *H. ovalis* and *H. cornelii* (Table 2). Unlike in *Eutima*, species of *Helgicirrha* may or may not have excretory pores either on papillae (e.g. *H. medusifera*) or directly on the bulbs and warts (e.g. *H. weaveri*); however, pores were not observed on *H. angelicae* papillae.

The presence of medusa buds on every gonad of all adult specimens of *H. angelicae* n. sp. is also an outstanding character that is useful to distinguish it from all other species but *H. gemmifera* and *H. medusifera*. As cited above, the former is quite different from *H. angelicae* n. sp. However, *H. medusifera* differs mainly in the position of the gonads, which are located on the distal third of the radial canals (Table 2), while in our specimens they are in the middle (Fig. 3). The large number of specimens found in our samples allowed us to observe the complete development of medusae, and in any case the gonads approached the ring canal or were even located on the distal region of the radial canals, while in *H. medusifera* they are clearly very close to it (Bigelow 1909). The different geographical distribution of the two species (the western Atlantic and the eastern Pacific) also argues against the possibility that they are morphological variations of the same species. Furthermore, in adult medusae of *H. medusifera* most marginal warts turn into developed bulbs with tentacles and few warts are present (Bigelow 1909), and this is not the case for *H. angelicae* n. sp. because the number of warts increased with medusa development in similar proportion to the tentacles (Fig. 3). Future studies based on molecular data of both species could completely elucidate this question.

Among the 177 samples analysed, covering the northern Brazilian continental shelf and adjacent equatorial Atlantic oceanic waters (see Fig. 1 from Tosetto et al. 2019), both species had very restricted distributions. Currently, *E. marajoara* n. sp. has been found only in the waters of Marajó Bay, an estuarine environment (18.2 salinity) located in the mouth of the Pará and Amazon rivers, and is perhaps an endemic species to the area. *H. angelicae* n. sp. was restricted to coastal waters under the influence of the Amazon River plume. Knowledge on the zooplankton community inhabiting waters of the Amazonian coast is still scarce (Boltovskoy and Valentin 2018). Recently, this unique ecosystem has attracted attention from scientific and public society because of the presence of hard-bottom reefs (Moura et al. 2016) and oil exploitation in the area (Silva Junior and Magrini 2014), which may lead to significant impacts and losses in the rich, but still poorly known, biodiversity in the area.

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# APÊNDICE D – SAMPLING PLANKTONIC CNIDARIANS WITH PAIRED NETS: IMPLICATIONS OF MESH SIZE ON COMMUNITY STRUCTURE AND ABUNDANCE

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# Sampling planktonic cnidarians with paired nets: Implications of mesh size on community structure and abundance

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ABSTRACT

Mesh selectivity is an important factor to be considered when sampling zooplankton. Selectivity may differ according to the environment and taxon, but his has not been evaluated for cnidarians in neritic and/or oceanic ecosystems. In this study, efficiency of plankton nets with two different mesh sizes (120 and 300 μm) were compared to assess the cnidarian assemblage from neritic and oceanic habitats in the equatorial Atlantic Ocean. No statistical differences between meshes were observed in species richness, total and most dominant taxa abundance, or taxonomic and size structure of the community in both oceanic and neritic habitats. Only for the small (0.5–2 mm) neritic *Persa incolorata* did the meshes differ, with higher abundances in the finer one. Despite small particularities, our results show that the 120 and 300 μm meshes produce similar results.

## 1. Introduction

Marine planktonic animals have a wide variability in size and swimming ability, constituting a quite heterogeneous community which, together with the typical patch distribution, makes it difficult to establish standard sampling protocols in ecological studies and quantitative assessments (Omori and Hamner, 1982; Harris et al., 2000). The accuracy of a particular sampling instrument typically is related to species size, morphology, flexibility, behavior and distribution, and environmental characteristics (Vannucci, 1968; De Bernardi, 1984). Among the many factors that may influence zooplankton sampling, mesh size selectivity is one of the most important (Skjodal et al., 2013). While a small mesh may filter high rates of unwished particles, obstructing water passage and rapidly clogging the mesh, a coarse one may lose smaller species and early life stages (Riccardi, 2010; Vannucci, 1968).

Mesh selectivity and catch efficiency is a controversial subject. For copepods, where mesh size effect is relatively well understood, 200 μm meshes may lose a significant proportion of small species, copepodites and nauplii abundance (up to 90%) and biomass (up to 50%; Hopcroft et al., 1998; Hwang et al., 2007; Di Mauro et al., 2009; Favareto et al., 2009; Riccardi, 2010; Wu et al., 2011). However, the reported underestimation of larger species and individuals by smaller meshes due to the bow wave effect and mesh obstruction (Vannucci, 1968; Hopcroft et al., 2001; Favareto et al., 2009) is not ubiquitous (Antacli et al., 2010; Miloslavić et al., 2014).

The effects of different mesh sizes on other invertebrate zooplanktonic taxa are poorly known. Few particular information is available considering appendicularians, chaetognaths, mollusks, polychaetes, cnidarians and non-copepod crustaceans (Almeida Prado, 1962; Vidjak, 1998; Di Mauro et al., 2009; Riccardi, 2010; Skjodal et al., 2013; Miloslavić et al., 2014; Nogueira Júnior et al., 2015). Despite most of this literature showing that specific groups and/or sizes are better estimated by particular mesh sizes, the lack of detailed information, such as seasonality and habitat variability, hinders the development of standard sampling protocols. Given the requirement of precise methods to estimate zooplankton abundance, detailed information of taxa-specific mesh size effects considering habitat heterogeneity is a matter of great importance.

Planktonic cnidarians have aroused recent interest in the scientific community due to their high feeding rates and unexpected population blooms (e.g. Purcell et al., 2007). For a complete understanding of these processes, precise quantitative methods need to be established. Although the choice of the mesh size will depend on particular targets in each study, the 500 μm mesh, frequently used in planktonic cnidarian sampling (e.g. Gili et al., 1991; Loman-Ramos et al., 2007; Segura-Puertas et al., 2010), was found to largely underestimate hydrozoan estuarine assemblages (Nogueira Júnior et al., 2015). Since the estuarine cnidarian community usually is dominated by small-sized hydromedusae (Xu and Huang, 1983; Nogueira Júnior et al., 2015), the

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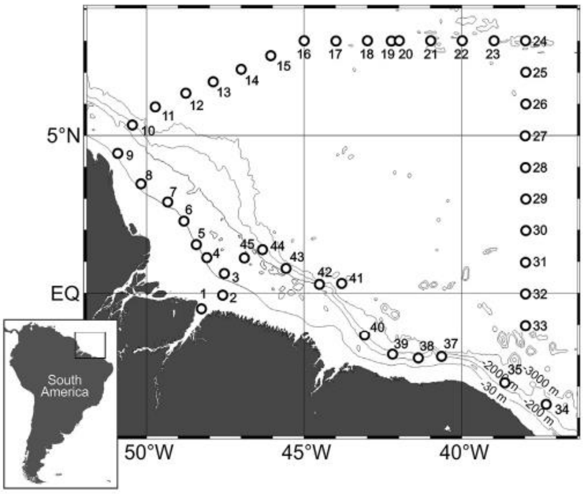

**Fig. 1.** Map of the North Brazilian continental shelf and adjacent equatorial Atlantic Ocean, showing the sampled stations.

absence of studies testing the effect of mesh sizes in neritic and oceanic waters precludes the possibility to expand the results to other taxonomic and size composition ecosystems.

In aiming to improve the understanding of this subject, in this study we evaluated the efficiency of plankton nets with two different mesh sizes (120 and 300 µm) to assess the cnidarian assemblage from neritic and oceanic habitats in the equatorial Atlantic. This is based on the hypothesis that the meshes will provide different results regarding diversity, abundance and community structure.

## 2. Material and methods

### 2.1. Study area and sampling

Samples were obtained between October 9th and November 1st, 2012 during the oceanographic cruise Camadas Finas III, aboard the research vessel NHo. Cruzeiro do Sul - H38 (DHN/Brazilian Navy) along the North Brazilian continental shelf and adjacent equatorial Atlantic Ocean (Fig. 1). The area is a heterogenic environment, affected by the large freshwater discharge of the Amazon River, strong currents, eddies, wind fields and high tidal variation (Molleri et al., 2010; Nittrouer and DeMaster, 1996). Zooplankton samples were obtained at 44 stations in oblique hauls, using nets with 120 and 300 µm mesh and 0.3 and 0.6 m opening respectively (except for station 39, where only the 300 µm mesh sample was available). The 300 µm net was hauled immediately after the 120 µm one. Stations were sampled from the near bottom to the surface on the continental shelf, and from 200 m to the surface in the open ocean. These nets were towed at approximately 2 knots, at various times of day and night. Due to differences in depth, duration of hauls was variable, ranging from 6 to 35 min. Both nets were fitted with a flowmeter (Hydro-Bios) to estimate the volume filtered during each trawl. Volume sampled averaged (± SD) 65.1 ± 42.7 and 196.2 ± 172.9 $m^3$ in the 120 and 300 µm mesh respectively. Samples were fixed with 4% formaldehyde buffered with sodium tetraborate ($0.5\,g\,l^{-1}$).

### 2.2. Analysis of samples

Whole samples of both meshes (N = 87) were analyzed under a stereomicroscope and specimens were identified (Boltovskoy, 1999) and counted. Abundances were standardized as number of individuals.100 $m^{-3}$ for medusae and number of colonies.100 $m^{-3}$ for siphonophores. For calycophorans, the number of anterior nectophores was used for estimating the polygastric stage abundance, and eudoxid bracts for the eudoxid stage abundance (e.g., Hosia and Båmstedt, 2007). Physonects and the calycophoran *Hippopodius hippopus* were not considered in the analysis due to the well-known difficulties in accurate quantifying them from net samples. In each sample, up to 30 individuals per species were measured, considering the medusae bell diameter and siphonophore largest width.

### 2.3. Data analysis

Stations were grouped into neritic and oceanic habitats based on their location, considering the shelf break at the isobath of 100 m. Species richness, total abundance, and abundance of individual dominant taxa estimated with both meshes in neritic and oceanic habitats were compared using Bi-Factorial ANOVA (Zar, 2010). PERMANOVA was used to test whether the taxonomic and size structure of the cnidarian community changed according to mesh size, type of habitat (neritic or oceanic) and possible interactions between these factors. PERMANOVA were based on a Bray–Curtis similarity matrix after data transformation (log (x + 1); Anderson, 2001). P values $< 0.05$ were considered significant in both analyses. The collection efficiency of the 300 µm mesh ($CE_{300}$, %) in relation to the 120 µm mesh was calculated as follows: $CE_{300} = (Ab_{300} * 100)/Ab_{120}$; where $Ab_{300}$ and $Ab_{120}$ are abundance estimated by 300 and 120 µm meshes respectively. Bi-Factorial ANOVA was performed using Statistica 10. PERMANOVA analysis were performed using Primer v.6 + PERMANOVA.

## 3. Results and discussion

A total of 80 taxa were sampled (37 siphonophores, 41 hydromedusae and 2 scyphomedusae). The 300 µm mesh sampled more taxa in the neritic stations (33 vs 29) and the 120 µm sampled more in the oceanic ones (61 vs 47), but differences were not significant (see below). While 19 taxa were found exclusively in the 120 µm mesh, 12 were exclusive in the 300 one. All these taxa were rare, with very few individuals. Their absence in one of the meshes probably was random, as a consequence of increasing the sampling effort. However, some of the exclusive species found in the 120 µm mesh are small (~1 mm) hydromedusae such as *Cytaeis* sp. and Corynidae sp. which may have been missed by the 300 µm mesh. Damaged unidentifiable specimens represented 1.3% and 2% of 120 and 300 µm mesh respectively.

Significant differences ($p < 0.05$) were not observed in species richness and total abundance obtained with 120 and 300 µm meshes (Fig. 2; Table 1), the same pattern was obtained when considering the size and taxonomic structure in the PERMANOVA or the interaction in the neritic and oceanic habitats in all cases (Fig. 2; Table 1). In all analysis differences were observed between the habitats (Table 1). Although average $CE_{300}$ was slightly lower in the neritic stations, the index presented a high variability, ranging from 9.9 to 619.6% in the oceanic stations and from 24.3 to 289.4% over the continental shelf (Fig. 2e). No clear pattern in the $CE_{300}$ was observed when considering its distribution by size classes, with average values always around 100% and high variability (Fig. 2f).

Dominant taxa were similar in both meshes, only differing in rank order and proportion (Table 1). The neritic habitat was dominated by *Liriope tetraphylla*, *Persa incolorata*, *Enneagonum hyalinum*, *Muggiaea kochii* and *Diphyes dispar*. Oceanic stations were dominated by *Diphyes bojani*, *Aglaura hemistoma*, *Chelophyes appendiculata*, *Eudoxoides mitra* and *Bassia bassensis* (Table 1). This condition was shown both in the size and taxonomic structure, which differ significantly (PERMANOVA; $p < 0.05$) between the neritic and oceanic habitats, but not between the meshes or the interaction of the factors (Table 1).

Mesh pore aperture is often one of the main factors to be considered in the selection of the sampling procedure, and studies comparing paired nets such as the presented here provide substantial support to

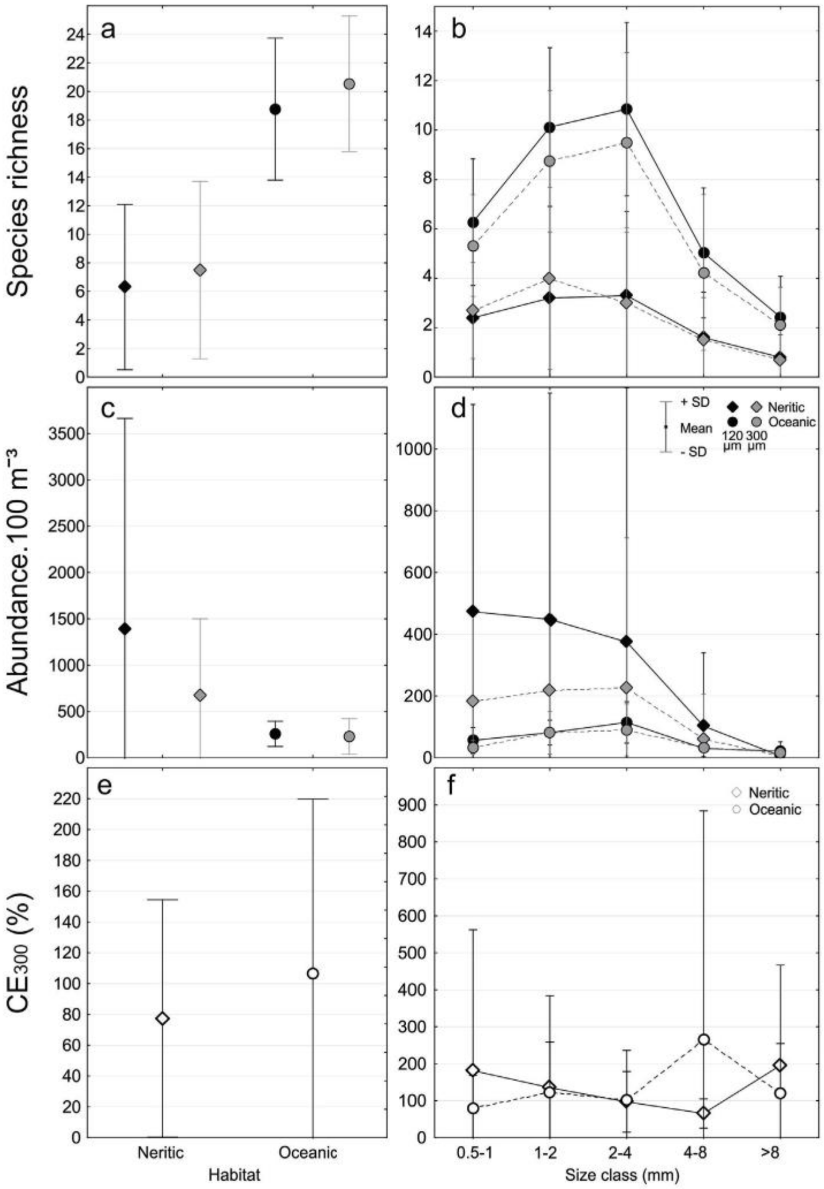

**Fig. 2.** Average species richness (a; b), abundance (c; d) and collection efficiency of 300 μm mesh (e; f) of total (a; c; e) and size-based (b; d; f) planktonic cnidarian community in neritic and oceanic habitats in the equatorial Atlantic Ocean.

help scientists choose the right equipment (Antacli et al., 2010). Overall, the results of this study show that the two mesh sizes tested produced similar results both at neritic and oceanic habitats. Yet, the use of multiple net sizes in zooplankton sampling may enhance the understanding of the community structure and the prediction power of ecological models by demonstrating its whole size spectrum was correctly considered, particularly for ecosystems where such variability has not been tested (Antacli et al., 2010; Miloslavić et al., 2014; Nogueira Júnior et al., 2015), emphasizing the importance of methodological tests such as the present study.

Even though general ecological results were similar, anomalies were observed in specific taxa such as the small trachymedusa *Persa incolarata* (0.5–2 mm), in which abundance differed between the two meshes, habitats and the interaction of the factors (Table 1). It occurred almost exclusively in a few neritic stations, where average abundance estimated by the 120 μm mesh was nearly six times that estimated by the 300 μm mesh (Fig. 3b). Most of the sampled individuals were juveniles, smaller than 1 mm bell diameter, and probably lost by 300 μm mesh. Similar effects probably occurred with less-abundant small-species such as *Obelia* spp. (< 1 mm). In general, a particular mesh would efficiently sample organisms at least 1/3 larger than its pore apertures (Bernhard et al., 1973; Nichols and Thompson, 1991). Thus, the 120 and 300 μm meshes would work well for specimens > 160 and > 400 μm respectively and filtering capacities of 300 μm mesh would be sufficient even for the smaller hydromedusae found (approximately 0.5 mm). However, the absence of rigid structures such as appendices, antennae and spines and gelatinous fragile body of small hydromedusae may facilitate deformation of mesoglea and the passage of larger specimens through the mesh pores.

Although the other dominant species and total abundance in neritic

**Table 1**

Dominant planktonic cnidarian taxa relative abundance and size (mean and range) in neritic and oceanic stations sampled with two mesh sizes. Summary of Bi-factorial ANOVA testing differences in individual taxa abundance, species richness and total abundance, and PERMANOVA (Pseudo F) testing differences in size-based and taxonomic structure of planktonic cnidarian community considering mesh size and habitat as factors. E = Calicophoran eudoxid stage. P = Calicophoran poligastric stage. Bold = significant ($p < 0.05$) differences.

| Habitat/Taxa/Indicator | Relative abundance | | Mean species size and interval (mm) | | Mesh | | Habitat | | Mes x Hab | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 120 µm | 300 µm | 120 µm | 300 µm | F | p | F | p | F | p |
| **Neritic** | | | | | | | | | | |
| *Liriope tetraphylla* | 31.07% | 32.53% | 2.6 (0.5–10) | 2.2 (0.5–9) | 2.46 | 0.12 | 20.0 | < **0.01** | 2.09 | 0.15 |
| *Persa incolorata* | 27.84% | 9.31% | 1.17 (0.5–2) | 1.17 (0.8–2) | 4.42 | **0.03** | 8.51 | < **0.01** | 4.40 | **0.03** |
| *Enneagonum hyalinum* | 17.67% | 25.52% | E = 2.8 (0.8–9) P = 3.5 (2–10) | E = 3.2 (2–8) P = 2.9 (2–10) | 0.25 | 0.61 | 8.34 | < **0.01** | 0.25 | 0.61 |
| *Muggiaea kochii* | 9.59% | 8.88% | E = 0.8 (0.6–1) P = 2.5 (0.8–4) | E = 0.8 (0.8–1.2) P = 2.5 (1–4) | 1.11 | 0.29 | 7.79 | < **0.01** | 1.12 | 0.29 |
| *Diphyes dispar* | 6.63% | 7.9% | E = 4 (1.5–5) P = 4.8 (2–15) | E = 3.4 (1.5–6) P = 4.9 (2–17) | 0.68 | 0.41 | 9.55 | < **0.01** | 0.73 | 0.39 |
| Others (n = 31 spp.) | 7.2% | 15.86% | 2.3 (0.5–9) | 2 (0.5–8.8) | | | | | | |
| **Oceanic** | | | | | | | | | | |
| *Diphyes bojani* | 17.58% | 24.31% | E = 2.4 (0.8–5) P = 5.4 (1–12) | E = 2.1 (0,7–5) P = 5 (0.9–13) | 0.42 | 0.51 | 2.39 | 0.12 | 0.01 | 0.90 |
| *Aglaura hemistoma* | 16.02% | 10.92% | 1.4 (0.5–3) | 1.4 (0.5–3) | 0.40 | 0.52 | 6.19 | **0.01** | 1.27 | 0.26 |
| *Chelophyes appendiculata* | 14.01% | 17.08% | E = 1.2 (0.8–2) P = 7 (2–12) | E = 1.1 (0.7–2) P = 6.9 (1–14) | 0.73 | 0.39 | 10.4 | < **0.01** | 0.28 | 0.59 |
| *Eudoxoides mitra* | 7.64% | 13.92% | E = 2.8 (0.8–5) P = 5.8 (1–13) | E = 2.8 (2–5.5) P = 6.5 (1–13) | 0.04 | 0.84 | 13.2 | < **0.01** | 0.06 | 0.79 |
| *Bassia bassensis* | 5.25% | 8.61% | E = 2.5 (0.5–5) P = 2.4 (0.8–5) | E = 2 (0.5–5) P = 2 (0.5–4) | 0.03 | 0.85 | 23.6 | < **0.01** | 0.04 | 0.83 |
| Others (n = 64 spp.) | 39.5% | 25.16% | 2.7 (0.5–13) | 2.7 (0.6–15) | | | | | | |
| **Species richness** | | | | | 1.29 | 0.26 | 95.9 | < **0.01** | 0.05 | 0.83 |
| **Total abundance** | | | | | 3.24 | 0.08 | 14.6 | < **0.01** | 2.76 | 0.10 |
| **Size structure** | | | | | 2.41 | 0.07 | 11 | < **0.01** | 0.79 | 0.5 |
| **Taxonomic structure** | | | | | 0.8 | 0.66 | 42.4 | < **0.01** | 0.81 | 0.64 |

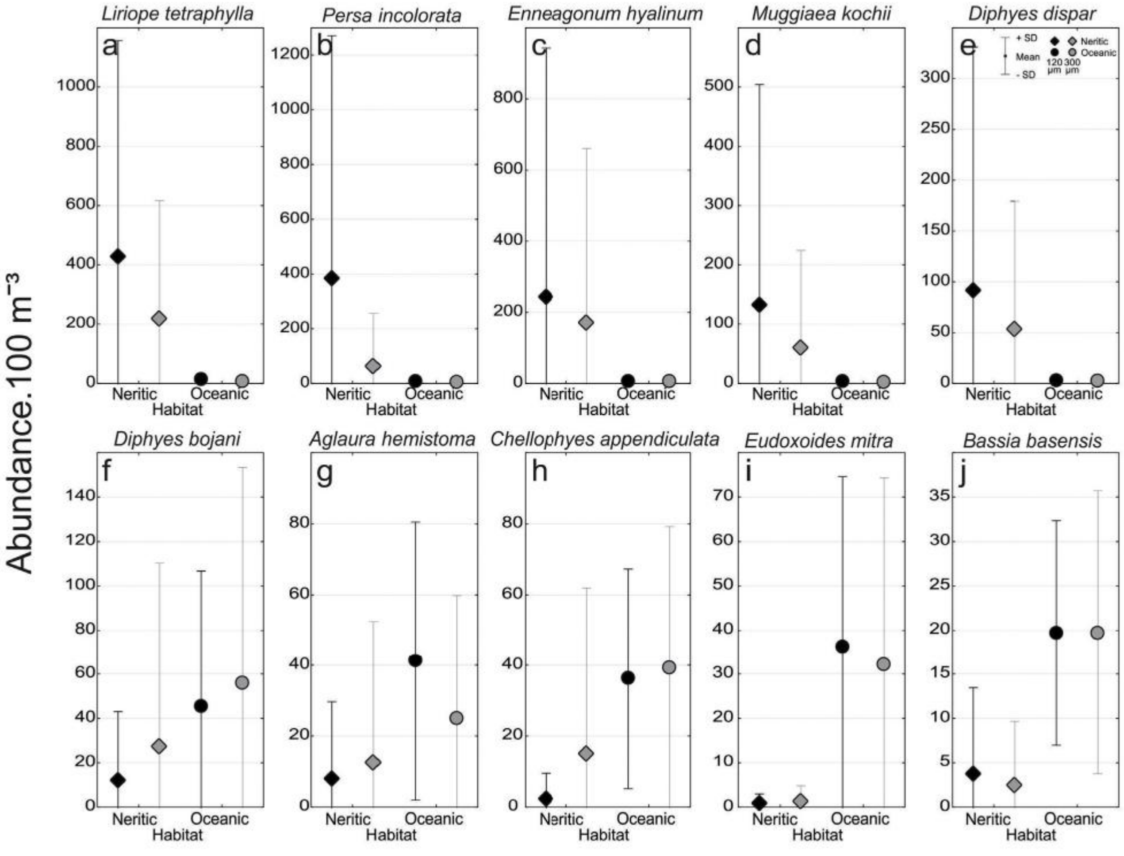

**Fig. 3.** Average abundance (ind. 100 $m^{-3}$) of dominant planktonic cnidarians sampled with 120 and 300 µm meshes in neritic and oceanic habitats in the equatorial Atlantic Ocean.

stations did not significantly differ between the two meshes, mean values were quite higher at the 120 μm one (Figs. 2c–d, 3a-e). The absence of significant results may in part be a consequence of the high variance in the data, a common feature of biological communities in general and of marine zooplankton in particular in part due to the patchy distribution common of zooplanktonic organisms in many spatial scales (Steele, 1978; Omori and Hamner, 1982; Messié and Chavez, 2017). This may be particularly true in the present study, with a high variability of habitats over the large area sampled, with many oceanographic processes occurring simultaneously (Lentz and Limeburner, 1995; Nittrouer and DeMaster, 1996; Molleri et al., 2010), where even adjacent stations presented high variability as can be seen by the high standard deviations.

Despite small anomalies (mostly *P. incolorata*), our results show that the 120 and 300 μm meshes produce similar results sampling planktonic cnidarians in neritic and oceanic habitats. Studies use meshes usually ranging from 150 to 500 μm for oceanic and neritic environments (Pagès and Gili, 1992; Lo and Biggs, 1996; Thibault-Botha et al., 2004; Nogueira Júnior et al., 2014), although coarser and finer meshes also may be used (e.g. Pagès and Kurbjeweit, 1994; Morita et al., 2017). Since these studies did not evaluated mesh efficiency, this divergence in the sampling procedures hinders the possibility of direct comparisons considering abundance, species richness and assemblage structure. Thus, future ecological studies with the group in oceanic habitats should also consider mesh selectivity aiming to produce better estimates, more comparable results, and for eventual calibrations due to possible regional particularities.

Although the frequency of ecological studies involving planktonic cnidarians has increased significantly in the last decades, the discussion of the most accurate way to sample them is still in the early stages. Much is to be done to define the best way of sampling planktonic cnidarian with net hauls. While the actual evaluations indicate 200 μm mesh is adequate for estuarine environments (Nogueira Júnior et al., 2015) and both 120 and 300 μm are adequate to neritic and oceanic habitats (present study), these and coarser meshes need be tested elsewhere in the world to endorse our results. Other aspects such as tow duration, speed and shape, net opening and size, and bow wave effect also were never evaluated and may influence the samplings. In addition to nets, new technologies such as video recorders (Luo et al., 2014) and active acoustics (Båmstedt et al., 2003) are promising zooplankton sampling techniques for the future and combination of these approaches and others to come are likely to broaden our perspectives on the functioning of ecological systems.

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