HELLEN CERIELLO

Relações interespecíficas: diversidade, métodos de ancoragem e hábitos alimentares associados aos tubos de espécies de Ceriantharia (Cnidaria; Anthozoa)

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DEDICATÓRIA

Dedico este trabalho aos meus Ophélios que tanto amo: *"[...] talvez você não veja nada neles. E eu vejo tudo neles; e é quando a imagem deles não está por perto que eles se fazem mais presentes em meu trabalho." (Oscar Wilde)*

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CERIELLO, Hellen. **Relações interespecíficas: diversidade, métodos de ancoragem e hábitos alimentares associados aos tubos de espécies de Ceriantharia (Cnidaria; Anthozoa)**. 2018. 69p. Dissertação (Mestrado Acadêmico em Biociências). – Universidade Estadual Paulista (UNESP), Faculdade de Ciências e Letras, Assis, 2018.

RESUMO

O filo Cnidaria é caracterizado por animais em cujos tecidos encontram-se células tóxicas denominadas cnidócitos. Devido à liberação de substâncias tóxicas, os cnidários apresentam poucas associações com outras espécies, entretanto as associações mais conhecidas são frequentemente descritas como obrigatórias ou comensais facultativas. Um dos grupos deste filo, Ceriantharia, é representando por membros genericamente conhecidos por ceriantários ou anêmonas-de-tubo cuja característica mais marcante é a presença de uma secreção celular única (pticocisto) que auxilia na construção de um tubo, sintetizado pelo próprio animal, que fica inserido no substrato e abriga o animal. Embora existam estudos quanto ao histórico, taxonomia e posição sistemática, análises moleculares e morfológicas e ciclo de vida, estudos a respeito de associações interespecíficas ocorrendo em tubos de ceriantários são escassos. Logo, pouco se conhece sobre essas associações bem como os métodos que as espécies utilizam para se ancorarem aos tubos desses animais. Sendo assim, esse estudo elencou espécies que ocorrem em tubos de Ceriantharia, abordando principalmente os métodos de ancoragem e hábitos alimentares envolvidos nas relações observadas. Os tubos de 8 espécies de ceriantários foram analisados, fornecendo dados quanto a associações de Annelida, Crustacea e Mollusca aos tubos.

PALAVRAS-CHAVE: associações simbióticas. Simbiose. Invertebrados marinhos. Taxonomia.

CERIELLO, Hellen. **Interspecific relationships: diversity, anchoring methods and feeding habits associated to the tubes of Ceriantharia species (Cnidaria; Anthozoa)**. 2018. 69p. Dissertation (Masters in Biosciences). São Paulo State University (UNESP), School of Sciences, Humanities and Languages, Assis, 2018.

ABSTRACT

The phylum Cnidaria is characterized by animals that carry stinging cells named cnidocytes in their tissues. Due to the release of toxic substances, cnidarians have few associations with other species, however mostly known associations are often described as mandatory or optional commensalism. One of the groups in this phylum, Ceriantharia, is represented by members generally known as cerianthariansor tube-dwelling anemones whose most remarkable feature is the presence of a peculiar cell secretion (ptychocyst) that supports the construction of a tube, synthetized by the animal itself, and inserted into the substrate, lodging the animal. Although there are some studies concerning the history, taxonomy and systematic position, molecular and morphological analyzes and life-cycle, studies regarding interspecific associations occurring with ceriantharian tubes are scarce. Thus, little is known about these associations as well as the methods that the species use in order to anchor on these tubes. Thereby, this study listed species occurring in ceriantharian tubes mainly discussing the anchoring methods and feeding habits involved in the associations observed. The tubes of 8 Ceriantharia species were analyzed, yielding data about interactions with Annelida, Crustacea and Mollusca to the tubes.

KEYWORDS: marine invertebrates. Symbiosis. Symbiotic associations. Taxonomy.

SUMÁRIO

INTRODUÇÃO

O filo Cnidaria é caracterizado por animais em cujos tecidos encontram-se células urticantes denominadas cnidócitos. Esse filo é dividido em dois grandes subfilos, Anthozoaria e Medusozoa, e nele são incluídas as hidras, águas-vivas, anêmonas-do-mar e corais (Daly et al. 2007; Stampar et al., 2014). A classe Anthozoa, único agrupamento no subfilo Anthozoaria, é o maior grupo do filo, abrangendo mais de seis mil espécies de animais (Daly et al. 2007). Todos os representantes desse grupo apresentam formas polipoides sem estágio medusoide em seu ciclo de vida, podendo ser tanto coloniais quanto solitários. A história evolutiva dessa classe ainda é motivo de muita disputa, sendo que três grupos são claramente reconhecidos, Ceriantharia, Hexacorallia e Octocorallia (Kayal et al. 2013; Stampar et al. 2014).

Ceriantharia é representado por membros genericamente conhecidos por ceriantários ou anêmonas-de-tubo (Daly et al. 2007) que exibem formato corporal alongado, cilíndrico e levemente pigmentado. São solitários, semi-sésseis, hermafroditas com fecundação externa e habitam fundos marinhos onde seus corpos são alojados em tubos (secretados por eles mesmos) enterrados em meio aos sedimentos (Kim & Huys 2012) (Fig. 1). Atualmente, estima-se que esse grupo seja composto por 85 espécies (Molodtsova 2004; Stampar 2015a).

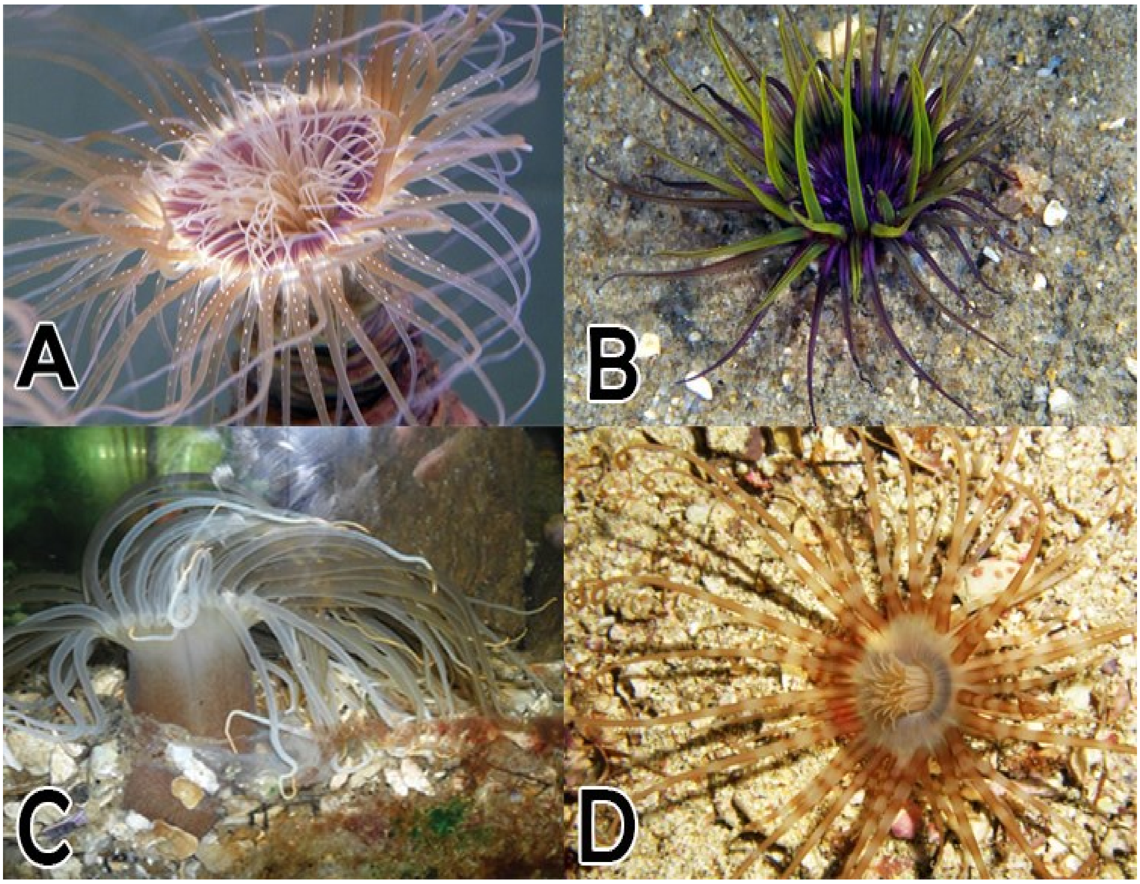

Fig 1. Alguns membros de Ceriantharia. **A.** *Pachycerianthus schlenzae* Stampar, Morandini and Silveira, 2014 (imagem: Sérgio N. Stampar). **B.** *Ceriantheopsis lineata* Stampar, Scarabino, Pastorino and Morandini, 2015 (imagem: Marcelo Krause). **C.** *Ceriantheomorphe brasiliensis* Carlgren, 1931 (imagem: Daphne Spier). **D.** *Isarachnanthus nocturnus* Hartog, 1977 (imagem: Arley Eishma).

Embora haja estudos sobre a taxonomia e sistemática deste grupo (ex. Stampar et al. 2014), as associações faunísticas com os tubos de Ceriantharia e os métodos necessários para ancoragem de outras espécies a eles são pouco conhecidos, assim como sua importância ecológica (Stampar et al. 2015a). Apesar disso, associações faunísticas com ceriantários não são incomuns (ex. Stampar et al. 2010; Kim & Huys 2012; Stampar et al. 2014; Vieira & Stampar 2014; Stampar et al. 2015b) e os compartes mais marcantes observados realizando essas associações são foronídeos, anfípodes e sipunculídeos (Tiffon 1987).

Associações simbióticas com cnidários nem sempre são bem definidas e suas categorias, tais como parasitismo, comensalismo, inquilinismo e mutualismo podem variar de acordo com os autores que as descreveram (Östlund-Nilsson et al. 2005; Anderson & Midgley 2007). Tais interações podem ser influenciadas tanto pela biologia dos organismos envolvidos quanto por fatores ambientais que ao se alterarem podem impactar nas características da suposta interação (Miller et al. 2006; Schwanz 2006). Ainda assim, o hospedeiro é responsável por fornecer recursos como alimento, abrigo e proteção ao seu simbionte enquanto que esse não necessariamente lhe fornecerá algo em troca (Leung & Poulin 2008).

É comum observar invertebrados marinhos associados a estruturas rígidas que parecem ser muito adequadas às suas ancoragens (Farrapeira & Calado 2010). Entretanto, alguns estudos correlacionam o sucesso ou insucesso do estabelecimento do espécime não à estrutura em si, mas à região estrutural em que o espécime se encontra instalado (Bonaldo et al. 2004). Desta forma, a textura filamentosa e macia apresentada pelo tubo ceriantário não seria uma opção inviável para o estabelecimento de invertebrados marinhos.

A composição do tubo de Ceriantharia é essencialmente uma sobreposição de filamentos oriundos de organelas de células especializadas (pticocistos) sobrepostos e mesclados com muco aderente e, ocasionalmente, alguns sedimentos (Stampar et al. 2015a). Apesar de sua composição inconspícua, muitas espécies, tais como *Ancylomenes pedersoni* Chace, 1958 (Crusctacea; Caridae), *Phoronis australis* Haswell, 1883 (Phoronida), *Stramonita brasiliensis* Claremont e D. G. Reid, 2011 (Mollusca; Gastropoda) e *Dragmacidon reticulata* Ridley e Dendy, 1886 (Porifera; Demospongiae) (Fig. 2) são encontradas nos tubos de Ceriantharia (Tiffon 1987). Consequentemente, para que essas interações ocorressem, foi necessário que as espécies associadas desenvolvessem estruturas especiais para a ancoragem (ex. Vieira & Stampar 2014).

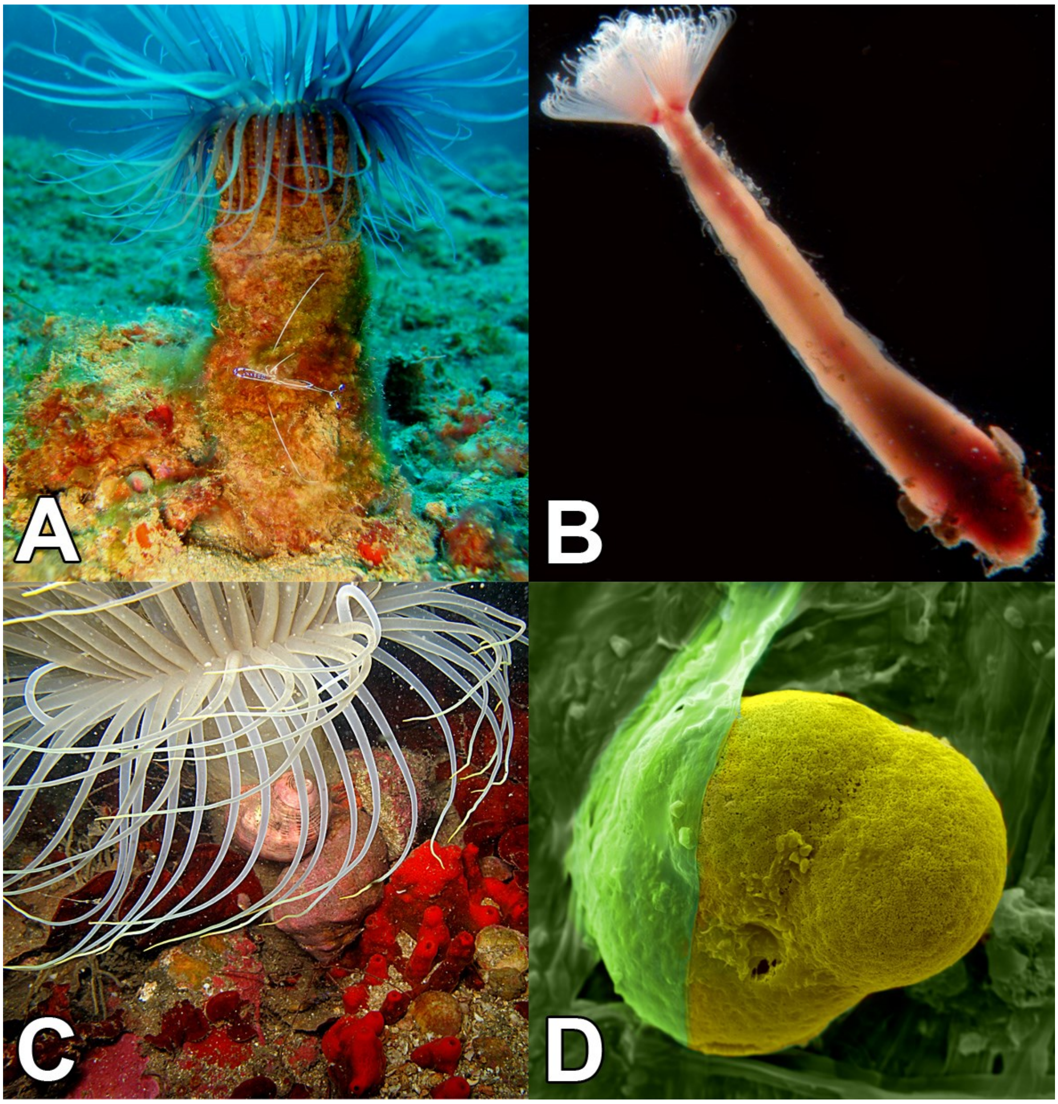

Fig 2. Organismos vivos nos tubos de Ceriantharia. **A.** *Ancylomenes pedersoni* encontrado sobre o tubo de *Pachycerianthus schlenzae*. **B.** *Phoronis australis* encontrado dentro do tubo de *Ceriantheomorphe brasiliensis* e *Ceriantheopsis lineata*. **C.** *Stramonita brasiliensis* e *Dragmacidon reticulate* encontrados sobre o tubo de *Ceriantheomorphe brasiliensis*. **D.** Foraminífero não-identificado encontrado sobre o tubo de *Pachycerianthus schlenzae*. (Imagens: Sérgio N. Stampar).

Desta forma, o foco principal neste estudo foi identificar as espécies que ocorrem em tubos de Ceriantharia e reconhecer possíveis padrões de alimentação e adaptações morfológicas que viabilizaram a ancoragem a tal estrutura.

OBJETIVOS

O objetivo geral nesse estudo foi reconhecer a diversidade e os padrões no uso dos tubos de Ceriantharia como substrato para a vida de outras espécies. De forma a atingir tal objetivo, foram delineados os seguintes objetivos específicos:

- Elencar as espécies de invertebrados que utilizam os tubos de Ceriantharia como substrato;
- Entender a forma de relação para cada espécie bem como sua maneira de ancoragem;
- Identificar a relação alimentar e/ou reprodutiva de cada espécie encontrada associada com tubos de ceriantários.

Os resultados obtidos foram organizados em capítulos que abordam as relações observadas entre grupos taxonômicos distintos encontrados associados ao tubo ceriantário.

CAPÍTULO 1.

CONCHAS DE MOLLUSCA EM TUBOS CERIANTÁRIOS (CNIDARIA; ANTHOZOA)

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RESUMO

Nesse estudo é discutido o uso de conchas de moluscos na construção de tubos ceriantários. Os tubos de sete espécies (n= 10 espécimes) de Ceriantharia da Noruéga, Portugal, Estados Unidos, Japão e Brasil foram estudados. As análises revelaram o primeiro registro de *Microgaza rotella* no Sudeste do Brasil e foram encontrados um total de 24 espécies de moluscos pertencentes a 21 famílias que estavam associadas aos tubos ceriantários; Basterotiidae, Caecidae, Calyptraeidae, Carditidae, Cerithiidae, Chamidae, Colloniidae, Columbellidae, Eulimidae, Fissurellidae, Myidae, Mytilidae, Potamididae, Pyramidellidae, Scaliolidae, Semelidae, Skeneidae, Solariellidae, Tellinidae, Veneridae e Zebinidae. Nossos resultados sugerem que conchas de moluscos são um importante componente na construção de tubos ceriantários e permitem a descoberta de padrões de biodiversidade da fauna de Mollusca em uma região.

Palavras-chave: Bivalvia. Bioconstrução. Ceriantharia. Engenheiros do ecossistema. Gastropoda. Recifes alternativos.

MOLLUSCA SHELLS ON CERIANTHARIAN (CNIDARIA; ANTHOZOA) TUBES

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ABSTRACT

In this study we discuss the use of mollusks shells in the construction of cerianthariantubes. The tubes of seven species (n= 10 specimens) of Ceriantharia from Norway, Portugal, United States, Japan, and Brazil were assessed. Analyses revealed the first record of *Microgaza rotella* in southeastern Brazil, and we found a total of 24 mollusk species belonging to 21 families that were associated with ceriantharian tubes; Basterotiidae, Caecidae, Calyptraeidae, Carditidae, Cerithiidae, Chamidae, Colloniidae, Columbellidae, Eulimidae, Fissurellidae, Myidae, Mytilidae, Potamididae, Pyramidellidae, Scaliolidae, Semelidae, Skeneidae, Solariellidae, Tellinidae, Veneridae and Zebinidae. Our results suggest that mollusk shells are an important component in the construction of ceriantharian tubes and enable the discovery of biodiversity patterns of the Mollusca fauna found at a site.

Keywords: alternative reefs. Bivalvia. Bioconstruction. Ceriantharia. Ecosystem engineers. Gastropoda.

INTRODUCTION

Some marine organisms can build multi-stratified structures through the aggregation and accumulation of components found on the sea floor or via components synthesized by themselves (Moore 2006). Such organisms are called “ecosystem engineers” or “ecosystem builders” (Jones et al. 1994). The resulting structures from the activities of ecosystem builders can vary in shape, size, dimensions and some can also provide suitable microhabitats for the settlement of many other species. Consequently, these structures can also be used by researchers as a tool to acquire knowledge about otherwise hard to find or unaccessible fauna of a location (Jones et al. 1994; Cocito 2004; Calcinai et al. 2015; Bürkli and Wilson 2017).

Given their tube-building behavior, ceriantharians (Cnidaria; Anthozoa) can be thought of as one kind of ecosystem builder. The ceriantharian tube is a very soft and flexible structure due to its basic composition of mucus and ptychocysts (cnidae filaments specific for this group). Other than these components, small sediments, found on the soft bottoms where the tube burrows into, adhere to the tube layers and give resistance and structural support to the tube (Stampar et al. 2015a).

Because of the soft texture of ceriantharian tubes, it would be expected that such substrates are not attractive anchoring points for invertebrate species considering that usually such organisms use rigid structures such as ship hulls (Carraro et al. 2012), offshore platforms (Bomkamp et al. 2004), and marine invertebrate shells (Farrapeira and Calado 2010) as anchoring locations. However, a few studies investigating the invertebrate fauna associated with ceriantharian tubes have reported some species settled on this unusual microhabitat (Emig 1979; Tiffon 1987; Stampar et al. 2010).

Mollusca is a highly diverse phylum with various species widespread throughout different marine and terrestrial habitats (Zhi-Qiang 2011), and both bivalve and gastropod mollusks can be found associated with a wide variety of taxonomic groups either acting as hosts or as symbionts (Humes 1974; Humes 1988; Spotte 1996; Gittenberger et al. 2000; Gittenberger 2003; Smith and Gosliner 2003; Boehs and Magalhães 2004; Zvereva and Vysotskaya 2005; Torgan et al. 2009; Ramos et al. 2010; Banaszak et al. 2013; Espinosa et al. 2013; Quirós Rodríguez and Campos 2013; Dufour et al. 2014; Queiroz and

Dias 2014; Ramos and Banaszak 2014; Salas-Moya et al. 2014; Mackie et al. 2015; Goto and Ishikawa 2016; Goto et al. 2016). However, studies reporting interactions between mollusks and ceriantharians are quite scarce (e.g. Goto et al. 2012) and the few studies that exist do not fully characterize the manner that the associations were observed, and thus it remains unclear what kind(s) of interactions occur between mollusks and ceriantharians. Thereby, the current study aimed to report on the fauna of Mollusca present on the tubes of different ceriantharian species and to discuss the characteristics of these occurrences.

MATERIAL AND METHODS

Ten tubes from seven ceriantharia species (Table 1) preserved in 4% seawater formalin were studied. The specimens were collected via scuba diving surveys from a wide range of locations; Norway, Portugal, United States, Japan, and Brazil. All mollusk shells adhered to each of the tubes were removed, photographed, and measured using a Zeiss AxioCam MRc5 and Zeiss AxioVision SE64 Rel 4.8 imaging software. Subsequently, the mollusk specimens were morphologically identified based on Penna (1971), Abbott (1974), Okutani (2000), Rios (2009), and Dornelas and Simone (2011). The ceriantharian specimens were identified based on Carlgren (1912), Spier et al. (2012), Stampar et al. (2012), and Stampar et al. (2016).

In order to evaluate if the shells were harboring living or dead mollusks adhered to the tubes, we observed the presence or absence of the periostracum (Meenakshi et al. 1969; Taylor and Kennedy 1969).

The mollusk shells in this study are deposited in the Museum of Zoology of the University of São Paulo (MZSP) and University Museum, Norwegian University of Science and Technology, Trondheim (NTNU-VM).

RESULTS

Every mollusk shell specimen (Figs. 1–2) in this study was found adhered on the outside of a ceriantharian tube, and none had a periostracum coating. The conchological results included both Gastropoda and Bivalvia (Table 1).

Table 1. List of species, number of specimens, and collection localities of Ceriantharia with mollusks attached to their tubes.

SPECIES	NUMBER OF SPECIMENS	LOCALITY	GASTROPODA	BIVALVIA
***Arachnanthus* sp.**	1	Brazil: São Sebastião, São Paulo	*Schwartziella bryerea* (MZSP 136925) *Turbonilla* sp. (MZSP 136926)	*Ervilia nitens* (MZSP 136927) *Chama* sp. (MZSP 136928) *Cardites micellus* (MZSP 136929) *Tivela* sp. (MZSP 136930)
Ceriantheopsis americana	1	USA: St. Andrews Bay, Florida	**-**	*Cumingia lamelosa* (MZSP 136931)
Ceriantheomorphe brasiliensis	3	Brazil: Angra dos Reis, Rio de Janeiro; Florianópolis, Santa Catarina; Laje de Santos, São Paulo	*Finella dubia* (MZSP 136945) *Parvanachis obesa* (MZSP 136948) *Bittiolum varium* (MZSP 136946) *Bostrycapulus odites* (MZSP 136944) *Caecum regulare* (MZSP 136952) *Microgaza rotella* (MZSP 136950)	*Ervilia nitens* (MZSP 136949) *Sphenia fragilis* (MZSP 136947) *Musculus lateralis (*MZSP 136951)
***Ceriantheomorphe* sp.**	1	Portugal: Aveiro Lagoon, Aveiro	**-**	*Macomopsis melo* (MZSP 136932)
Cerianthus lloydii	1	Norway: Trondheim	*Puncturella noachina* (NTNU-VM 40513)	**-**
Isarachnanthus bandanensis	1	Japan: Mizugama, Okinawa	*Cerithidea balteata* (MZSP 136938) *Eulima* sp. (MZSP 136939) *Liotella* sp. (MZSP 136940) *Emarginula* sp. (MZSP 136941) *Chrysallida* sp. (MZSP 136942) *Collonista rubricincta* (MZSP 136943)	**-**
Isarachnanthus nocturnus	2	Brazil: Salvador, Bahia and São Sebastião, São Paulo	*Bittiolum varium* (MZSP 136953)	*Basterotia elliptica* (MZSP 136935) *Ervilia nitens* (MZSP 136936) *Musculus lateralis* (MZSP 136937)

Material examined

Mollusks found on the ceriantharian tubes: **Norway**, Trondheim, on the tube of *Cerianthus lloydii* Gosse, 1859 (coll. 07.viii.1929), NTNU-VM 40513 (Fig 1O), 1 shell, Fissurellidae, *Puncturella noachina* Linnaeus, 1771. **Portugal**, Aveiro, Aveiro lagoon, on the tube of *Ceriantheomorphe* sp. Carlgren, 1931 (C. Hernandez and technical group of Aveiro University coll. 08.vi.2016), MZSP 136932 (Fig 2E, F), 3 shells, Tellinidae, *Macomopsis melo* G.B. Sowerby II, 1866. **USA**, Florida, St. Andrews Bay, on the tube of *Ceriantheopsis americana* Agassiz in Verrill, 1864 (coll. 23.ix.1993), MZSP 136931 (Fig 2G, H), 2 shells, Semelidae, *Cumingia lamellosa* G. B. Sowerby I, 1833. **Japan**, Okinawa, Mizugama, on the tube of *Isarachnanthus bandanensis* Carlgren, 1924 (coll. 07.xi.2016), MZSP 136938 (Fig 1D), 1 shell, Potamididae, *Cerithidea balteata* A. Adams, 1855; MZSP 136942 (Fig 1E), 1 shell, Pyramidellidae, *Chrysallida* sp. Carpenter, 1856; MZSP 136940 (Fig 1F), 1 shell, Skeneidae, *Liotella* sp. Iredale, 1915; MZSP 136941 (Fig 1G), 1 shell, Fissurellidae, *Emarginula* sp. Lamarck, 1801; MZSP 136943 (Fig 1I), 1 shell, Colloniidae, *Collonista rubricincta* Mighels, 1845; MZSP 136939 (Fig 1J), 1 shell, Eulimidae, *Eulima* sp. Risso, 1826. **Brazil**, São Paulo, São Sebastião, on the tube of *Arachnanthus* sp. Carlgren, 1912 (21.vii.2015), MZSP 136925 (Fig 1A), 1 shell, Zebinidae, *Schwartziella bryerea* Montagu, 1803; MZSP 136926 (Fig 1M), 1 shell, Pyramidellidae, *Turbonilla* sp. Risso, 1826; MZSP 136927 (Fig 2C, D), 6 shells, *Ervilia nitens* Montagu, 1808; MZSP 136928, 3 shells, Chamidae, *Chama* sp. Linnaeus, 1758; MZSP 136929 (Fig 2J), 1 shell, Carditidae, *Cardites micellus* Penna-Neme, 1971; MZSP 136930 (Fig 2K), 1 shell, Veneridae, *Tivela* sp. Link, 1807; Rio de Janeiro, Angra dos Reis and Santa Catarina, Florianópolis, on the tubes of *Ceriantheomorphe brasiliensis* Carlgren, 1931 (S. Stampar and A. Morandini coll. 08.vii.2009), MZSP 136948 (Fig. 1B), 1 shell, Columbellidae, *Parvanachis obesa* C. B. Adams, 1845; MZSP 136946 (Fig. 1C), 1 shell, Cerithiidae, *Bittiolum varium* Pfeiffer, 1840; MZSP 136944 (Fig. 1H), 1 shell, Calyptraeidae, *Bostrycapulus odites* Collin, 2005; MZSP 136945, 1 shell, Scaliolidae, *Finella dubia* d'Orbigny, 1840; MZSP 136947 (Fig. 2L), 1 shell, Myidae, *Sphenia fragilis* H. Adams & A. Adams, 1854; São Paulo, Laje de Santos, on the tube of *C. brasiliensis* (S. Stampar and G. Kodja coll. 22.vii.2007), MZSP 136950 (Fig 1K, L), 1 shell, Solariellidae, *Microgaza rotella* Dall, 1881; MZSP 136952 (Fig 1N), 1 shell, Caecidae, *Caecum regulare* Carpenter, 1858; MZSP 136949 (Fig. 2C, D), 1 shell, *E. nitens*; MZSP 136951 (Fig. 2I), 1 shell, *Musculus lateralis* Say, 1822; São Paulo, São Sebastião, on the tube of *Isarachnanthus nocturnus* Hartog, 1977 (S. Stampar and A. Morandini coll. 16.ix.2011), MZSP 136953 (Fig. 1C), 1 shell, *B. varium*; Salvador, Boa Viagem beach, on the tube of *I. nocturnus* (coll. 05.iv.2009), MZSP 136935 (Fig 2A, B), 1 shell, Basterotiidae, *Basterotia elliptica* Récluz, 1850; MZSP 136936 (Fig 2C, D), 1 shell, Semelidae, *E. nitens*; MZSP 136937 (Fig 2I), 1 shell, Mytilidae, *M. lateralis*.

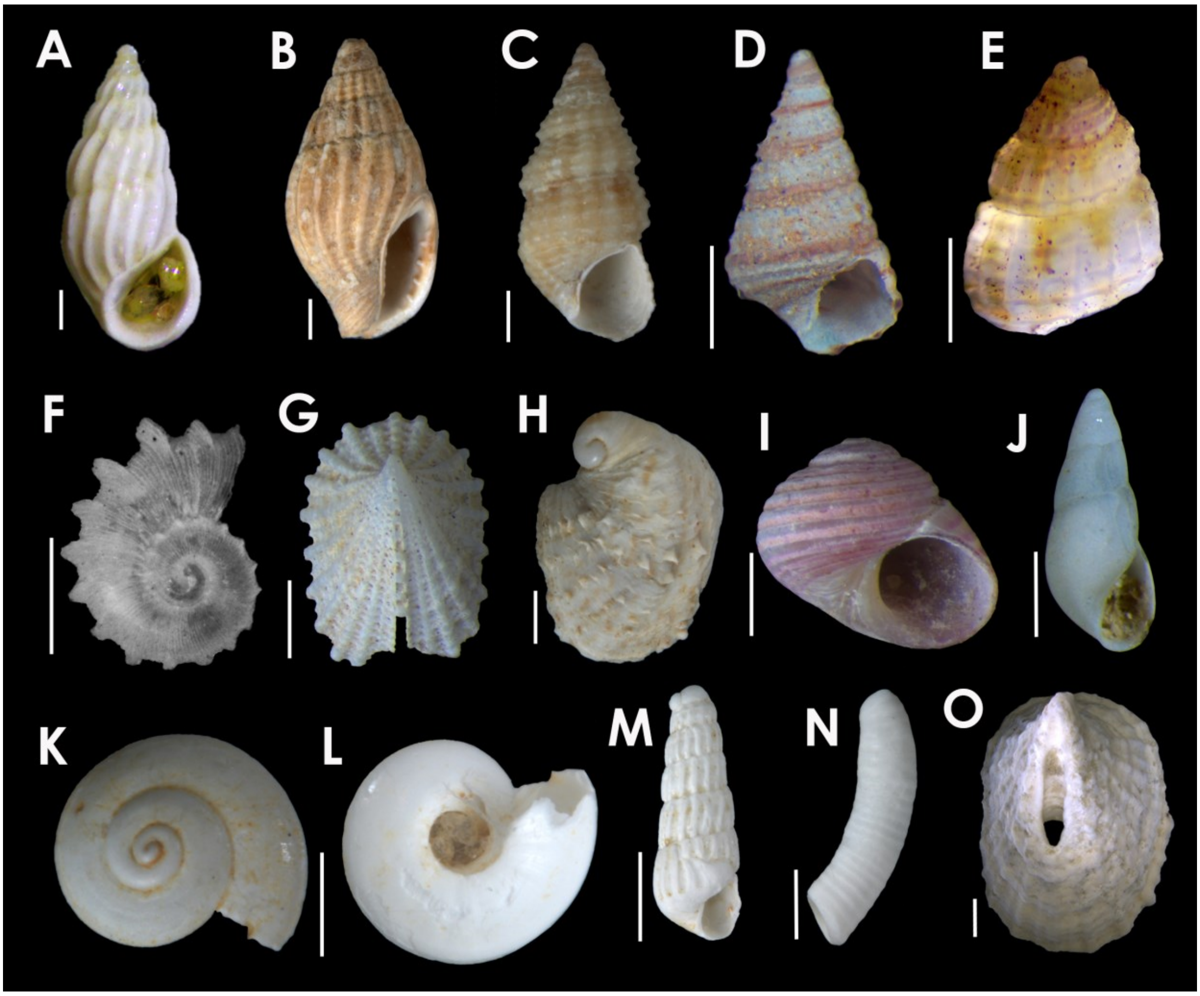

Fig 1. Gastropoda shells found on the ceriantharian tube. **A.** *Schwartziella bryerea*. **B.** *Parvanachis obesa*. **C.** *Bittiolum varium*. **D.** *Cerithidea balteata*. **E.** *Chrysallida* sp. **F.** *Liotella* sp. **G.** *Emarginula* sp. **H.** *Bostrycapulus odites*. **I.** *Collonista rubricincta*. **J.** *Eulima* sp. **K.** *Microgaza rotella*. **L.** Same in ventral view. **M.** *Turbonilla* sp. **N** *Caecum regulare*. **O.** *Puncturella noachina*. Scale: 500μm.

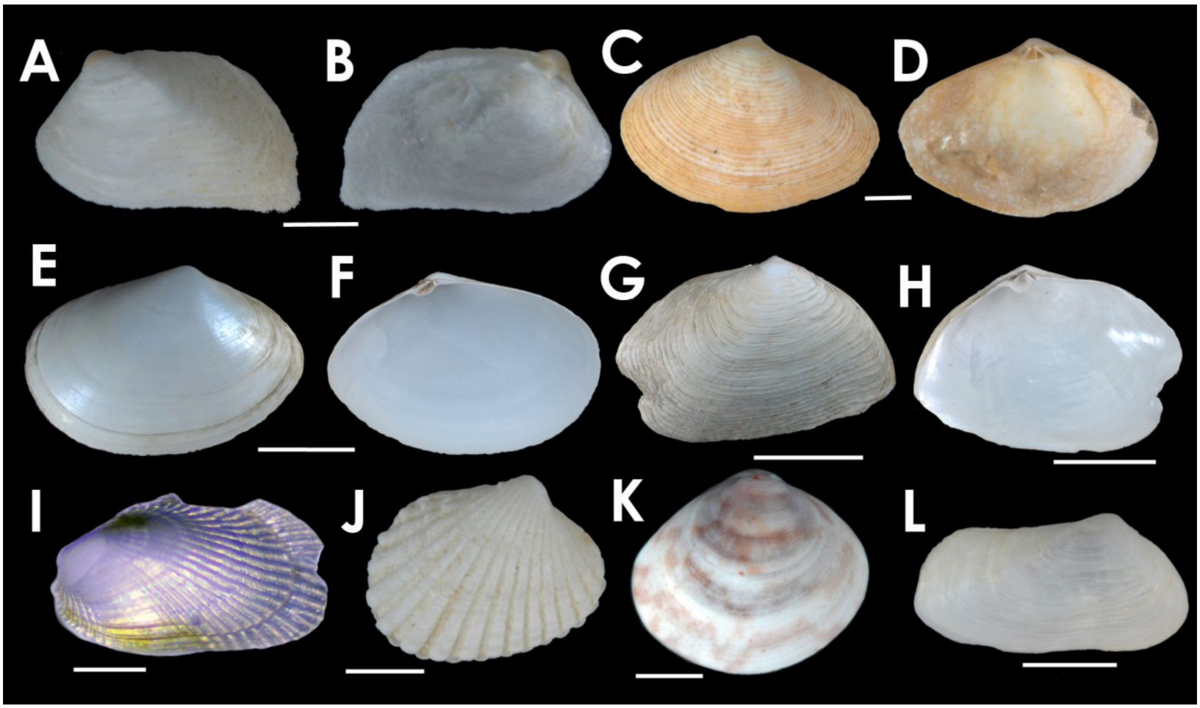

Fig 2. Bivalvia shells found on the ceriantharian tube. **A.** *Basterotia elliptica.* **B.** Same in ventral view. **C.** *Ervilia nitens*. **D.** Same in ventral view. **E.** *Macomopsis melo*. **F.** Same in ventral view. **G.** *Cumingia lamellosa*. **H.** Same in ventral view. **I.** *Musculus lateralis*. **J.** *Cardites micellus*. **K.** *Tivela* sp. **L.** *Sphenia fragilis*. Scale: **A–K** 500µm and **L** 100 µm.

Gastropods

Among the many sediments that surrounded *Arachnanthus* sp. and adhered to its fragile tube, shells of *Schwartziella bryerea* and *Turbonilla* sp. were observed. Numerous shells of *Cerithidea balteata*, *Eulima* sp., *Liotella* sp., *Emarginula* sp., *Chrysallida* sp. and *Collonista rubricincta* were found attached to the entire length of the thin and delicate tube of *Isarachnanthus bandanensis*. *Bittiolum varium* was found attached to the entire length of tubes of *Isarachnanthus nocturnus*. *Puncturella noachina* was in part adhered to the thin and fragile tube of *Cerianthus lloydii*.

On the tubes of *Ceriantheomorphe brasiliensis* the shells of *B. varium*, *Finella dubia, Parvanachis obesa*, *Bostrycapulus odites*, *Caecum regulare* and *Microgaza rotella* were noted. The tubes of *C. brasiliensis* usually have a high amount of overlap of filaments, and although this feature was also observed in the specimens in this study, no mollusk shells were found between layers, and shells were only found on the most external surfaces of the tubes.

Bivalves

Numerous shells of *Ervilia nitens*, *Chama* sp., *Cardites micellus* and *Tivela* sp. were observed adhered to the tube of *Arachnanthus* sp., while several *E. nitens*, *Basterotia elliptica* and *M. lateralis* were observed adhered to the tubes of *Isarachnanthus nocturnus*.

The shells of *E. nitens*, *Sphenia fragilis* and *Musculus lateralis* were observed upon the tubes of *Ceriantheomorphe brasiliensis* and shells of *Macomopsis melo* were observed covering considerable areas of the tube of *Ceriantheomorphe* sp. from Aveiro, Portugal.

Different from the tubes above, the only area on the tube of *Ceriantheopsis americana* where the presence of mollusk shells was observed was on its thin end that was inserted upwardly into the soft bottom. Only specimens of *Cumingia lamellosa* were observed on the tube and these were numerously and very attached to the tube.

New location report

This is the first record of *Microgaza rotella* occurring in Laje de Santos, São Paulo, in southeastern Brazil (Fig. 3I). To date, this species has been reported occurring from the southeastern United States to northern Brazil (Fig. 3A–H) (Rios 2009), and since that there are no other records in the literature compiling habitat information regarding this species in southeastern Brazil, *M. rotella* may occur naturally at this location and may be rare or allochthonous (i.e. originated in a region other than where it was found) and transported by other species.

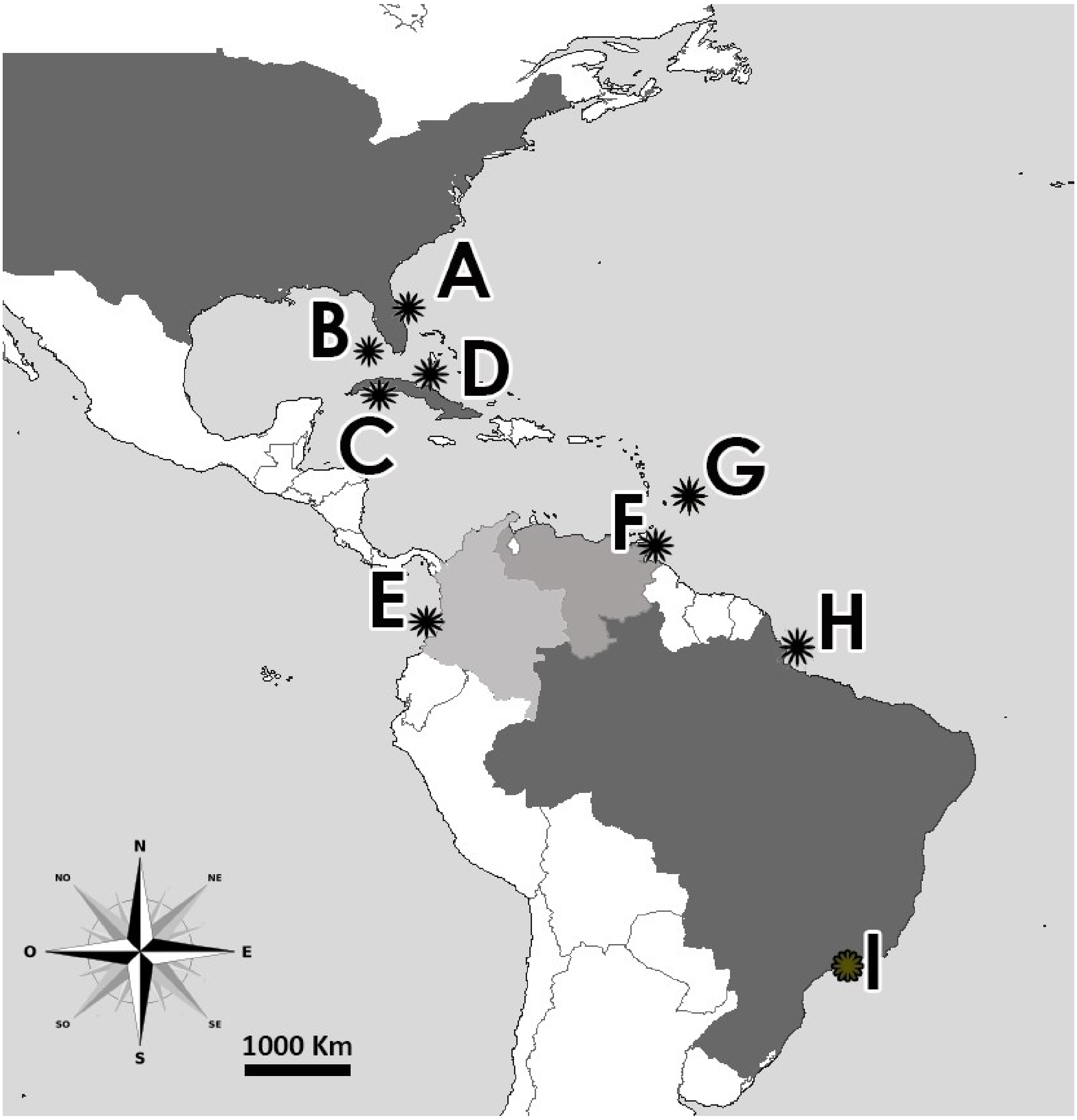

Fig 3. Records of *Microgaza rotella* in North and South Atlantic. The golden marker represents the new record of this species in southeastern Brazil. **A.** East Florida. **B.** Florida Keys. **C.** Pinar del Rio. **D.** Havana. **E.** Puerto Rico. **F.** Los Testigos. **G.** Barbados. **H.** Amapá **I.** Laje de Santos.

DISCUSSION

In our study the presence of mollusk shells was observed on all ceriantharian tubes examined. Although Schiaparelli and colleages (2005) have suggested that associations between some gastropods and ceriantharians are unlikely to happen due to mobility exhibited by the latter, we disagree with this theory as we have demonstrated that interactions between gastropod and bivalve mollusks and ceriantharians are not at all uncommon.

The absence of periostracum coating the shells suggests that the ceriantharians were not sheltering living mollusks when they were adhered to the ceriantharian tubes. Moreover, this observation can also be supported by the fact that all the shells' external surface were very worn out, indicating that they were part of the sediment of the soft bottom where the ceriantharian tubes were burrowed into. Future studies examining tube construction will be useful to provide information on the manner that mollusk shells are obtained (e.g. is there any special behavior associated?) and if it is possible that ceriantharian tubes shelter living mollusks.

Although the shells in our study were empty, mollusk shells are used by ceriantharians as an important component in the construction of their tubes. Thereby there is an architectural relationship between ceriantharians and mollusks. As well, the presence of shell remains reflects the species richness that was once present in the habitat where they were found. Bürkli and Wilson (2017) have also suggested that empty mollusk shells enable the understanding of biodiversity patterns of the Mollusca fauna found at a site and can be used to provide data on ecological and evolutionary timescales.

As in all cnidarians, ceriantharians exhibit defense strategies against predation such as the discharge of nematocysts, however the construction of tubes used as a shelter by ceriantharian species are one of the most remarkable strategies of this group. The tubes of *Arachnanthus* sp., *Cerianthus lloydii*, *Isarachnanthus bandanensis* and *Isarachnanthus nocturnus* are all arranged similarly with thin and delicate compositions. Specimens of the genus *Isarachnanthus,* different from most Ceriantharia species, move from their tubes constantly, not adding many overlapping filaments. Instead, as a protection mechanism, they produce thin branched tubes with alternative openings that allow the specimens to easily escape from predators (Stampar et al. 2015b). The thin nature of the tubes alone does not contribute as effective protection, and the addition of mollusk shells and other sediments as constituents of the tube composition may provide resistance to the tubes.

All tubes examined were all found to include large amounts of sediments, including mollusks shells. Considering that tubes have the same coloration displayed by surrounding sediments, the color of the tubes matching the color of the seabed can be thought of as homochromy (Fehse 2001) that could grant certain protection to ceriantharians by misleading potential predators.

The large amounts of bivalve shells found adhered to the tubes of *Arachnanthus* sp., *Ceriantheopsis americana* and *Isarachnanthus nocturnus* suggest that it is possible that the soft bottom surrounded by bivalves is opportune to the insertion of the ceriantharian tubes because it is probably easier to burrow into a substrate that has already been burrowed by other organisms.

In light of the results obtained, no symbiotic relationship between living Mollusca and Ceriantharia was observed. However, the use of mollusk shells by ceriantharians is seemingly beneficial to acquire protection against predation, as well as through homochromy provided by mollusk shells, and in the structural resistance and strength of tubes.

ACKNOWLEDGEMENTS

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CAPÍTULO 2.

VIVENDO NO TUBO: PERACARIDA NOS TUBOS DE CERIANTHARIA (CNIDARIA; ANTHOZOA)

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RESUMO

Peracarídeos são crustáceos macrobênticos que em sua grande parte ocorrem em ecossistemas recifais. Entretanto, algumas espécies de peracarídeos podem habitar substratos vivos como os cnidários que ao os ancorarem fornecem abrigo e substrato alternativo para o seu estabelecimento. Interações entre peracarídeos e antozoários (Cnidaria) não são incomuns, contudo quando se trata de Ceriantharia, uma subclasse dentro de Anthozoa, associações entre peracarídeos e ceriantários são um tópico com poucos estudos. Neste estudo os tubos de *Ceriantheomorphe brasiliensis*, *Ceriantheopsis lineata* e *Isarachnanthus nocturnus* foram coletados ao longo da Costa Sudeste brasileira e Oeste da Argentina e analisados por meio de técnicas de microscopia óptica, fornecendo dados quanto à associação de 29 peracarídeos com 7 tubos ceriantários. Posterior identificação resultou em 5 espécies de anfípodes, 1 espécie de isópode e uma 1 espécie de tanaidáceo. Adicionalmente, foi reportado o primeiro registro de *Photis sarae* no Estado de São Paulo. Os diferentes tipos de associações observadas entre Ceriantharia e Peracarida foram discutidos assim como as possíveis razões que os levaram a se associar.

Palavras-chave: associação simbiótica. Bioincrustação. Crustacea. Relações-interespecíficas. Substrato alternativo.

LIVING ON THE TUBE: PERACARIDA ON CERIANTHARIAN (CNIDARIA; ANTHOZOA) TUBES

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ABSTRACT

Peracarideans are macrobenthic crustaceans that mostly occur in coral reef ecosystems. However, some peracaridean species can inhabit living substrates as cnidarians that by harboring them provide shelter and alternative substrate for their settlement. Interactions between peracarideans and anthozoans (Cnidaria) are not at all uncommon, yet when it comes to Ceriantharia, a subclass belonging to Anthozoa, associations between these groups are restricted to few studies. In this study, the tubes of *Ceriantheomorphe brasiliensis*, *Ceriantheopsis lineata* and *Isarachnanthus nocturnus* were sampled along the southeastern Brazilian coast and western Argentina coast and analyzed by means of optical microscopy techniques, providing data about the association of 29 peracarideans with 7 ceriantharian tubes. Subsequent identification resulted in 5 amphipod, 1 isopod and 1 tanaidacean species. Furthermore, herein it was made the first report of *Photis sarae* in the São Paulo State. The different kinds of associations observed between Ceriantharia and Peracarida were discussed as well as the possible reasons that lead them to associate.

Keywords: alternative substrate. Biofouling. Crustacea. Interspecific-relationships. Symbiotic association.

INTRODUCTION

Interspecific interactions involving invertebrates are very common to be observed in the marine environment. Such interactions as commensalism, inquilinism, mutualism and parasitism are often established according as the partners acquire advantages or disadvantages from the associations performed. Despite the type of the association, symbiotic interactions assist at least one of the partners associated to complete part of their life cycle (Leung and Poulin 2008).

Crustacea and Cnidaria are groups known to perform symbiotic associations with a wide range of species (Wirtz 1997). Some crustaceans such as peracarideans are shrimp-like macrobenthic animals spread worldwide but mostly found in coral reef ecosystems (Thomas 1993). In general, peracarideans are looked upon free-living animals, however some species of this group are found inhabiting living substrata as cetaceans, mollusks, echinoderms, sponges, urochordata, chelonians, decapods and cnidarians (Barnard 1967; Harbison et al. 1977; Laval 1980; Vader 1983; Oshel and Steele 1985; Dittrich 1987; Dalby 1996; Vader and Krapp 2005; Thomas and Klebba 2007; Voultsiadou et al. 2007). Some anthozoans (Cnidaria) can host peracarideans providing shelter, feeding grounds and alternative substrate during part or whole life-cycle stages (Harbison et al. 1977; Dittrich 1988; Gasca and Haddock 2004). Contrarily, some others such as ceriantharians (Anthozoa; Ceriantharia) present few studies reporting interactions with other groups. Ceriantharians or tube-dwelling-anemones belong to a group of animals with tubes produced by cnidae filaments. The composition of these tubes is based on the addition of sediments, found in the vicinity of the soft bottom where the tubes are lodged, to an adherent mucus containing filaments of ptychocysts produced by the ceriantharians (Stampar et al. 2015a). Some species might be negatively affected by the toxins contained in the filaments, yet members of some groups such as Bryozoa, Phoronida, Sipuncula and Foraminifera are found associating with the ceriantharian tube (Tiffon 1987; Stampar et al. 2010; Vieira and Stampar 2014).

In view of the peculiar composition exhibited by the ceriantharian tube, species associated with these tubes must retain or develop adaptations that enable interspecific associations with ceriantharians (Landmann et al. 2015). Once that these adaptations are sufficiently effective to overcome the barriers that prevent associations with these animals, interspecific interactions with anthozoans can be highly profitable for both or at least one associated partner given the host's great longevity and the capability of providing protection against potential predators (Ross 1971) and food resources to their symbionts (Vader 1983).

Associations between peracarideans and anthozoans are not uncommon (Ansell 1969; Vader 1983), however most of the reported associations are often described occurring between specimens of Peracarida and Actiniaria (Della Valle 1893; Vader 1967) while the associations between Peracarida and Ceriantharia are described in a restricted number of studies.

Ansell (1969) first reported a possible association between a peracaridean, *Acidostoma neglectum* Bate and Westwood, 1861 and a ceriantharian, *Cerianthus lloydii* Gosse, 1859 suggesting an apparent ectoparasitism by the crustacean due to its mouthparts arrangement (Dahl 1959b) suitable to suck the internal fluids of the polyp and thus steal part of its food. This was verified by the presence of nematocysts in their stomach content. Later, Moore and Cameron (1999) described the association between *Photis longicaudata* Bate and Westwood, 1862 (Peracarida; Amphipoda) and again *Cerianthus lloydii*. In their study, it was observed a massive fouling of amphipods assembled on the top of the ceriantharian tube.

The above scenario indicates that information about the use of alternative soft substrata such as the ceriantharian tube are scarce, thus the aim in this study is to investigate, analyze and record the Peracarida community inhabiting ceriantharian tubes and to discuss the possible reasons that lead these groups to associate in Western South Atlantic.

MATERIAL AND METHODS

Sampling and preservation

The sampling was carried out by SCUBA diving in northwestern Argentina and in southeastern Brazil (Table 1). The collected ceriantharians were dislodged from their tubes and the latter were kept separately in glass containers duly labelled regarding the species name, date and collect location. The preservation of the tubes was made initially with formalin 4% and posteriorly all the material was transferred to ethanol 70% for maintenance.

Table 1. List of Ceriantharia species, number of specimens and locations where the ceriantharians that exhibited peracarideans attached to their tubes were collected.

SPECIES	SPECIMENS	LOCATION
***Ceriantheomorphe brasiliensis* Carlgren, 1931**	5	Brazil: Angra dos Reis (RJ) Arraial do Cabo (RJ) Laje de Santos (SP) São Sebastião (SP)
***Ceriantheopsis lineata* Stampar, Scarabino, Pastorino & Morandini, 2015**	1	Argentina: Port of Quequén (Bs.As.)
***Isarachnanthus nocturnus* Hartog, 1977**	1	Brazil: São Sebastião (SP)

Identification

The tubes were assessed, both outside and inside, regarding the fauna inhabiting them. The specimens found adhered to them or in between layers were removed, photographed and identified morphologically to species and family using specific keys and figures.

The specimens found on the ceriantharian tubes were sent to the Museum of Zoology, University of Campinas (UNICAMP) – (ZUEC).

RESULTS

In our study, 29 peracarideans were observed associating with tubes of three ceriantharian species. We found 8 families, including 5 amphipod species, 2 isopod species and 1 tanaidacean species (Table 2).

Table 2. List of Peracarida found on the ceriantharian tubes.

	PERACARIDA		
HOST	**AMPHIPODA**	**ISOPODA**	**TANAIDACEA**
Ceriantheomorphe brasiliensis	*Cymadusa filosa* Savigny, 1816 (Ampithoidae – 4 specimens) *Elasmopus pectenicrus* Bate, 1862 (Maeridae – 1 specimen) *Photis sarae* Souza-Filho & Serejo, 2010 (Photidae – 10 specimens) *Ampelisca* sp. Krøyer, 1842 (Ampeliscidae – 1 specimen)	*Paranthura urochroma* Pires, 1981(Paranthuridae – 1 specimen)	*Chondrochelia savignyi* Kroyer, 1842 (Leptocheliidae – 9 specimens)
Ceriantheopsis lineata	*Monocorophium* sp. Bousfield and Hoover, 1997 (Corophiidae – 1 specimen)	*Idotea balthica* Pallas, 1772 (Idoteidae – 1 specimen)	-
Isarachnanthus nocturnus	*Photis sarae* (1 specimen)	-	-

Most of the peracarideans were settled in areas of the tubes far from the ceriantharian tentacles, thus it is likely that they were not easily reached by the ceriantharian. No specimen was found inside or among tube layers.

Description of the tubes and associations

<u>*Ceriantheomorphe brasiliensis*</u>

This species usually builds a single tube with nearly the same size exhibited by the polyp. The tube is placed in a vertical position into unconsolidated sediments and normally present only one opening through where the ceriantharian can extent their tentacles (Stampar et al. 2015a).

<u>Rio de Janeiro/Angra dos Reis:</u> the tube presented an extremely soft and fragile texture with variable coloration from light brown inside to a light brown mixed with darker layers outside. It was easily disrupted into a goo-like substance when handled. Although delicate, the tube was stout in its medial portion while its ends were slim and carried few layers overlapped. In the stouter areas small fragments of mollusk shells were observed and internally it was noticed many perforations filled with orange sediments.

Some specimens of *Cymadusa filosa* (Amphipoda) and *Paranthura urochroma* (Isopoda) were found soaked in a great number of ptychocyst filaments detached from the tube and floating on the water, thereby it was not possible to distinguish whether the filaments had been released by the internal or external wall of the tube.

<u>Rio de Janeiro/Arraial do Cabo:</u> the soft and malleable dark gray tube of this specimen presented few layers overlapped along with a slender but consistent thickness. In its external wall, it presented some rugged areas where it was observed superficial perforations, however no specimen was found between the layers in these areas.

Although the internal wall of the tube presented an absolute flat and flawless texture, some regions, mainly the sides, were tearing apart into a cotton-like consistency possibly because of the time and/or mode of preservation. Amphipods *Photis sarae* were found covered in filaments that adhered them to the external wall of the tube.

São Paulo/Laje de Santos: the tube was partially thick with few sediments found on its outer wall that presented a slightly rugged texture with cotton-like regions. However, internally, its texture was smooth and no sediment or interaction with other species was noted. The coloration varied from brown on the outside and lighter brown on the inside.

The amphipods *P. sarae* and *Ampelisca* sp. were observed only on the smoother cotton-like external regions of the tube coated by filaments.

São Paulo/São Sebastião: in general, the tubes were composed by uneven layers that granted that its medial portion was thicker than the ends. Due to these uneven areas, externally the tubes displayed many smooth gaps alternating with rugged areas where there were layers overlapping heavily. However, the internal part of the tubes exhibited a smooth and resistant texture. Some of the internal and external regions could be easily mistaken with each other because the external smooth gaps resembled the internal part of the tube. Externally, the tubes coloration was brown and internally it exhibited a chestnut brown color with some remarkable lighter lines arranged along the tubes.

The amphipods *Cymadusa filosa* and *Elasmopus pectenicrus* were both coated by filaments and found anchored to one of the tubes while a group of uncoated tanaidaceans *Chondrochelia savignyi* were observed on the external gaps of the other tube where its texture was smoother.

Ceriantheopsis lineata

This species is restricted to Atlantic waters Their tubes are dead-end sacks, vertically positioned into the soft bottom and usually built in less than 2 days (Stampar et al. 2016).

Buenos Aires/Port of Quequén: externally, it was observed the overlapping of many layers along with ripples that contributed to the thick and resistant aspect of this tube. Internally however it was utterly smooth, apart from a few bulges in some areas, and more resistant than outside. On the outside, it exhibited a brown coloration and on the inside a chestnut brown color.

Although the heavy tube of *C. lineata* enabled that many layers were ripped off it without compromising its structure, no specimen was found among layers. However, the specimens observed, *Monocorophium* sp. (Amphipoda) and *Idotea* *balthica* (Isopoda), were found adhered to the filaments that covered the external wall of the tube.

Isarachnanthus nocturnus

The construction of the tube pattern of this species differs from the pattern observed for most of the species of Ceriantharia. Instead of building one single tube positioned vertically into the bottom and with only one opening, this species builds a tube system with several openings, providing alternative escape routes from predators (Stampar et al. 2015b).

São Paulo/São Sebastião: the tube texture was uneven outside and highly covered by algae stalks where one specimen of *Photis sarae* was observed. This amphipod was not directly anchored to the tube nor adhered to it, instead it was found among the algae covering the tube. Coarse gravel as crystals were observed on the external wall of the tube as well as in between the layers of it. Internally, it exhibited a bright gray color that was clouded by a slim and smooth translucent membrane that allowed the view of crinkles on the outside wall of the tube.

DISCUSSION

Most of the amphipods and isopods observed anchored to the ceriantharian tubes were coated by ptychocyst filaments (e.g. *Ampelisca* sp., *Cymadusa filosa*, *Idothea balthica*, *Monocorophium* sp., *Paranthura urochroma*, and *Photis sarae*) while the uncoated specimens such as the tanaidaceans were not observed hardly attached to the tubes. Thus, it is likely that the ptychocyst filaments own an adhesive property used by peracarideans as an anchoring method to settle on the ceriantharian tube while uncoated specimens must present an alternative anchoring method to keep them on the tube. Nonetheless, the stinging property exhibited by ptychocyst filaments can be harmful to many species. In this way, peracarideans must carry or develop adaptation mechanisms that enable the contact with ptychocysts. Similar to the study of Crawford (1992) with *Ancylomenes pedersoni* Chace, 1958 (Crustacea; Decapoda) and its anthozoan host, it is possible that the coated peracarideans gradually acclimate to the ptychocyst filaments and eventually endure the toxins contained in them. As a consequence to the endurance acquired, peracarideans remain protected when associated with the ceriantharian tube.

In our study, we observed the tube-dwelling tanaidacean *Chondrochelia savignyi* associating with the tubes of *Ceriantheomorphe brasiliensis*. Since no specimen was coated by filaments their adhesion to the tubes layers was minimal. Although the Tanaidacea biology is poorly known (Greve 1967; Suárez-Morales et al. 2011), the wide morphological diversity exhibited by these animals enables the distribution in several habitats and support the interaction with species from many taxonomic groups (Kitsos et al. 2005; Larsen 2005; Morales-Vela et al. 2008). *Chondrochelia savignyi* is a suspension-feeder that possibly found food and shelter in the ceriantharian tube. The water currents caused by the ceriantharian tentacles favor the suspension-feeding of the associate tanaidaceans that use the suspended food scraps from the ceriantharian feeding activity as a nutritional source, as Sepúlveda and colleagues (2003) proposed for peracarideans associating with ascidians.

Although the tube-dwelling amphipods, isopods and tanaidaceans in our study could burrow directly into the soft bottom forming mucous tubes where they usually inhabit (Greve 1967; Johnson and Attramadal 1982; Thistle et al. 1985), the peculiar composition exhibited by the ceriantharian tube can offer an additional protection from predators playing an important role as an alternative substrate to harbor these animals. Furthermore, to inhabit the ceriantharian tube seems to be energetically beneficial. For instance, the amphipod *Photis sarae* observed associating with the tubes of *Isarachnanthus nocturnus* and *C. brasiliensis* usually build soft tubes from the adhesion of mucus secreted by themselves to sediments and at times organisms such as algae (Souza-Filho and Serejo 2010) which is very similar to the way that the ceriantharian tube is built. However, no tube of this species was found. Thereby, making use of the ceriantharian tube instead of building their own can also be a profitable alternative to save energy and acquire shelter altogether.

Similar to the tanaidaceans mentioned hitherto, *P. sarae* observed on the tube of *I. nocturnus* also had no filaments coating its body. Despite that, staying among the algae stalks presented all over the ceriantharian tube is seemingly a good camouflage strategy to mislead predators and remain unnoticed. Moreover, it is noteworthy that *P. sarae* had only been reported in the State of Rio de Janeiro (Souza-Filho and Serejo 2010) and this is the first record of this species in the São Paulo State.

The addition of sediments from the seabed to the layers of the ceriantharian tube gives the tube a certain similarity with the bottom's coloration. Such factor could support the tubes predation by demersal fishes (i.e. bottom feeders). However, it does not occur due to the tube's ptychocyst-rich composition that is harmful to species unadapted to this feature. It is possible that the tubicolous specimen *Ampelisca* sp. observed in association with the tube of *Ceriantheomorphe brasiliensis* has found refuge in such substrate against the predation by demersal fishes that have ampeliscids as an important food resource (Valerio-Berardo et al. 2005; Valerio-Berardo and Wakabara 2006).

Although inconspicuous, the ceriantharian tube is a very soft structure that could be used on the nutrition of amphipods once their mouthparts were modified for the consumption of soft-bodied organisms (Harbison et al. 1977). The tubes of *Ceriantheomorphe brasiliensis* and *Ceriantheopsis lineata* were very thick and resistant. Such consistency is not uncommon since ceriantharians are able to constantly build their tubes and repair them from eventual damages (e.g. predation) by adding layers to it throughout time (Stampar et al. 2015a). Five Amphipoda species (*Ampelisca* sp., *Cymadusa filosa*, *Elasmopus pectenicrus*, *Monocorophium* sp. and *Photis sarae*) were observed associating with these tubes. There are authors that consider amphipods as parasites (Dahl 1959a,b), food-parasites (Orton 1922) and others as both depending on the developmental stage of the specimen (Dittrich 1987). Vader (1983) however established that the associations between amphipods and other marine invertebrates are mostly ectocommensalism, endocommensalism or occur over protection or micropredation. Since we observed no evident predation sign on the tubes of *C. brasiliensis* and *C. lineata*, and no apparent damage on the amphipods, we suggest that the amphipod-ceriantharian association is not based on predation and is more likely an ectocommensalism or inquilinism. Yet, in order to validate this hypothesis a more detailed study of the amphipods stomach contents and mouthparts is required (Dahl 1936; Dahl 1959a; Oshel and Steele 1985; Dittrich 1992).

Association between peracarideans and ceriantharian tubes can be very profitable to peracarideans (Moore and Cameron 1999) that acquire protection, shelter and food resources by anchoring on such substrate. On the other hand, ceriantharians do not acquire any advantage or disadvantage from the association, thereby the ceriantharian-peracaridean associations can be either assigned as both ectocommensalism or/and inquilinism. Moreover, ceriantharian tubes seem to be a suitable alternative substrate for the dwelling of Peracarida crustaceans, especially for tubicolous and infaunal specimens that usually burrow into sediments or anchor on fixed or mobile habitats seeking shelter.

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CAPÍTULO 3.

COLONIALISMO EM CERIANTHARIA (CNIDARIA; ANTHOZOA)

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RESUMO

Ceriantários ou anêmonas-de-tubo são conhecidos por sintetizarem tubos macios e flexíveis feitos de muco, filamentos de células urticantes (pticocistos) e sedimentos encontrados em fundos marinhos macios onde este é inserido. Os tubos têm por função alojar e proteger ceriantários de condições hostis como a predação. Muitas espécies utilizam o tubo ceriantário como um substrato alternativo, entretanto pouco se sabe quanto a estrutura organizacional de espécies de Ceriantharia em seus próprios tubos. Normalmente ceriantários são considerados animais solitários, neste estudo no entanto reportamos o primeiro registro de uma colônia de Ceriantharia envolvendo espécimes de *Botrucnidifer norvegicus.* Apesar disso, mais estudos a respeito da estrutura de populações em colônias de ceriantários são essenciais para um melhor entendimento desse novo hábito.

Palavras-chave: agregações. Anêmonas-de-tubo. Cnidaria. Estrutura de populações.

COLONIALISM IN CERIANTHARIA (CNIDARIA; ANTHOZOA)

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ABSTRACT

Ceriantharians or tube-dwelling anemones are known for synthetizing soft and flexible tubes made of mucus, cnidae filaments (ptychocysts) and sediments found on the soft bottom where the tube is buried. These tubes are used to lodged and protect ceriantharians from hostile conditions such as predation. Many species use the ceriantharian tube as an alternative substrate, however little is known about how is the organizational structure of Ceriantharia species in their own tubes. Usually, ceriantharians are taken as solitary animals, in this study however it is reported the first record of a Ceriantharia colony involving *Botrucnidifer norvegicus* specimens. In spite of that, more studies regarding the population structure in ceriantharian colonies are essential for a better understanding of this new habit.

Keywords: assemblages. Cnidaria. Population structure. Tube-dwelling anemones.

INTRODUCTION

Ceriantharians or tube-dwelling anemones are animals known by the ability to produce flexible and soft tubes from the adhesion of sediments from the seabed to cnidae filaments (ptychocysts) covered by mucus in order to acquire protection (Stampar et al. 2015a).

These animals are always assigned as solitary organisms with a single tube as their home (Kim and Huys 2012). However, some evidences in the family Arachnactidae indicate that the above-mentioned pattern is not very cohesive, and a polyp can produce more than one tube or branched tubes structured as a tube system (Den Hartog 1977; Stampar et al. 2015b). However, still retaining the solitary condition.

Assemblages are usually formed in response to changes in environmental conditions inadequate for single organisms with limited resources. Consequently, environmental changes can lead to a possible competition over space. In this way, specimens can gather together and vary their niches in order to more efficiently use the few resources available (Jackson 1977; Edwards and Stachowicz 2010).

The organization of marine invertebrate colonies is habitat-dependent and it is related to many factors such as space, specimen sizes, energy intake and cost, prey availability, prey capture surface and physiological stress (Jackson 1977; Sebens 1979; Hughes 1984). Furthermore, mortality rate plays an important role determining both growth and fecundity rates in colonies (Sebens 1979; Hughes 1984; Edwards and Stachowicz 2010).

Based on this scenario, the present study focuses on the description of the first colony of Ceriantharia specimens and discusses the implication of this behavior for the ecology of these animals.

MATERIAL AND METHODS

Five tubes of *Botrucnidifer norvegicus* Carlgren, 1912 deposited in the zoological collection of the University Museum, Norwegian University of Science and Technology, Trondheim (NTNU-VM) were observed through optical microscopy techniques. The specimens were observed and photographed with the use of a Leica MZ16A stereomicroscope, a Leica DFC 420 camera and the Las 4.5 (Leica application Suite) imaging software. All the tubes were preserved in ethanol 70%.

RESULTS AND DISCUSSION

The tube of *B. norvegicus* is usually nearly as long as the polyp, narrow, slim, presenting either a grey or brownish color, one opening and is inserted uprightly in the soft bottom (personal observation). However, the ceriantharian tube in general may vary in its singularity, size and how deeply it is buried in the soft bottom according to the habit of the species (Den Hartog 1977; Stampar et al. 2015a; Stampar et al. 2015b). The tube of *Isarachnanthus nocturnus* Hartog 1977, for example, is a branched system with more than one opening and alternatives routes (Jensen 1992; Stampar et al. 2015b) while most of the ceriantharian species build single tubes with only one opening. Regarding the size, species like *Ceriantheomorphe brasiliensis* Carlgren, 1931 and *Pachycerianthus schlenzae* Stampar et al., 2014 present tubes nearly as long as their bodies (Stampar et al. 2010; Stampar et al. 2014) while others species such as *Ceriantheopsis lineata* Stampar et al., 2016 (Stampar et al. 2016) and *Cerianthus lloydii* Gosse, 1859 have tubes much longer than their bodies. The tube of *Arachnanthus sarsi* Carlgren, 1912 can be found buried in shallow waters (Picton and Manuel 1985) while the branched tube of *Cerianthus vogti* Danielssen, 1890 is found deeply buried in deep waters (Jensen 1992).

In 3 of the 5 samples (NTNU-VM 40494, NTNU-VM 40506, NTNU-VM 40515) observed in our study, there were several small sized (0.5 – 5cm) specimens of *B. norvegicus* organized in a tube system with several openings, forming a colony.

These tube systems were similar to a soft grey amorphous mass and they lodged from 6 to 17 ceriantharians (Fig. 1) not uniformly spread throughout the tube, with some specimens found very close to each other and others further away. Furthermore, we also observed a delicate membrane covering the portion of the ceriantharians body lodged inside the tube (Fig. 2) and, given the difficulty on removing the specimens out of the tube, we believe that this membrane prevents that other specimens succeed at pulling the ceriantharians out of the tube easily.

Fig. 1 Tube lodging many specimens of *Botrucnidifer norvegicus*.

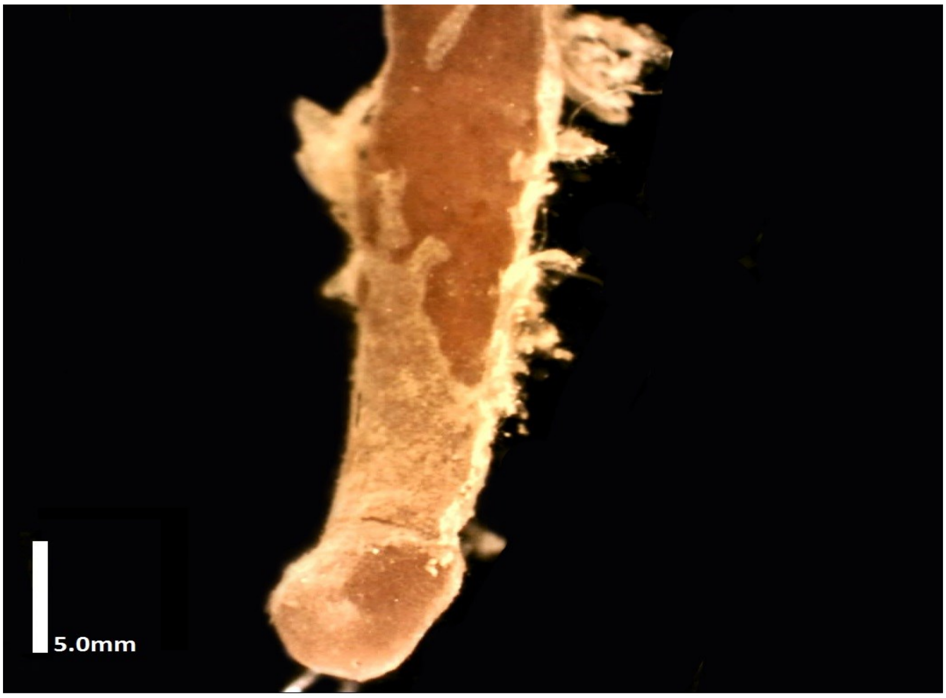

Fig. 2 Membrane covering *Botrucnidifer norvegicus* body.

The specimens varied in the depth they were housed in the tubes, some with whole body and others with only half enclosed inside the tube. But all polyps presented their tentacles outside the tube, as expected in their natural behavior (Fig. 3).

Fig. 3 Tentacles of *Botrucnidifer norvegicus* outside the tube.

Solitary specimens of *B. norvegicus* are bigger than colonial ones (personal observation). That is expected in most marine invertebrate species (Marshall et al. 2006) since colonial specimens are physiologically connected (Boardman et al. 1973) and thus all the organisms that compose a colony share small amounts of energy, maximizing the energy intake and cost in general to the entire colony (Sebens 1979).

This is the first record of a Ceriantharia colony ever reported, thus it is essential more studies regarding the population structure. How does these assemblages occur? How is the tube built? What about the effects that the organisms hold on each other when it comes to competition for space and food resources? These questions remain open, but are interesting subjects for further studies.

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CAPÍTULO 4.

VIVENDO EM UMA CASA ARDENTE: POLIQUETA EM TUBOS CERIANTÁRIOS (CNIDARIA; CERIANTHARIA

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RESUMO

Fundos marinhos são os habitats mais difundidos. Suas amplas extensões cobertas por sedimentos são utilizadas por muitas espécies de diversas formas. Entre os organismos que vivem nesses ambientes, poliquetas e ceriantários podem ser incluídos. Poliquetas são muito diversos em composição de espécies, comportamentos alimentares, reprodução, formas corporais e, logo, sua alta plasticidade os permite ocupar uma ampla variedade de ambientes e também os permitem se enterrarem e/ou habitarem substratos incomuns. A fauna de Polychaeta é frequentemente reportada em regiões tropicais cujas condições ambientais amenas contribuem para coletas com maior facilidade. O mesmo, entretanto, não é observado para a fauna Nórdica também devido a condições ambientais, neste caso adversas. Além disso, relações simbióticas envolvendo poliquetas Nórdicos com outras taxa não são amplamente discutidas e registros quanto a associações com ceriantários são incomuns. Ainda assim, as muitas adaptações desenvolvidas por poliquetas ao longo da evolução os permitiu se associarem com muitos grupos. Embora improvável de abrigar espécies devido a sua organização macia aliada à sua composição peculiar, o tubo ceriantário é um adequado substrato alternativo amplamente utilizado por muito grupos. Estudos que discutem interações entre Ceriantharia e Polychaeta do Norte e Oeste da Europa e América do Sul nunca foram reportados antes. Desta forma, neste estudo foram descritas associações entre 16 famílias de poliquetas e 6 espécies de Ceriantharia, discutindo as possíveis razões que levaram essas associações a ocorrerem.

Palavras-chave: anêmonas-de-tubo. Associação simbiótica. Relações interespecíficas. Substrato alternativo. Fundos macios.

LIVING IN A SPICY HOUSE: POLYCHAETA IN CERIANTHARIAN TUBES (CNIDARIA; CERIANTHARIA)

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ABSTRACT

Sea bottoms are the most widespread habitats. Their large extensions covered by sediments are utilized by many species in very diverse ways. Among the bottom-dwellers polychaetes and ceriantharians can be encompassed. Polychaetes are very diverse in species composition, feeding behaviors, reproduction, body shapes and, so, their high plasticity enables them to be found in a broad range of environments and also allows them to burrow into unusual substrata or/and to inhabit it. The polychaete fauna is often reported in tropical regions whose environmental conditions contribute to an easier sampling. The same however is not observed to the Nordic polychaete fauna also due to environmental conditions, in this case adverse. Moreover, symbiotic relationships involving Nordic polychaetes with other taxa is not widely discussed and reports with regard to associations with ceriantharians are uncommon. Still, the many adaptations developed by polychaetes in general along evolution enabled them to associate with many groups. Although unlikely to harbor species due to its very soft organization allied to its peculiar composition, the ceriantharian tube is a suitable alternative substrate widely used by many groups. Studies discussing Ceriantharia-Polychaeta interactions from northern and western Europe and South America has never been reported. In such way, in this study it was described associations occurring between 16 polychaete families and 6 Ceriantharia species, discussing the possible reasons that lead these associations to occur.

Keywords: alternative substrate. Interspecific-relationships. Soft bottoms. Symbiotic association. Tube-dwelling anemones

INTRODUCTION

Sea bottoms are one of the most prevalent habitats on Earth, only losing in habitable spaces to the water column above it. Most of the bottoms present large extensions covered by many kinds of sediments, from gravel to fine grains and muds utilized by distinct species in different ways (e.g. feeding, lodging, tubes construction) (Snelgrove 1997,1999). Evidently, these areas are habitats of several bottom-dwellers, including polychaetes and ceriantharians.

Benthic forms such as polychaetes are commonly found on soft-bottoms (Knox 1977) where they play an essential role in bioturbation and in the seabed's renewal conditions by altering the sediment properties and abundance on the bottom during burial of organic matter gathered on the seabed. Consequently, this process affects trophic webs (Snelgrove 1997; Díaz-Castañeda and Reish 2009; Díaz-Castañeda et al. 2014). Nonetheless, polychaetes are also highly sensitive to environmental alterations that occur on soft bottoms and therefore are great indicators of environmental conditions (e.g. pollution, benthic environment quality, organic matter abundance) (Dauvin et al. 2007; Martinez-Garcia et al. 2013).

The diversity of species composition, feeding behaviors, reproduction and body shapes exhibited by polychaetes is noteworthy (Fauchald and Jumars 1979; Hutchings 1998; Petersen 1999; Jumars et al. 2015). Furthermore, the plasticity presented by these animals varies according to the particular behavior exhibited by the specimen (Blake and Hilbig 1994) which enables polychaetes to be found in a broad range of environments, conditions, depths and also allow them to burrow into unusual substrata or/and to inhabit it (Glasby et al. 2016).

Along evolution, polychaetes have developed gradual adaptations regarding their shape, coloration and behavior. These adaptations granted them a great diversity of life styles and enabled that several species could symbiotically interact with distinctive partners such as sponges, crustaceans, mollusks, ascidians and cnidarians as commensals or parasites in order to obtain some profit (e.g. shelter, food, reproduction site) or to increase their lifespan (Knox 1977; Martin and Britayev 1998). Despite the kind of symbiotic relation performed, one of the partners involved always obtain some benefit (Leung and Poulin 2008).

In general, species descriptions and estimates of abundance are related to the biogeographical region in which the species are found (Hutchings 1998). Due to the environmental conditions, mild temperatures and facility in sampling, the polychaete fauna in tropical regions is well reported and thus abundant when compared to other regions (Carvalho et al. 2017; Dean 2017). Inversely, although the faunal composition varies according to habitat heterogeneity and depths, species found in deeper slopes are bathymetrically restricted and therefore in deep seas the fauna is poorly known due to the low sampling coverage, glaciation events, and adverse environment conditions (Gray 1994,1997; Buhl-Mortensen et al. 2012; Oug et al. 2017). Moreover, symbiotic relationships involving polychaetes with other taxa is not widely discussed and reports with regard to associations with ceriantharians are uncommon.

Ceriantharians (Cnidaria; Anthozoa) are tube-dwelling animals that synthetize their tubes primordially with the use of mucus containing a special type of cnida, ptychocyst, only found in this group. Although unlikely to harbor species due to its very soft organization allied to its peculiar composition (see more in Stampar et al. 2015), the ceriantharian tube is a suitable alternative substrate to a considerable number of marine invertebrates like copepods, phoronids, amphipods and sipunculans (Ansell 1969; Stampar et al. 2010; Kim and Huys 2012).

Up to now, Ceriantharia-Polychaeta interactions were only poorly reported, especially in Atlantic Ocean. In such a way, this study is focused on describing and ecologically discuss the relation between families of polychaetes and ceriantharians.

MATERIAL AND METHODS

The studied material (Table 1) was collected by SCUBA diving in western Argentina, northeastern and southeastern Brazil, western Portugal and western Norway (Fig. 1).

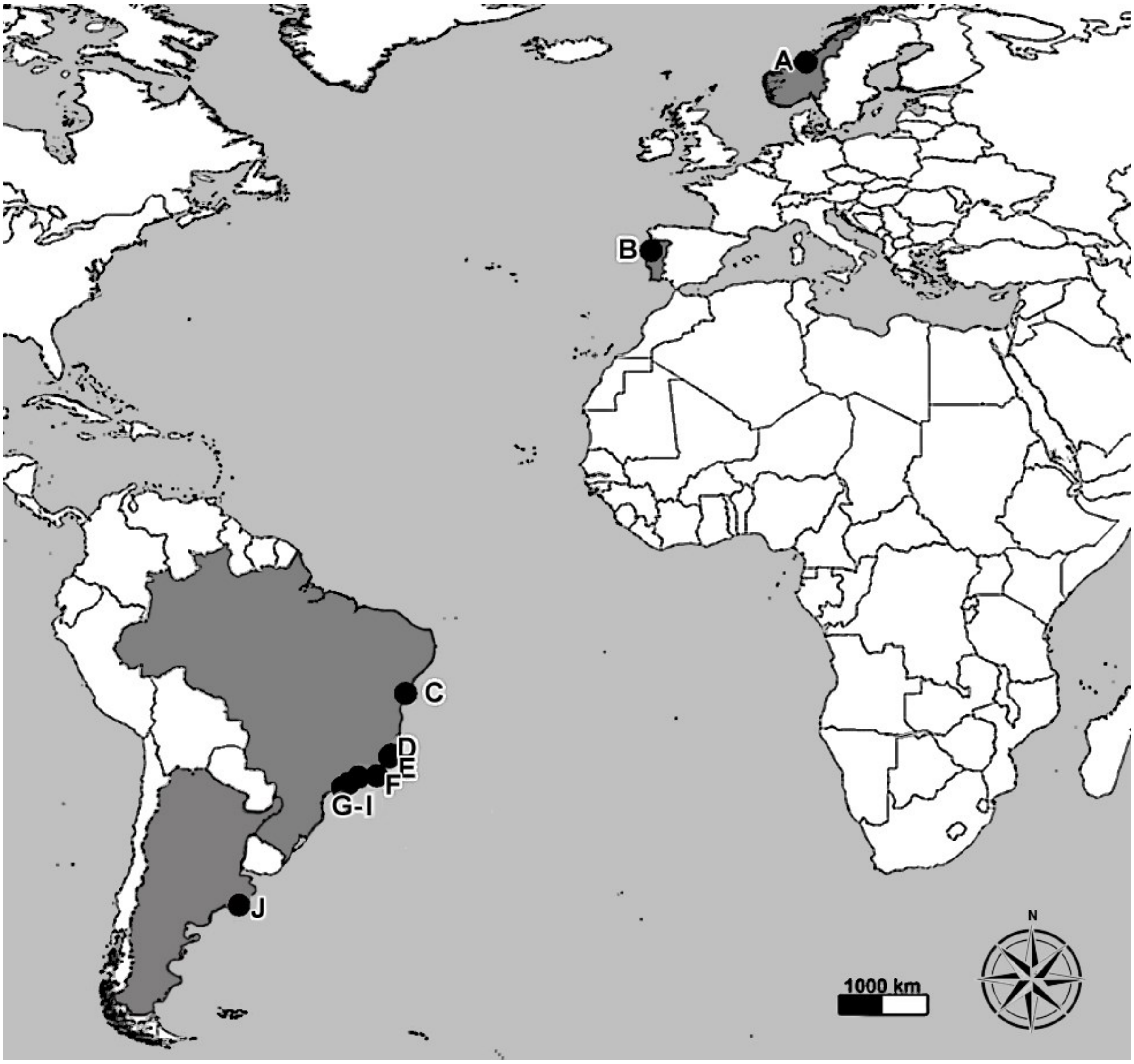

Fig 1. Map with sampling areas. **A.** Stadsbygd and Agdenes Norway; **B.** Aveiro, Portugal; **C.** Salvador, Brazil; **D.** Vitória, Brazil; **E.** Guaraparí, Brazil; **F.** Arraial do Cabo, Brazil; **G-I.** Angra dos Reis, Laje de Santos and São Sebastião, Brazil; **J.** Quequén, Argentina.

Two specimens that had been previously deposited in the zoological collection of the Norwegian University of Science and Technology, NTNU University Museum, Trondheim (NTNU-VM) were also analyzed (NTNU-VM 40494/NTNU-VM 40515).

The material collected in Argentina, Brazil and Portugal was preserved in formalin 4% and posteriorly maintained in ethanol 70%.

The tubes were preserved along with their ceriantharians, except some of *Isarachnanthus nocturnus* and *Ceriantheomorphe* sp., these were dislodged from the tubes and put in separate labelled trails containing ethanol 70% before the tube analyzes were carried out.

The analyzes performed on the ceriantharian tubes aimed to detect symbiotic interactions occurring between marine polychaetes and ceriantharians. All the polychaetes found anchored to the tubes were removed and put into separate vials containing 70% ethanol and labelled with the ceriantharian tube species name and location where it was collected.

The identification of polychaete specimens was based on Holthe (1986), Ryland et al. (1995), Rouse and Pleijel (2001) and Harris et al. (2009).

RESULTS

The ceriantharian tubes studied presented 123 associated specimens from 16 families of polychaetes, in which *Ceriantheomorphe brasiliensis* presented the highest number, including 11 families, while *Pachycerianthus schlenzae* presented the lowest number, encompassing only 2 polychaete families (Table 1). The family Lumbrineridae was the one with the highest number of specimens (32%) (Table 2), while the families Magelonidae, Polynoidae and Serpulidae were the families with the lowest number of specimens (1% each).

The polychaetes observed on the tubes of *Botrucnidifer norvegicus* were not firmly attached or burrowed into it, instead they were observed on the surface of the tubes and among folds of layers, as well as most of the specimens associated with *Ceriantheomorphe brasiliensis*. One of the tubes of *C. brasiliensis*, however, displayed several strips where many spionids and polynoids were found.

On the surface and also burrowed between layers of the tubes of *Ceriantheopsis lineata*, *Isarachnanthus nocturnus* and *Pachycerianthus schlenzae* were observed many specimens from different families, however, most of the specimens observed were lumbrinerids, of which some specimens were burrowed and coated by cnidae filaments while others were anchored on the surface of the tubes, not presenting any coating.

Many perforations were observed along the tubes of *Ceriantheopsis lineata.* By removing some layers of the tubes at these perforations, we found Capitellidae, Cirratulidae, Phyllodocidae, Spionidae and Syllidae polychaetes inside. Some specimens were deeply burrowed in the tubes while others only superficially. The layers removal also revealed a boring hole under the layers, indicating that phyllodocids and syllids are possibly able to move along the tube.

A group of sternaspids were found both superficially anchored and deeply burrowed in the layers of the tube of *Ceriantheomorphe* sp.; among the branches that covered the tube of *Isarachnanthus nocturnus* many cirratulids, lumbrinerids, oenonids and serpulids were found (Table 1). In this last case, these specimens were not attached to the tube nor presented filaments coating them.

Table 1. Ceriantharian host species and polychaete families associated with their tubes.

HOST	NUMBER OF SPECIMENS	LOCATION	POLYCHAETA
Botrucnidifer norvegicus Carlgren, 1912	2	Norway: Stadsbygd, Agdenes/ Trondheim/	Cirratulidae Ryckholt, 1851 Oenonidae Kinberg, 1865 Syllidae Grube, 1850 Terebellidae Johnston, 1846
Ceriantheomorphe brasiliensis Carlgren, 1931	6	Brazil: Angra dos Reis (RJ) Arraial do Cabo (RJ) Guanabara Bay (RJ) São Sebastião (SP) Laje de Santos (SP)	Capitellidae Grube, 1862 Cirratulidae Eunicidae Berthold, 1827 Magelonidae Cunningham & Ramage, 1888 Nereididae Blainville, 1818 Phyllodocidae Örsted, 1843 Polynoidae Kinberg, 1856 Sabellidae Latreille, 1825 Spionidae Grube, 1850 Syllidae Terebellidae
***Ceriantheomorphe* sp.** Carlgren, 1931	1	Portugal: Aveiro Lagoon	Maldanidae Malmgren, 1867 Nereididae Sternaspidae Carus, 1863
Ceriantheopsis lineata Stampar, Scarabino, Pastorino & Morandini, 2015	2	Argentina: Port of Quequén (Bs. As.) Brazil: Vitória (ES)	Capitellidae Cirratulidae Lumbrineridae Schmarda, 1861 Phyllodocidae Spionidae Syllidae
Isarachnanthus nocturnus Hartog, 1977	4	Brazil: Boa Viagem beach (BA) São Sebastião (SP)	Cirratulidae Lumbrineridae Oenonidae Serpulidae Rafinesque, 1815
Pachycerianthus schlenzae Stampar, Morandini & Silveira, 2014	2	Brazil: Guaraparí (ES) Vitória (ES)	Lumbrineridae Syllidae

Table 2. Quantity and percentage of polychaete specimens represented by their families found on the ceriantharian tube.

FAMILY	SPECIMENS	PERCENTAGE (%)
Lumbrineridae	39	32%
Cirratulidae	28	23%
Spionidae	15	12%
Syllidae	9	7%
Nereididae	6	5%
Sternaspidae	6	5%
Sabellidae	4	3%
Eunicidae	3	2%
Capitellidae	2	2%
Maldanidae	2	2%
Oenonidae	2	2%
Phyllodocidae	2	2%
Terebellidae	2	2%
Magelonidae	1	1%
Polynoidae	1	1%
Serpulidae	1	1%

DISCUSSION

Energetic cost to specimens adapted to hard substrata when associated with ceriantharian tubes

Some polychaetes exhibit a subsurface behavior and present burrowing mechanisms suitable for digging into diverse substrata (Trueman 1966; Du Clos 2014; Francoeur and Dorgan 2014; Grill and Dorgan 2015). Given these burrowing mechanisms, the soft layers on the ceriantharian tube would not be an obstacle to these polychaetes.

On the tubes of *Ceriantheomorphe brasiliensis* we found cirratulids, eunicids, phyllodocids, spionids, syllids and nereidids. The latter is known to avoid rigid sediments (Du Clos 2014), however, the other groups are well adapted to burrow into hard substrata, with exception of Spionidae whose great plasticity allows them to be successful in all kinds of environments from hard to soft substrata, depths and temperatures (Fauchald 1977). Yet these hard substrate burrowers were observed in between soft layers of the ceriantharian tubes. The burrowing method and behavior as well as the specimen’s morphology, such as body size, are related to the type of substrate in which the animal is located (Dorgan et al. 2008; Che and Dorgan 2010; Grill and Dorgan 2015). Harder substrata, for example, require from the worm certain morphological and behavioral adaptations that may not be necessary in softer substrata. In this way, the use of ceriantharian tube as an alternative substrate is less costly to these animals. Nonetheless, the polychaete must retain or develop some defense mechanism against the ptychocysts filaments present on the tube, enabling a successful interaction. This kind of mechanism was already observed to bryozoans (Vieira and Stampar, 2014).

Mechanisms that enable the anchoring on the ceriantharian tube

Filaments of ptychocysts are the material with the largest amount in ceriantharian tubes (Stampar et al. 2015) and might be harmful to some species, including polychaete predators. This indicates that the polychaetes found on the surface and layers of the tubes possibly use the ceriantharian tube as a defense mechanism against predators (e.g. refuge), and also could be well adapted to the tube composition, not being harmed by the filaments of the ptychocysts.

Lumbrinerids observed in layers of the tubes of *Isarachnanthus nocturnus* and *Pachycerianthus schlenzae* were coated by mucus that possibly provided an additional protection from the contact with the ptychocyst present all over the ceriantharian tube. Some species of phyllodocids can release mucus as a response to disturbance (Fauchald 1977), and it is possible that this mucus could be used to coat and protect them while in between layers of the ceriantharian tube.

Capitellids are opportunistic organisms able to inhabit highly disturbed areas and likely unfavorable to the living of most species (Grassle 1974). It is no wonder that their high resiliency to destructive environments could also be applied to the ceriantharian tube since the specimens found were not supposedly facing any adversity due to the anchoring.

Mobility in the tube

It is noteworthy that phyllodocids and syllids were able to move through the layers of the tube of *Ceriantheopsis lineata*. These specimens are active omnivorous predators (Fauchald 1977; Fauchald and Jumars 1979), so it is possible that they move around the tube seeking food resources.

Ceriantharian tube as an alternative substrate

In view of the capacity that ceriantharian tubes have to provide an alternative habitat to numerous species that associate with them, and thus affecting their abundance, ceriantharians can be taken as ecosystem builders.

As observed in our study, Lumbrineridae was the richest family in number of specimens associating with ceriantharian tubes. This evidence is likely due to the fact that species of this family are among the most common polychaetes found burrowed in muddy and sandy soft bottoms (Fauchald 1977). Thereby, the soft organization presented by the tubes of *Ceriantheopsis lineata*, *Isarachnanthus nocturnus* and *Pachycerianthus schlenzae*, where these specimens were found, is not very contrasting to the kinds of substrata that they are used to dwell and, so, the ceriantharian tube is suitable to conduct both the harboring and burrowing of lumbrinerids, taking part as an alternative substrate.

A group of six sternaspids was observed associating with *Ceriantheomorphe* sp., however sternaspids are not very common to be observed in large numbers (Sendall and Salazar-Vallejo 2013). Yet, the ceriantharian tube could offer an intra/interspecific competition partially free substrate that contributes to polychaetes small assemblages.

Tubiculous worms and ceriantharian tubes

Commonly, many species display an antipredator hiding behavior (Dill and Fraser 1997). Specimens of tubeworms and ceriantharians, for instance, acquire shelter against predators in protective self-built-tubes. Apart from serpulids, whose tube is calcareous (Hove and Vandenhurk 1993; Díaz-Castañeda and Reish 2009), the tubes secreted by the tube-builders observed in our study (eunicids, magelonids, maldanids, sabellids, spionids and terebellids) are very similar to the ceriantharian tube, considering the soft structure composed by sediments and mucus secreted by the specimens (Blake and Hilbig 1994). Díaz-Castañeda and Reish (2009) observed that polychaetes are able to use the havens built by other species. In our study, we observed the same pattern with the ceriantharian tube. Although adapted to build tubes, it is somewhat costly to perform it and, so, being able to inhabit another species tube, as similar as the tube dwelled by the specimen, could be a very profitable strategy for polychaetes in regard of saving energy and acquiring protection and refuge altogether.

Hiding, feeding and protection

Several polychaetes burrow into sediments seeking for protection. However, according to Dill and Fraser (1997), the cost-benefit of hiding lies on the food availability in the environment when the specimen withdrew into the tube to protect itself. For example, in an environment with a considerable availability of food, to stay hidden for too long deprives the specimen from eating and breathing, thereby the benefits of hiding are not so beneficial when assessed by this angle. In contrast, when the specimen remains hidden in a food-scarce environment, it is not affected negatively by the food deprivation. Our observations concerning feeding behaviors, related to the feature of hiding, approached polychaetes with suspension and deposit food habits, as observed in spionids (see more in Taghon and Greene 1992). The use of ceriantharian tube as an alternative substrate can be very profitable to polychaetes not only by the protection and refuge obtained, but also because of the possibility of making use of the suspended food scraps from the ceriantharian feeding activity as food resources while hiding, instead of actively exploring them on the bottom, which is energetically more demanding and possibly risky due to the exposure to predators. Our observation about this feeding strategy supports the study of Zibrowius et al. (1975) in which lumbrinerids feed on the food of their anthozoan hosts. Furthermore, even though the food scarceness increases along with the depth and it is likely that such conditions are unfavorable to deep-sea bottom-dwellers (Snelgrove 1999), the Nordic cirratulids, oenonids, syllids and terebellids observed in our study did not appear to be facing any feeding adversity.

Similarly to the study of Casoli and collaborators (2016), in which the polychaete abundance is related to the environmental composition capable of providing resources (e.g. food and shelter), smooth sandy bottoms do not offer as many shelters and feeding sites as well sorted ones that support a higher benthic macrofaunal diversity (Buhl-Mortensen et al. 2012; Carvalho et al. 2017). Thereby, there is a balance between the availability of food resources and refuge in which both are essential to the survival of species viz. food-richness is not enough to maintain species in a region since the lack of shelter in this region may be risky to specimens that forage in the area and, thus, the use of ceriantharian tubes can be an interesting alternative shelter and feeding site to polychaete species.

Camouflage and mimicry

Some families in our study (e.g. capitellids, eunicids, nereidids, sabellids and serpulids) have members whose bodies can display eye-catching colors. According to Blake and Hilbig (1994), bright colors are very attractive to predators, thereby the inconspicuous color exhibited by the ceriantharian tube could be beneficial to polychaetes found burrowed between filament layers, as an option of camouflage to mislead predators. Despite the variable color patterns presented by members of Phyllodocidae, in this study specimens of this family were found near the soft bottom and presented an inconspicuous coloration, as suggested by Blake and Hilbig (1994). Moreover, the resemblance to some of the hosts structures is a mechanism widely used by many species to be overlooked by predators (Patton 1972; Buhl-Mortensen and Mortensen 2004; Schiaparelli et al. 2005; Pawlik 2012). In this way, it is possible that the spionids and polynoids observed among strips of the tube of *Ceriantheomorphe brasiliensis* were performing mimicry in order to avoid predation.

Symbiotic associations

There were no evidences on the ceriantharian host acquiring any benefit or disadvantage while harboring polychaetes. Although in our study we observed one family that presents some parasitic species (Oenonidae) (Fauchald 1977), the specimen observed was among branches covering the tube of *Isarachnanthus nocturnus* and not directly in contact with it. Furthermore, no sign of predation surrounding the area where this specimen was placed was noted. Therefore, it is more likely that the oenonid observed was hiding among branches than parasitizing the ceriantharian tube. Additionally, no predation sign was observed on the tube of *Botrucnidifer norvegicus*, where another oenonid was found as well.

Regarding the symbionts, polychaetes acquire both protection and food resources from the associations with the ceriantharian tube while hidden or due to the tube's composition. In this way, interactions between polychaetes and ceriantharian tubes are an apparent commensalism.

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CONCLUSÃO GERAL

Com base nos resultados obtidos, o aspécto inconspícuo e textura macia do tubo de Ceriantharia não aparentaram ser fatores limitantes para a ancoragem de invertebrados marinhos que, em sua grande parte, são geralmente encontrados aderidos a estruturas rígidas. Contrariamente, tal estrutura se mostrou propícia para o estabelecimento de certos grupos podendo os fornecer um substrato alternativo parcialmente livre de competição inter/intraespecífica.

Membros dos filos Annelida e Mollusca e do subfilo Crustacea possuem ou desenvolveram mecanismos de adaptação que os permitiram se ancorar ou habitar tubos ceriantários, além de também poderem utilizá-los como sítios de alimentação.

Além disso, os simbiontes associados aos tubos podem adquirir possíveis benefícios como refúgio, abrigo, proteção e, por vezes, alimento. Em contrapartida, não foram observados ganhos ou prejuízos obtidos pelos hospedeiros ceriantários na maior parte das interações observadas. Ainda assim, a composição peculiar do tubo ceriantário lhe confere extrema maciez e flexibilidade o que o torna uma estrutura frágil e passível de sofrer danos. Contudo, a adição de conchas de moluscos às camadas do tubo o auxilia a obter maior resistência, garantindo sua integridade. Não obstante, a homocromia obtida a partir da adesão de conchas ao tubo contribui para que esse se assemelhe ao fundo marinho, permanecendo inconspícuo e praticamente imperceptível a predadores. Sendo assim, a adesão de conchas de moluscos em tubos ceriantários acarreta certos benefícios para o último.

Associar-se com o tubo de Ceriantharia pode ser favorável a animais que se alimentam por suspensão, como sugerido para interações envolvendo o tubo ceriantário, crustáceos e poliquetas. Os últimos podem adquirir recursos alimentares a partir de restos de comida provenientes da alimentação de seu hospedeiro ceriantário sem haver necessidade de forragearem pelo ambiente ao passo que se mantém abrigados e protegidos.

De forma geral, ceriantários são classificados como solitários. Entretanto, em nosso estudo demonstramos que a espécie *Botrucnidifer norvegicus* é capaz de viver em colônia. Isto indica que o hábito solitário, embora aplicado para grande parte dos ceriantários, é uma exceção para *B. norvegicus*.

Ainda, por meio deste estudo foi possível realizar o primeiro registro de espécies de Crustacea e Mollusca em novas localidades antes não encontradas.

Registros como estes são importantes para auxiliar no conhecimento da biodiversidade de espécies em uma região assim como acrescentar informação quanto a disseminação de espécies.

Por fim, conclui-se que as associações mais comuns que ocorrem entre ceriantários e invertebrados marinhos tenham caráter de inquilinismo e/ou comensalismo.

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