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Distribuição espacial, diversidade e conectividade genética de Chaetognatha no Atlântico Oeste Tropical

Recife
2019

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Tese de doutorado apresentada ao Programa de Pós-Graduação em Oceanografia da Universidade Federal de Pernambuco, como requisito para a obtenção do Grau de Doutor em Oceanografia

Área de concentração: Oceanografia Biológica

Orientadora: Profa. Dra. Sigrid Neumann-Leitão

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RESUMO

A presente Tese teve como objetivo conhecer em maior profundidade o filo Chaetognatha no Atlântico Oeste Tropical. O primeiro artigo reuniu as principais informações do grupo no Brasil, publicadas entre a década de 50 até agosto de 2018. Foi demonstrado que das 26 espécies catalogadas para águas brasileiras, apenas 11 têm sido registradas com alta frequência. Essa questão foi associada a maior disponibilidade de publicações direcionadas a sistemas costeiros; e, a relativa escassez de investigações compreendendo estratos superiores a 200 m de profundidade. O segundo artigo apresentou como objetivo principal avaliar a diversidade e conectividade genética de *Flaccisagitta enflata* entre localidades neríticas (Porto do Recife e Tamandaré) e oceânicas (Arquipélago de Fernando de Noronha, Atol das Rocas, monte submarino Guará e Arquipélago de São Pedro e São Paulo) do nordeste do Brasil. Fragmentos de 425 pb foram sequenciados para um total de 116 espécimes, a partir do gene mitocondrial COI. Em geral, altos níveis de diversidade foram registrados, com média de 0,98 de diversidade haplotípica. Indicações de uma população panmítica foram fornecidas pela filogenia, rede de haplótipos e análise do Migrate-n. Contudo, diferenças significativas foram detectadas pela AMOVA geral e comparações Φst par-a-par, sugerindo níveis mais baixos de conectividade entre algumas áreas, especialmente entre o Porto do Recife e todas as localidades oceânicas ($p < 0,05$). Foi sugerido que a topografia de entrada do porto, cercada por uma barreira de recifes, pode restringir a taxa de renovação da água local e, portanto, as taxas de migração de *F. enflata* na região. Esta investigação demonstrou que mesmo uma espécie holoplanctônica e cosmopolita pode se desviar da homogeneidade genética esperada em uma abordagem regional. O terceiro estudo atuou em conjunto ao segundo, no intuito de ampliar a disponibilidade de sequências *barcode* de Chaetognatha no Atlântico Tropical. Neste artigo foi analisada a variabilidade molecular intra e interespecífica de espécies do filo, incluindo as primeiras sequências COI de *Parasagitta friderici*. Os valores de diversidade registrados foram elevados (média K2P diferenças intraespecíficas = 0,017; média K2P diferenças interespecíficas 0,333), o que pode estar relacionado aos grandes tamanhos populacionais relatados para o zooplâncton. O sequenciamento do COI ainda permitiu gerar um quarto artigo, que inferiu uma relação trófica entre *F. enflata* e Cnidaria. Esta proposta foi sugerida a partir de sequências COI deste grupo detectadas em amostras teciduais de dois espécimes de *F. enflata*. A possibilidade de contaminação foi considerada improvável. Uma busca realizada no BLAST mostrou que ambas as sequências apresentaram uma combinação de maior cobertura e identidade com *Nemopilema nomurai* (Scyphozoa), apoiando a hipótese de que elas pertencem a uma espécie de medusa. Uma vez que táxons gelatinosos podem integrar a vasta dieta de Chaetognatha, é possível que *F. enflata* tenha ingerido este tipo de item, o qual não foi totalmente digerido até o momento da amostragem e não foi visualizado pelo método de transparência. Esta Tese representa um primeiro passo na investigação de aspectos ainda não explorados em águas brasileiras, constituindo uma importante ferramenta de auxílio a estudos futuros envolvendo espécies do zooplâncton.

Palavras-chave: Zooplâncton. Sagittidae. Filogeografia. DNA. COI. Sistemas costeiros. Ilhas oceânicas.

ABSTRACT

The present Thesis aimed to know in greater depth the Chaetognatha phylum in the Tropical Western Atlantic. The first study gathered the group's main information in Brazil, published between the 50's decade and August 2018. It has been demonstrated that of the 26 species cataloged for Brazilian waters, only 11 have been registered with high frequency. This issue was associated the greater availability of publications directed to coastal systems (where usually occurs few species); and the relative scarcity of investigations comprising strata greater than 200 m deep. The second study had as main objective to evaluate the diversity and genetic connectivity of *Flaccisagitta enflata*, between neritic (Port of Recife and Tamandaré) and oceanic (Fernando de Noronha Archipelago, Rocas Atoll, Guará seamount and Saint Peter and Saint Paul's Archipelago) locations in northeastern Brazil (Tropical Western Atlantic). Fragments of 425 bp were sequenced for a total of 116 specimens, from the mitochondrial COI gene. In general, high levels of diversity were recorded, with an average of 0.98 of haplotype diversity. Indications of a panmitic population were provided by phylogeny, haplotype network and Migrate-n analysis. However, significant differences were detected by the general AMOVA and pairwise Φst comparisons, suggesting lower levels of connectivity between some areas, especially between the Port of Recife and all oceanic locations ($p < 0.05$). Was suggested that the topography of the port inlet, enclosured by a reef barrier, may constrain the local water turnover ratio and thus migration rates of *F. enflata* in region. This investigation demonstrated that even an holoplanktonic and cosmopolitan species may deviate from genetic homogeneity expected in a regional approach. The third study acted in conjunction with the second, in order to increase the availability of Chaetognatha *barcode* sequences in the Tropical Atlantic. In this article were analyzed the intra and interspecific molecular variability of phylum species, including the first COI sequences of *Parasagitta friderici*. The recorded diversity values were high (mean K2P intraspecific differences = 0.017, mean K2P interspecific differences = 0,333), which may be related to the large population sizes reported for zooplankton. The COI sequencing still allowed generate a fourth article, which inferred a trophic relation between *F. enflata* and Cnidaria. This proposal was suggested through COI sequences of this group detected in tissue samples from two specimens of *F. enflata*. The possibility of contamination was considered unlikely. A search carried in BLAST showed that both sequences provided here presented a combination of highest query coverage and match identity with *Nemopilema nomurai* (Scyphozoa), supporting the hypothesis that they belong to a species of jellyfish. Since gelatinous taxa are known to integrate the broad diet of Chaetognatha, it is possible that *F. enflata* has ingested this type of item, which was not fully digested until the moment of sampling and was not visualized by the transparency method. This Thesis represents a first step in the investigation of aspects not yet explored in Brazilian waters, constituting an important aid tool to future studies involving species of zooplankton.

Keywords: Zooplankton. Sagittidae. Phylogeography. DNA. COI. Coastal systems. Oceanic islands.

SUMÁRIO

1 INTRODUÇÃO

O zooplâncton constitui um grupo altamente heterogêneo nos ecossistemas aquáticos, caracterizando-se por uma grande diversidade de tamanhos e formas, reduzida capacidade natatória, diversos tipos de alimentação e uma ampla distribuição espacial (PALMA, S.; KAISER, 1993). Sua importância ecológica reside no papel que desempenham na teia alimentar marinha, onde atuam na transferência da biomassa e energia produzida pelo fitoplâncton aos níveis tróficos superiores (CASANOVA, 1999; GROSS, 1996; LENZ, 2000; RODRÍGUEZ-SÁENZ; MORALES-RAMÍREZ, 2012); contribuem com a ciclagem e exportação de nutrientes orgânicos e inorgânicos presentes na coluna d'água, abrigam estágios iniciais de organismos nectônicos e bentônicos (incluindo aqueles de relevância comercial), bem como apresentam espécies indicadoras das condições ambientais dominantes (GROSS, 1996). Esta última característica pode ainda ocasionar alterações quantitativas rápidas em suas populações, como resposta a impactos gerados sobre o ecossistema. Investigar aspectos relacionados ao zooplâncton no domínio pelágico é desta forma, de significativa importância para a ciência e para a sociedade como um todo.

Dentre os principais grupos que compõem esta comunidade, Chaetognatha geralmente destaca-se por apresentar altas taxas de frequência e abundância no meio estudado (e.g. REEVE, 1970; PEARRE JR., 1980; NEUMANN-LEITÃO; SANT'ANNA et al., 2008). O filo reúne espécies distribuídas desde sistemas costeiros a oceânicos, em águas superficiais até profundidades relativas à zona abissopelágica (0 - 5000 m) (OZAWA et al., 2007). São animais de pequeno tamanho corporal (2-120 mm), com hábito alimentar comumente oportunista e estritamente carnívoro. Embora sua dieta seja composta por uma ampla variedade de itens, as espécies demonstram marcada preferência por Copepoda. Este fato concede a Chaetognatha grande importância ecológica como elo trófico entre o referido grupo e níveis tróficos mais elevados, contribuindo na transferência de biomassa e energia entre pequenos a grandes predadores, incluindo peixes de interesse comercial (ALVARIÑO, 1985; ROGER, 1994; VEGA-PÉREZ; SCHINKE, 2011) `Pearre, 1974`. Quetognatos também são considerados grandes produtores de matéria orgânica particulada (PEARRE JR., 1980; BONE; KAPP; PIERROT-BULTS, A. C., 1991; VEGA-PÉREZ; SCHINKE, 2011), e alguns ainda demonstram alta afinidade por massas d'água específicas, o que os torna relevantes como indicadores hidrológicos regionais. Atualmente são conhecidas 209 espécies em todo o mundo, 29 das quais apresentam registro no Atlântico Sul (VEGA-PÉREZ; SCHINKE, 2011) e 26 em águas brasileiras (CASANOVA, 1999).

Dispersão, Diversidade e Conectividade Genética

A maior parte das espécies de Chaetognatha possui ciclo de vida holoplanctônico (CASANOVA, 1999; BOLTOVSKOY, 2005; VEGA-PÉREZ; SCHINKE, 2011). Esta característica é geralmente associada a organismos com altas taxas de fecundidade, grandes tamanhos populacionais e um alto potencial de dispersão pelas correntes marinhas (PALUMBI, 1992). Por muito tempo acreditou-se que estes fatores tornavam espécies holoplanctônicas unidades populacionais de dispersão ilimitada, ideia que era sustentada pela dificuldade em identificar barreiras eficazes à sua migração e a falta de descontinuidades de habitats no reino pelágico (PEIJNENBURG; BREEUWER et al., 2004; HELLBERG, 2009). De fato, estudos realizados nas últimas décadas já demonstraram que esses fatores podem proporcionar elevada diversidade genética em espécies holoplanctônicas (e.g. DEAGLE et al., 2015; NOBLEZADA, M. M. et al., 2016), em associação a elevados níveis de conectividade estabelecidos entre ambientes geograficamente distantes (e.g. NORRIS, 2000; NORRIS; VARGAS, 2000; DARLING et al., 2000). No entanto, evidências cada vez mais consistentes vêm sugerindo que muitas espécies não apresentam dispersão desenfreada, uma vez que variados níveis de estruturação geográfica têm sido detectados entre suas populações (BUCKLIN; LAJEUNESSE et al., 1996; LEE, 2000; PEIJNENBURG; BREEUWER et al., 2004; GOETZE, 2005; KIRBY; LINDLEY; BATTEN, 2006; CHEN; HARE, 2011). Este fato justifica a importância da aplicação de ferramentas moleculares ao holoplâncton, no tocante à investigação dos parâmetros filogeográficos que moldam sua distribuição.

No Atlântico Oeste Tropical (AOT), tais investigações são particularmente necessárias, visto que aspectos como diversidade e conectividade genética têm sido avaliados principalmente em espécies meroplanctônicas. Embora que estas apresentem apenas o estágio larval pelágico para se dispersar através das correntes marinhas, a maior parte das populações investigadas nesta região demonstram ser geneticamente homogêneas. Exemplos deste tipo foram registrados para o peixe recifal *Cephalopholis fulva* (SOUZA, A. S. et al., 2015) e para o cefalópode *Octopus insularis* (LEITE, T. S. et al., 2008), estudados entre a costa e ilhas oceânicas brasileiras. Adicionalmente, espécies de decápodes semi-terrestres como os caranguejos *Grapsus grapsus* (TESCHIMA et al., 2016) e (RODRÍGUEZ-REY; HARTNOLL; SOLÉ-CAVA, 2016) também apresentaram evidências de alta conectividade entre ambientes insulares da região nordeste do Brasil. Em todos estes estudos, as correntes parecem desempenhar um papel significativo na dispersão dos organismos, contribuindo para o estabelecimento de suas populações nas diferentes áreas avaliadas. Tais conclusões também foram sustentadas por análises de modelagem realizadas em vários ambientes do Atlântico Sul, desenvolvidas para monitorar larvas de lagosta com longo período de dispersão (12 meses de estágio planctônico) (RUDORFF et al., 2009a; RUDORFF et al., 2009b). No AOT, exemplos alternativos de populações geneticamente diferenciadas já foram relatados para outras espécies de peixes recifais, entre a costa e ilhas oceânicas brasileiras (CUNHA et al., 2014; NEVES, J. M. M. et al., 2016).

Informações referentes à genética populacional de Chaetognatha ainda são escassas na região. Dados sobre diversidade e filogeografia genética no Atlântico envolvendo o Brasil, estão disponíveis apenas para espécies oceânicas, habitantes de maiores profundidades (KULAGIN; STUPNIKOVA et al., 2013; KULAGIN; NERETINA, 2017). A conectividade foi superficialmente abordada; no entanto, estes estudos mostraram uma maior similaridade genética entre indivíduos coletados na porção Sudoeste (*Eukrhonia hamata* - KULAGIN; STUPNIKOVA et al., 2013); e, na porção equatorial deste oceano (*Pseudosagitta maxima* - KULAGIN; NERETINA, 2017). No Atlântico Norte, Jennings, Bucklin e Annelies Pierrot-Bults (2010) não chegaram a detectar associação entre a diversidade e localização geográfica para várias espécies do grupo, o que foi atribuído ao elevado potencial de mistura genética de Chaetognatha, ou a um tempo evolutivo relativamente curto para a separação das populações em linhagens geneticamente isoladas. Em comum, estes três estudos utilizaram o marcador molecular COI do DNA mitocondrial (subunidade I da citocromo c oxidase - COI) para atender aos objetivos propostos, considerando-o de maneira isolada (JENNINGS; BUCKLIN; PIERROT-BULTS, A., 2010; KULAGIN; STUPNIKOVA et al., 2013) ou em conjunto a marcadores nucleares (KULAGIN; NERETINA, 2017).

A escolha deste gene por tais publicações reflete sua eficácia em avaliar aspectos filogeográficos gerais (HEBERT; RATNASINGHAM; WAARD, 2003). O COI (1,5 Kb) é atualmente conhecido como a principal sequência de DNA que permite a identificação e descoberta de espécies em inúmeros sistemas terrestres e aquáticos (e.g. HAJIBABAEI et al., 2006; CLARE et al., 2007; BUCKLIN; STEINKE; BLANCO-BERCIAL, 2011). Sua utilização está relacionada a uma série de circunstâncias, como (i) a ampla distribuição que apresenta entre os metazoários, uma vez que trata-se de um gene mitocondrial; (ii) taxas de evolução suficientemente rápidas para permitir a discriminação de espécies muito relacionadas na maioria dos grupos; (iii) ausência de sobreposição entre distâncias genéticas intraespecíficas, o que contribui para a detecção de diversidade críptica; e, (iv) primers universais aplicáveis ao sequenciamento de uma ampla gama de metazoários (HEBERT; RATNASINGHAM; WAARD, 2003; BUCKLIN; STEINKE; BLANCO-BERCIAL, 2011). Em sistemas marinhos, a literatura fornece muitos exemplos da utilidade do COI na investigação da estrutura populacional, através da qual, padrões de distribuição de espécies puderam ser esclarecidos em uma série de escalas espaciais (e.g. HELLBERG, 2009; AVISE, 2009; BUCKLIN; STEINKE; BLANCO-BERCIAL, 2011). A identificação de presas no conteúdo estomacal, detecção de espécies invasoras, utilização na perícia forense e na segurança de consumo de pescado ainda são algumas das outras áreas de estudo as quais o COI também pode ser submetido (BUCKLIN; STEINKE; BLANCO-BERCIAL, 2011). De maneira geral, a ampla magnitude do banco de dados deste gene (`http://www.barcodinglife.org` e `www.ncbi.com`) representa uma importante vantagem para este marcador em comparação a muitos outros genes (por ex. COII).

Esta Tese fornece dados inéditos sobre espécies de Chaetognatha em águas brasileiras (AOT). O marcador COI foi aplicado à avaliação da diversidade e conectividade genética em ambientes neríticos e oceânicos do AOT, fornecendo novas perspectivas ao estudo de dispersão e distribuição do holoplâncton na região. Embora ainda onerosas, ferramentas moleculares mostram-se eficazes em várias esferas científicas, e o aperfeiçoamento de técnicas à investigação do zooplâncton pode render importantes avanços ao seu conhecimento. Espera-se que esta pesquisa possa incentivar a continuidade de estudos filogeográficos direcionados a esse grupo, incluindo áreas ainda não avaliadas do oceano Atlântico. Muito ainda se tem a descobrir.

2 ESTRUTURA E OBJETIVOS DA TESE

Esta Tese foi dividida em sete capítulos, para a melhor apresentação das informações e resultados obtidos. Os dois primeiros referem-se à Introdução Geral e aos Objetivos, e os quatro posteriores constituem os estudos desenvolvidos e submetidos a diferentes Revistas Científicas. O último capítulo apresenta as considerações finais alcançadas.

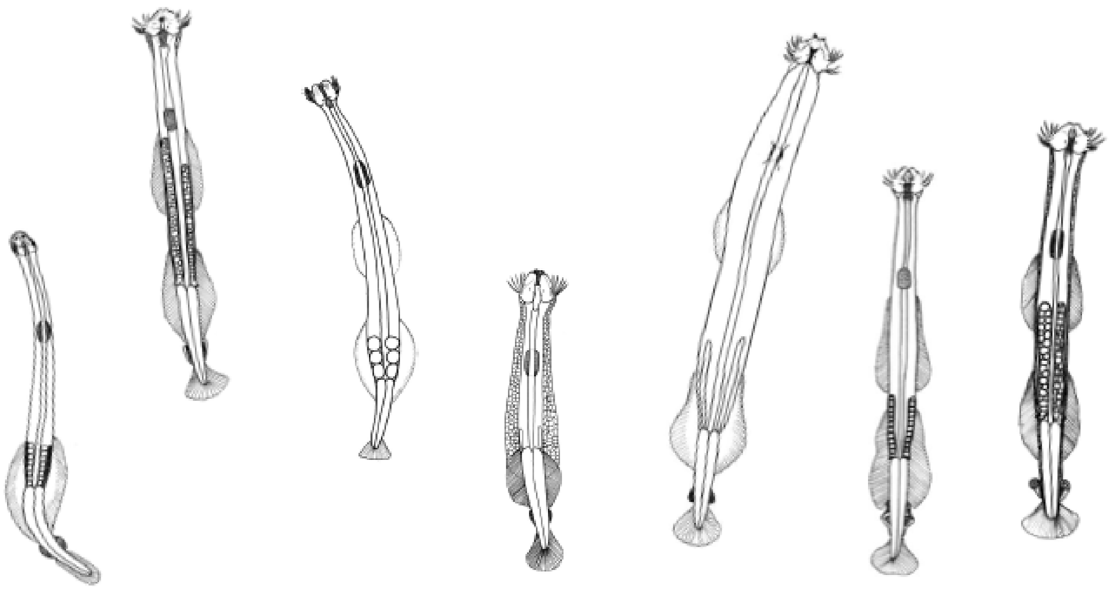
Na presente seção, o **Objetivo Geral** desta Tese foi:

- Apresentar um estudo de revisão sobre Chaetognatha no Brasil, e investigar aspectos genéticos de espécies deste grupo, incluindo variações intra e interespecíficas, diversidade, conectividade e possível relação trófica, baseando-se em sequências do gene subunidade I da citocromo c oxidase (COI) do DNA mitocondrial (DNA *barcode*).

E, compondo os estudos desenvolvidos, os **Objetivos Específicos** foram:

- Fazer um levantamento bibliográfico dos estudos sobre Chaetognatha publicados em ambientes brasileiros entre a década de 50 e a atualidade, abordando principalmente a composição das comunidades nas regiões estudadas e sua distribuição espacial (Capítulo 3)
- Determinar o nível de diversidade genética do quetognato *Flaccisagitta enflata* (Sagittidae), descrever o padrão de conectividade genética exibido por essa espécie entre a região nerítica e oceânica do nordeste do Brasil (Atlântico Oeste Tropical); e, fornecer uma visão geral de sua história demográfica, empregando a análise de sequências do gene COI do DNA mitocondrial (Capítulo 4)
- Investigar os níveis de diversidade genética intra e entre espécies de Chaetognatha, utilizando sequências do gene COI do DNA mitocondrial (Capítulo 5)
- Propor uma relação trófica entre Chaetognatha e Cnidaria, com base em sequências do gene COI do DNA mitocondrial (Capítulo 6)

3 ARTIGO 1 - INVESTIGATIONS ON CHAETOGNATHA IN BRAZIL (SOUTHWESTERN ATLANTIC OCEAN): A REVIEW



Imagens ilustrativas representando a diversidade de Chaetognatha em águas brasileiras. **Fonte**: www.ufrj.com.br/chaetognatha

ABSTRACT

Chaetognatha constitutes a phylum of planktonic invertebrates with world distribution, occurring from coastal to oceanic systems and in wide vertical range in the water column (0-5000 m depth). The ecological importance of the species refers to their role as key-predators of Copepoda, producers of particulate organic matter and regional hydrological indicators. Given its relevance, the present study represents an effort in to gather the main data of Chaetognatha in Brazil, since there are relatively few publications devoted to the specific knowledge of this phylum in the region. The bibliographic research was performed using different electronic databases. Were considered scientific articles, books and book chapters published, as well as printed books of identification of the species. The literature obtained was selected, so that gathered specific and general of zooplankton publications from the decade of 1950 until August 2018. This review was structured in sections, among which the spatial distribution (horizontal and vertical) was emphasized. According to the obtained data, of the 26 species of Chaetognatha cataloged for Brazil, only 11 have been registered with high frequency in the studies performed, the equivalent to 42% of the total taxa described. This issue reflects certain factors, such as a greater availability of publications directed to coastal systems, and relative scarcity of investigations comprising strata greater than 200 m deep. Still, aspects related to the progress of the Chaetognatha study in the state of São Paulo were described as valid for Brazil as a whole, and included: (i) the incentive to training of specialists, (ii) the creation and maintenance of scientific collections, and (iii) the importance of publications aimed at greater investigation of benthic and deep environments. The adoption of these practices can broaden the cataloged taxonomic list for Brazil, clarify patterns of vertical distribution of species and encourage group research in new scientific areas.

Keywords: Zooplankton. Bibliographic research. Biodiversity. Distribution. Coastal systems. Oceanic islands.

INTRODUCTION

Chaetognatha is a phylum consisting of small animals invertebrates, strictly carnivores and with worldwide distribution (CASANOVA, 1999; BOLTOVSKOY, 2005; ÁVILA; ARRUDA; BONECKER, S. L. C., 2006). These organisms usually present high levels of frequency and abundance, being able to compose about 10% of the total biomass of zooplankton in the global oceans (eg., Ball and Miller, 2006).

There are several issues that define the ecological importance of this group. When establishing a trophic link between Copepoda and higher trophic levels, Chaetognatha is often related to areas with attractive fishing potential (BOLTOVSKOY, 1981; ALVARIÑO, 1985; ROGER, 1994). Aspects such as predatory character and rapid food digestion also characterize the species as key elements of particulate organic matter, providing an important contribution to the carbon flow of the oceans (PEARRE JR., 1980; BONE; KAPP; PIERROT-BULTS, A. C., 1991; VEGA-PÉREZ; SCHINKE, 2011). These factors, associated with a wide geographic distribution, make the phylum a strong structuring of the zooplanktonic marine community worldwide (PEARRE JR., 1980; HOSSFELD, 1996). Certain species are still recognized as good hydrological indicators, since they live in association with water masses or specific currents in the pelagic environment (BIERI, 1959; MCLELLAND, 1984; CHENEY, 1985; JOHNSON, W. S.; ALLEN, 2005; VEGA-PÉREZ; SCHINKE, 2011).

The first information about this animal group in the South Atlantic dates back to the nineteenth century, when specimens of the phylum were collected aboard the ship “*HMS Beagle*” by Charles Darwin. He verified that such organisms occurred frequently and in relative abundance along and in areas farther away the coast of countries covered by the expedition, such as Brazil (DARWIN, 1844). Subsequently, expeditions carried out from the years 1900 on board vessels as “*Nave Liguria*” (1915), “*Terra Nova*” (1930) and “*Meteor*” (1938) collected a significant amount of plankton samples in Brazilian environments. These provided the basis for the first studies of systematic classification, composition of communities and distribution of species of Chaetognatha registered in Brazil (e.g. VEGA-PÉREZ; SCHINKE, 2011). Currently it is estimated that of the 209 species registered in the world, 29 occur in the South Atlantic (VEGA-PÉREZ; SCHINKE, 2011; SOUZA, C. S. D.; LUZ; MAFALDA JR., 2014), and 26 in Brazilian waters (CASANOVA, 1999).

Although it is considered one of the taxa most cited in Brazil, due to the considerable amount of general zooplankton work that also addresses it, there are relatively few studies devoted specific to the knowledge of this phylum. Among these, the most was developed in shelf environments, and present data mainly about the occurrence, distribution and ecology of the species registered (e.g. ALMEIDA-PRADO, 1961, 1963, 1968; VEGA-PÉREZ; LIANG, T. H., 1992; LIANG, T. H.; VEGA-PÉREZ, 1994; MARAZZO; MACHADO; NOGUEIRA, C. S. R., 1997; LIANG, T.-H.; ARA, et al., 2003; FERNANDES; STERZA; NEVES, K. O., 2005; ARAÚJO, H. M. P.; RIBEIRO, V. A., 2005; ARRUDA; ÁVILA; BONECKER, S. L. C., 2010; FIGUEIRÊDO et al., 2018). For oceanic areas, the availability of specific works can be considered scarce, with most data directed to the islands and archipelagos of northeast Brazil (HOSOE, 1956; LIANG, T. H.; VEGA-PÉREZ, 2001; SOUZA, C. S. D.; LUZ; MAFALDA JR., 2014).

Something also important to mention relates to the identification of the species. It is often hinted by the little ideal method of fixation of the samples (eg., 4% formaldehyde neutralized) (JENNINGS; BUCKLIN; PIERROT-BULTS, A., 2010), which ends up degrading taxonomically important structures for its diagnosis, such as lateral fins. Perhaps this is one of the main reasons why there are still few specialists available to the study of this taxon, not only in Brazil, but worldwide. Recently, this limitation has been reduced by the use of molecular markers that allow a safe and efficient identification of the species (JENNINGS; BUCKLIN; PIERROT-BULTS, A., 2010; MIYAMOTO; MACHIDA; NISHIDA, 2010, 2012), however, genetic analyses are much more onerous when compared to traditional identification based on morphology. For Brazil, for example, there is a minimal availability of publications that have used molecular tools with application in Chaetognatha (KULAGIN; STUPNIKOVA, et al., 2013; KULAGIN; NERETINA, 2017).

Given the great ecological importance of the group, and relevant information dispersed by general publications of zooplankton, the present study is an effort to gather

the main data of the phylum Chaetognatha in Brazil (Southwestern Atlantic Ocean). The results essentially describe the composition of the communities in the regions studied, their spatial distribution, and ecological notes of the main species recorded, besides brief comments about future perspectives in Brazilian science, relating important issues to the progress of the study of Chaetognatha. The gathering of this information contributes to providing the current level of knowledge of the group, which may be relevant for the delimitation of further investigations into the species.

MATERIAL AND METHODS

GENERAL CHARACTERIZATION OF THE STUDY AREA

Circulation

The coast and the Brazilian oceanic portion are governed by complex currents systems originated from the South Equatorial Current (SEC). On its route from east to west, this component flows towards the northeast shelf of the country, where suffers an important bifurcation (SILVEIRA; MIRANDA; BROWN, 1994; LUMPKIN; GARZOLI, 2005), giving rise to the North Brazilian Subcurrent (NBUC), which transports surface and subsurface waters to the north (STRAMMA; FISCHER; REPPIN, 1995). Subsequently, at the extreme of the northeast region (Cabo de São Roque), a SEC merges to NBUC, generating the strong and continuous North of Brazil Current (NBC) (SILVEIRA; MIRANDA; BROWN, 1994; BOURLÈS et al., 1999), that flows on the surface carrying warm and saline waters along the entire north Brazilian shelf (STRAMMA; RHEIN, et al., 2005). The bifurcation of the SEC still originates the Brazilian Current (BC), which transports surface waters to the south with oligotrophic characteristics, in addition to high temperature and salinity, varying between 24-26°C and 36-38, respectively (SILVEIRA; SCHMIDT, et al., 2000; CIRANO et al., 2006; PALÓCZY et al., 2016). BC flows along of the north shelf, southeast and south Brazil, where at the height of 36°S separates from this region from the confluence Brazil-Malvinas (TALLEY et al., 2011; EKAU; KNOPPERS, 1999; STRAMMA; ENGLAND, 1999).

In the Brazilian oceanic portion, or in some cases, departing from the continent towards the ocean, formations of islands and seamounts are found in the northeast region (Saint Peter and Saint Paul’s Archipelago, North Brazilian Chain, Fernando de Noronha Chain) and at southeast of the country (Vitória-Trindade Chain). The Abrolhos Archipelago constitutes an exception, being situated on the limitations of the northeast continental shelf (SERAFINI; FRANÇA; ANDRIGUETTO-FILHO, 2010). All these features function as important obstacles to the marine currents, which often result in particular circulation pattern in these areas. The interaction flow-topography can modify the physical dynamics of the environment when generating vortices and meanders, in addition to local pulses of topographic resurgence (CASTRO; MIRANDA, 1998; EKAU; KNOPPERS, 1999).

Water Masses

Considering the classification proposed by Sverdrup, M. W. Johnson, and Fleming (1942), Miranda (1985) and Silveira, Schmidt, et al. (2000), the Brazilian oceanic zone under the influence of the Brazilian current presents four main water masses. Tropical Water (TW) is located on the surface. It is defined by high values of temperature and salinity, due to the intense solar radiation in the South Atlantic Tropical, where the precipitation-evaporation balance is negative. As a consequence, salinity is always higher than 36, and temperature values occur above 20°C. The South Atlantic Central Water (SACW) generally flows below the TW. This water mass occurs along the pycnocline, with temperatures varying between 6-20°C and salinities between 34.6-36. Below the SACW, the Antarctic Intermediate Water (AAIW) is defined by temperature limits and salinities varying between 3-6°C and 34.2-34.6, respectively. This water mass flows north from 25°S towards Ecuador; and, to the south, from 28°S (MÜLLER et al., 1998). By last, the North Atlantic Deep Water (NADW) flows below the AAIW, with temperature characteristics ranging between 3-4°C and salinity between 34.6-35. It occupies levels between 1500 and 3000 m along southeast Brazil, flowing south in the edge region of the shelf up to approximately 32°S, where it returns towards Ecuador.

On the eastern Brazilian shelf, in addition to the TW and SACW, the circulation is still formed by the Coastal Water (CW) and the Shelf Water (SW) (CASTRO; MIRANDA, 1998). The first is characterized by temperatures superior to 20°C and salinity below 35. The Shelf Water, in turn, is considered a water mass formed by the association of TW, SACW and SW. Its temperatures range from 20-27ºC and salinity from 35-36. According to Castro and Miranda (1998), the seasonal and latitudinal variations observed in the thermohaline dynamics occur mainly due to the local topography, currents flow and prevailing wind regimes along the continental shelf. The description of the respective water masses is also presented by T. H. Liang and Vega-Pérez (2001).

DATA COMPILATION AND PROCESSING

The bibliographic research was performed using different electronic databases (SCOPUS, Web of Science, Scielo, Google scholar and Lattes Platform) by inserting as Keywords: ”Chaetognatha” / “Chaetognath” and ”Brazil”. It was considered scientific articles, books and book chapters published and available on these platforms; in addition, it was considered printed books of identification of the species. The literature obtained according to this survey was then selected, gathering publications from the 1950 until August 2018. These publications specifically dealt about Chaetognatha or in general zooplankton, provided they had approached the identification of the species collected. Some specific studies were still required directly to the authors, since they were not found accessible on the researched platforms.

After the survey, the respective review was structured in sections. An inventory of the species registered in Brazilian waters was presented, followed by general comments about the areas of research that involved Chaetognatha until today. In order to better present the specific knowledge available to the group, each paper with emphasis on Chaetognatha was described in chronological order of publication. For each one of the locations investigated, were reported information regarding to the geographical coordinates, Brazilian region comprised in each study, methodology used (type of haul performed, mesh of the selected net), registered species, among other specifications. It is also important to mention that it was not considered with the designation ’species’ the quotations of morphotypes (e.g. *Sagitta* sp. or *Sagitta* spp.). This review provides special emphasis to the spatial distribution of Chaetognatha, in addition to ecological descriptions of the species most frequently recorded in Brazilian environments.

RESULTS AND DISCUSSION

INVENTORY OF REGISTERED SPECIES

In Brazil, are described 26 species of Chaetognatha distributed in five taxonomic families (Table 1). The family Sagittidae is the most numerous in worldwide scale, comprising more than 75% of fauna known to the present (PAPILLON et al., 2006), percentage similar to that observed in Brazilian waters (> 73%). On the other hand, Pterosagittidae is constituted by a single species also registered in Brazil; while Krohnittidae is represented by two of the three species currently known throughout the world. The other families (Eukrohnnidae and Spadellidae) comprise a larger number of species, however, are not well represented in Brazilian waters (Table 1). This fact may be related to the little knowledge available on deeper waters and benthic habitats, environments to which these groups are respectively linked, according to their ecology (CASANOVA, 1999; BOLTOVSKOY, 2005).

Table 1 – Species of Chaetognatha occurring in Brazilian environments. Adapted from Vega-Pérez and Schinke (2011)

FAMILY	**SPECIES**	**DESCRIPTOR**	**YEAR**
Sagittidae	*Parasagitta tenuis*	(Conant)	(1896)
	Parasagitta friderici	(Ritter-Záhoni)	(1911)
	Flaccisagitta enflata	(Grassi)	(1881)
	Flaccisagitta hexaptera	(d´Orbigny)	(1836)
	Ferosagitta hispida	(Conant)	(1895)
	Sagitta bipunctata	Quoy e Gaimard	(1828)
	Sagitta helenae	Ritter-Záhoni	(1911)
	Serratosagitta serratodentata	(Krohn)	(1853)
	Serratosagitta pacifica	(Tokioka)	(1940)
	Serratosagitta tasmanica	(Thompson)	(1947)
	Decipisagitta decipiens	(Fowler)	(1905)
	Decipisagitta sibogae	(Fowler)	(1906)
	Mesosagitta minima	(Grassi)	(1881)
	Pseudosagitta lyra	(Krohn)	(1853)
	Pseudosagitta gazellae	(Ritter-Záhoni)	(1909)
	Pseudosagitta maxima	(Conant)	(1896)
	Solidosagitta planctonis	(Steinhaus)	(1896)
	Solidosagitta zetesios	(Fowler)	(1905)
	Caecosagitta macrocephala	(Fowler)	(1905)
Pterosagittidae	*Pterosagitta draco*	(Krohn)	(1853)
Krohnittidae	*Krohnitta subtilis*	(Grassi)	(1881)
	Krohnitta pacifica	(Aida)	(1897)
Eukrohniidae	*Eukrohnia hamata*	(Mörbius)	(1875)
	Eukrohnia bathypelagica	Alvariño	1962
	Eukrohnia fowleri	Ritter-Záhoni	1909
Spadellidae	*Paraspadella nana**	(Owre)	(1963)

***Single benthic species ocurring in Brazil. Source:** Danielle Melo.

It is also relevant to mention that some species reported over the decades were subsequently synonymized, such as *Pterosagitta besnardi* (= *Pterosagitta draco*) and *Sagitta gloriae* (= *Ferosagitta hispida*), initially described by Vannucci and Hosoe (1952) and by Almeida-Prado (1963), respectively. Taxonomic questions about synonymies still involve other genus, as *Solidosagitta* (e.g MCLELLAND; PERRY, 1989; CASANOVA, 1999) and *Parasagitta*, this latter dividing opinions among different authors in Brazil (Table 1; See Horizontal Distribution section).

Among the specific publications of Chaetognatha considered by this review, the first study to register species of the group corresponds to that of Vannucci and Hosoe (1952), developed on the island of Trindade and seamount Jaseur (southeast region of Brazil). Figueirêdo et al. (2018), in turn, reports the last record of the group in Brazilian waters, comprising new occurrences of *Paraspadella nana* in the Bay of Tamandaré and Abrolhos Bank, both localities located in the northeast region (Table S3.1). The investigation of still poorly known environments can expand the list of the species catalogued so far (see Perspectives to the study of Chaetognatha section).

AREAS OF STUDY INVOLVING SPECIFIC PUBLICATIONS OF THE GROUP IN BRAZIL

Although it often represents one of the most abundant groups of the holoplankton in the marine environment (e.g. PEARRE JR., 1980; CAVALCANTI; LARRAZÁBAL, 2004; NEUMANN-LEITÃO; SANT'ANNA, et al., 2008), the specific publications of the phylum in Brazil grew significantly only from the decade of 90 (Figure 1), when subjects such as food ecology and trophic interactions began to be addressed by some authors in the southeast region of the country (VEGA-PÉREZ; LIANG, T. H., 1992; LIANG, T. H.; VEGA-PÉREZ, 1995; MARAZZO; NOGUEIRA, C. S. R., 1996; MARAZZO; MACHADO; NOGUEIRA, C. S. R., 1997; LIANG, T.-H.; VEGA-PEREZ, 2002; LIANG, T.-H.; ARA, et al., 2003). Data of this type can be considered of great relevance, since which expanded the knowledge beyond the already traditional aspects discussed of distribution, abundance and association of Chaetognatha with water masses in the domain pelagic

(Table S3.1).

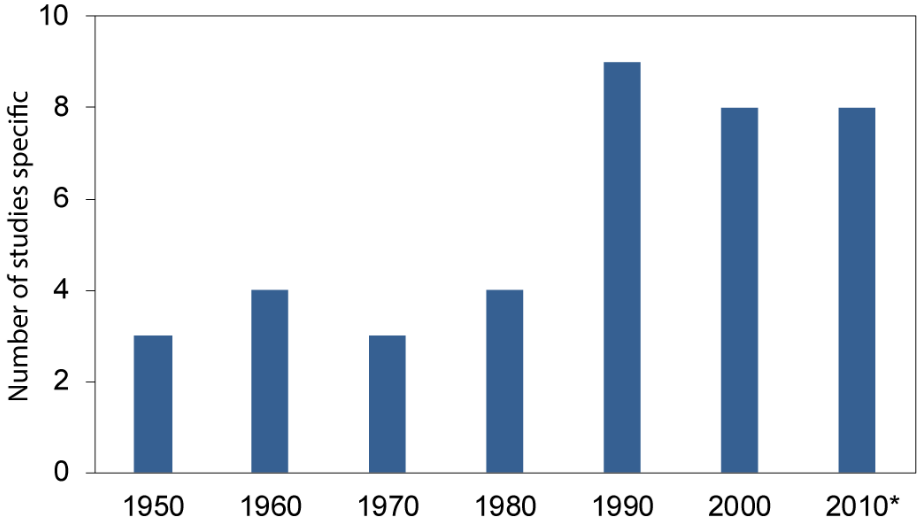


Figure 1 – Number of specific studies of the phylum Chaetognatha published by decade in Brazilian waters. Were considered publications from 1950 to August 2018*. **Source**: Alef Silva

Among the aforementioned studies, deeper investigations into food ecology were performed for the species *P. friderici*, in view of its high representativeness along the continental shelf (VEGA-PÉREZ; LIANG, T. H., 1992; LIANG, T. H.; VEGA-PÉREZ, 1995; LIANG, T.-H.; ARA, et al., 2003). On the other hand, something common to all these publications is the close relationship of Chaetognatha as an important predator of Copepoda. This could be demonstrated through the high percentage of species of this taxon in stomach contents (VEGA-PÉREZ; LIANG, T. H., 1992; LIANG, T. H.; VEGA-PÉREZ, 1995; MARAZZO; MACHADO; NOGUEIRA, C. S. R., 1997; LIANG, T.-H.; ARA, et al., 2003); Or even through the association between the spatial distribution of Chaetognatha and the Copepoda density, reflecting a perceptible trophic interaction between the groups (MARAZZO; NOGUEIRA, C. S. R., 1996). Other taxa, such as Appendularia, Annelida and other crustaceans also proved to be important prey to the diet of the species (VEGA-PÉREZ; LIANG, T. H., 1992; LIANG, T. H.; VEGA-PÉREZ, 1995; LIANG, T.-H.; ARA, et al., 2003). Inter-and intra-specific of cannibalism relations were observed in some of these studies, a behavior considered common in Chaetognatha (PEARRE JR., 1982; LIANG, T. H.; VEGA-PÉREZ, 1995; VEGA-PÉREZ; SCHINKE, 2011).

In association with quantitative data, of distribution or of trophic ecology, some publications still treated about other parameters involving the group. Among these, quotes the analysis of morphologic and/or anatomical characters (VANNUCCI; HOSOE, 1952; ALMEIDA-PRADO, 1961; BOLTOVSKOY, 1975), biomass measurement of species (LIANG, T. H.; VEGA-PÉREZ, 2001; LIANG, T.-H.; VEGA-PEREZ, 2002; LIANG, T.-H.; ARA, et al., 2003), investigation of the population structure based on developmental stages (e.g. ALMEIDA-PRADO, 1968; LIANG, T. H.; VEGA-PÉREZ, 1994; LIANG, T.-H.; VEGA-PEREZ, 2002; LIANG, T.-H.; ARA, et al., 2003; RESGALLA-JUNIOR, 2010; MENDES; FIGUEIREDO; VALENTIN, 2012), evaluation of reproductive cycles (MENDES; FIGUEIREDO; VALENTIN, 2012), and of infections by parasites (ALMEIDA; BARQUETE; JR., 2009). Two publications dedicated to the genetic investigation of specific taxa also carried out sampling in Brazilian waters (KULAGIN; STUPNIKOVA, et al., 2013; KULAGIN; NERETINA, 2017) (Table S3.1).

According to the bibliographical survey carried out in this review, the number of specific publications developed from the decade of 90 to the present remains at a constant level (Figure 1). The following sections comprise the main information (among specific and general publications) about the spatial distribution of Chaetognatha in Brazil.

HORIZONTAL DISTRIBUTION

Since richness and diversity of Chaetognatha remain relatively constant between 40°N and 40°S in the Atlantic (MACPHERSON, 2002; NOGUEIRA-JÚNIOR et al., 2018), there is a tendency for the same species to be found throughout different Brazilian latitudes (north, northeast, southeast and south regions). On the other hand, it is observed that in a coastal-ocean gradient, most species demonstrate preference for some characteristic environment. This occurs as a reflection of its adaptations to the different abiotic conditions governing the hydrodynamics of each environment, leading to the observation of general patterns of the horizontal distribution (BIERI, 1959; CASANOVA, 1999; BOLTOVSKOY, 2005; ÁVILA; ARRUDA; BONECKER, S. L. C., 2006). In this context, the species can be considered as typical of a coastal systems, usually presenting a more restricted distribution; or, like those found preferentially in open shelf waters and/or oceanic, may even occur in the transition zones between the two environments (LIANG, T.-H.; VEGA-PEREZ, 2002). Cosmopolitan or widely distributed species in the South Atlantic can still be registered from coast to the oceanic domain (CASANOVA, 1999; BOLTOVSKOY, 2005; ÁVILA; ARRUDA; BONECKER, S. L. C., 2006), in general showing intervals where they also occur preferentially.

Coastal Neritic Systems

When considering a coastal-oceanic gradient, it is noted that most of the works involving Chaetognatha was developed in coastal neritic environments, including river estuaries (SANKARANKUTTY; MEDEIROS; OLIVEIRA, 1995; SANKARANKUTTY; MEDEIROS; SILVA, A. C. C., 1996; LOPES; ALMEIDA PRADO, 1986; LOPES, 1994; LANSAC TÔHA; LIMA, 1993; MELO-MAGALHÃES et al., 1996; NEUMANN-LEITÃO; MATSUMURA-TUNDISI, 1998; PORTO-NETO et al., 1999; KRUMME; LIANG, T.-H., 2004; COSTA, K. G.; PEREIRA; COSTA, R. M., 2008; CAVALCANTI; NEUMANN-LEITÃO; VIEIRA, 2008; ARAUJO, H. M. P. et al., 2008; RESGALLA-JUNIOR; SOUZA, V. G. C., et al., 2008; SANTOS, T. G. et al., 2009; LEITE, N. D. R.; PEREIRA; COSTA, R. M. D., 2009; MARCOLIN et al., 2010; COSTA, R. M. et al., 2011; COSTA, K. G.; BEZERRA, et al., 2013; NOGUEIRA-JUNIOR et al., 2018); bays and coves (ALMEIDA-PRADO, 1963; COSTA, P., 1970; MARAZZO; NOGUEIRA, C. S. R., 1996; COELHO-BOTELHO et al., 1999; DIAS, C. O.; BONECKER, S. L. C.; NOGUEIRA, C. R., 1999; RESGALLA-JUNIOR, 2001; MARAZZO; VALENTIN, 2003, 2004; SILVA, A. P. et al., 2004; FERNANDES; STERZA; NEVES, K. O., 2005; VEADO, L. D. A. V.; RESGALLA JR., 2005; RESGALLA-JUNIOR; VEADO, L. D. A., 2006; STERZA; FERNANDES, 2006; DIAS, C. O.; BONECKER, S. L. C., 2008; BONECKER, S. L. C.; DIAS, C. O., 2009; MIYASHITA et al., 2012; DIAS, C. O.; CARVALHO, et al., 2018); and, reef areas (MELO, N. F. A. C. d. et al., 2002; MAYAL et al., 2009; NASCIMENTO-VIEIRA; NEUMANN-LEITÃO, et al., 2010).

Depending on the degree of geomorphological openness, these ecosystems many times presents a limited influence with the marine environment, which often conditions a low richness of recorded chaetognaths. Nogueira-Júnior et al. (2018), for example, described that the species *Parasagitta friderici*, *Parasagitta tenuis* and *Flaccisagitta enflata* are the most abundant and frequent chaetognaths in estuarine ecosystems (including river estuaries and bays), having been reported in more than 60% of the 25 Brazilian estuaries with data available about Chaetognatha. In these areas, communities richer in species constitute exceptions, and may be associated with greater openness of locality to marine influence, as the example of Guanabara Bay (5 species DIAS, C. O.; CARVALHO, et al., 2018), and Ribeira Bay, where six (DIAS, C. O.; BONECKER, S. L. C.; NOGUEIRA, C. R., 1999) up to twelve species belonging to the group were recorded (DIAS, C. O.; BONECKER, S. L. C., 2008). Both localities are situated in the state of Rio de Janeiro, southeast Brazil. In reefs areas, the pattern observed according to the few studies available is always turned on the occurrence of only one species: *P. tenuis* (MELO, N. F. A. C. d. et al., 2002; MAYAL et al., 2009) or *P. friderici* (NASCIMENTO-VIEIRA; NEUMANN-LEITÃO, et al., 2010).

Although what the richness of a taxon may vary according to the methodology used and the intrinsic characteristics of each site (PALMA, M. B. et al., 2013), the occurrence and pattern of distribution of Chaetognatha in coastal systems seem to be conditioned, above all, by the tidal regime (SANKARANKUTTY; MEDEIROS; SILVA, A. C. C., 1996; LIANG, T.-H.; ARA, et al., 2003; FERNANDES; STERZA; NEVES, K. O., 2005; NASCIMENTO-VIEIRA; NEUMANN-LEITÃO, et al., 2010) associated with variations of salinity which regulate a local hydrodynamics (MARAZZO; NOGUEIRA, C. S. R., 1996; MELO-MAGALHÃES et al., 1996; STERZA; FERNANDES, 2006; MENDES; FIGUEIREDO; VALENTIN, 2012). The association of these two main factors along a temporal approach can suggest whether the species maintain resident populations or if they are only trapped due to tidal currents entering the environment, creating a favorable way for their presence (NAIR; SANKARANKUTTY, 1988; MELO-MAGALHÃES et al., 1996; FERNANDES; STERZA; NEVES, K. O., 2005). Other environmental parameters, as speed and direction of the winds (MELO, N. F. A. C. d. et al., 2002; HERNÁNDEZ; SUÁREZ-MORALES; GASCA, 2005; NOGUEIRA-JÚNIOR et al., 2018); and biotic parameters, such as food availability (MARAZZO; NOGUEIRA, C. S. R., 1996; MARAZZO; MACHADO; NOGUEIRA, C. S. R., 1997; COELHO-BOTELHO et al., 1999; MARAZZO; VALENTIN, 2003; FERNANDES; STERZA; NEVES, K. O., 2005) and life cycle strategies (NOGUEIRA-JÚNIOR et al., 2018) may still interfere in the extent of the horizontal distribution of Chaetognatha in these ecosystems.

The two species of *Parasagitta* above mentioned are among the few Chaetognatha typical of a coastal systems in other parts of the world (DUCRET, 1962; MCLELLAND, 1980; PIERROT-BULTS, A. C.; NAIR, 1991; HOSSFELD, 1996). Although Nogueira-Júnior et al. (2018) have mentioned that the dominance of these species appears to be modified according to latitude (*P. tenuis* predominating in latitudes < 11°S, while *P. friderici* in latitudes > 22°S), the authors emphasize that this observation may be result of taxonomic problems involving its identification. (BOLTOVSKOY, 1981), for example, considers *P. friderici* and *P. tenuis* as synonymies, whose species may present morphological variations according to local hydrological conditions. Some authors clearly follow this thought (COELHO-BOTELHO et al., 1999; RESGALLA-JUNIOR; MONTÚ, 1995; RESGALLA-JUNIOR, 2010); others do not alluded to this information, leaving uncertain whether they agree with the respective classification (e.g. ALVARIÑO, 1968; MONTÚ; CORDEIRO, T. A., 1988). Even though most studies consider both taxa as valid, based on investigation studies and other identification guides (ALMEIDA-PRADO, 1961; CASANOVA, 1999; ÁVILA; ARRUDA; BONECKER, S. L. C., 2006), the latitudinal change mentioned should be in fact treated with caution, and investigated more deeply (NOGUEIRA-JÚNIOR et al., 2018).

Neritic and Oceanic Waters Adjacent to Brazilian Coastal Systems

Studies report that a gradual increase in richness of Chaetognatha occurs with the distance from the coast towards to the ocean (ARAÚJO, H. M. P.; RIBEIRO, V. A., 2005; LIANG, T. H.; VEGA-PÉREZ, 2001; LIANG, T.-H.; VEGA-PEREZ, 2002), similar pattern to that described for planktonic groups in general (NEUMANN-LEITÃO et al., 1991; LIANG, T.-H.; VEGA-PEREZ, 2002; BONECKER, S. L. C.; ARAUJO, A. V. de, et al., 2014; BONECKER, A. C. T.; ARAÚJO, A. V., et al., 2017). This tendency can be mainly related to the marine ecology of chaetognaths (HOSSFELD, 1996), which in open neritic and oceanic waters are favored by the continuous presence of water masses with this characteristic (SVERDRUP; JOHNSON, M. W.; FLEMING, 1942; MIRANDA, 1985; CASTRO; MIRANDA, 1998; SILVEIRA; SCHMIDT, et al., 2000). The reduction of continental and estuarine contributions also provides a greater stability of physical parameters, an important factor to increase the richness and diversity of zooplankton along the Brazilian Tropical region (NEUMANN-LEITÃO et al., 1991; NEUMANN-LEITÃO; SILVA TDA, et al., 1999; NEUMANN-LEITÃO; SANT'ANNA, et al., 2008). In general, a significant number of studies have addressed the composition of the Chaetognatha communities in continental shelf (ALMEIDA-PRADO, 1963; VALENTIN, 1984; MONTEIRO RIBAS; MUREB, 1989; PARANAGUÁ et al., 1990; NEUMANN-LEITÃO et al., 1991; VEGA-PERÉZ, 1993; VALENTIN; MONTEIRO-RIBAS, 1993; CAVALCANTI; LARRAZÁBAL, 2004; ARAÚJO, H. M. P.; RIBEIRO, V. A., 2005; ARAÚJO, H. M. P.; RIBEIRO, V., 2008), as well as in the shelf together with the Brazilian oceanic zone (involving slope and/or the oceanic domain) (PARANAGUÁ, 1966; COSTA, P. F., 1971; BOLTOVSKOY, 1975; VALENTIN, 1984; NASCIMENTO-VIEIRA; SANT'ANNA, et al., 1990; LIANG, T. H.; VEGA-PÉREZ, 1994; LIANG, T. H.; VEGA-PÉREZ, 2001; LIANG, T.-H.; VEGA-PEREZ, 2002; RESGALLA-JUNIOR; MONTÚ, 1995; NEUMANN-LEITÃO; MATSUMURA-TUNDISI, 1998; NEUMANN-LEITÃO; SILVA TDA, et al., 1999; NOGUEIRA, C. R. et al., 1999; NEUMANN-LEITÃO; SANT'ANNA, et al., 2008; RESGALLA-JUNIOR; SOUZA, V. G. C., et al., 2008; BONECKER, S. L. C.; ARAUJO, A. V. de, et al., 2014; BONECKER, A. C. T.; ARAÚJO, A. V., et al., 2017; BONECKER, S. L. C.; ARAÚJO, A. V., et al., 2017; BONECKER, A. C. T.; DIAS, C. D. O., et al., 2018). It is important to mention, however, that few of these studies detail the distribution of the species along the evaluated gradient. The lack of quantitative data is commonly observed.

Excluding those publications where the number of species was clearly underestimated (VEGA-PERÉZ, 1993; VALENTIN, 1984; VALENTIN; MONTEIRO-RIBAS, 1993), the richness of Chaetognatha demonstrates an average increase of two for six species in open neritic waters (not including coastal systems), and for ten when considering these latter together with oceanic areas. The species described in the first context, within the north and northeast Tropical region of Brazil, comprise: *F. enflata, P. friderici, P. tenuis, F. hispida, P. draco, Serratosagitta serratodentata, Sagitta bipunctata, Krohnitta pacifica* and *Flaccisagitta hexaptera* (PARANAGUÁ et al., 1990; NEUMANN-LEITÃO et al., 1991; CAVALCANTI; LARRAZÁBAL, 2004; ARAÚJO, H. M. P.; RIBEIRO, V. A., 2005). Detailed data on their distribution are provided only by the study of H. M. P. Araújo and V. A. Ribeiro (2005), which highlighted the species *F. enflata* and *P. tenuis* as the most frequent and abundant in the shelves of Alagoas and Sergipe (Brazilian northeast), with higher concentrations observed in the most internal stations of the evaluated gradient. As discussed earlier, these two species in association with *P. friderici* are the most frequent chaetognaths in Brazilian coastal systems, but that can also occur in open neritic waters due to their eurithermic and eurihaline characteristics; especially *F. enflata*, considered cosmopolitan and with wide horizontal distribution (CASANOVA, 1999; BOLTOVSKOY, 2005).

Most of the other species recorded are typically oceanic (see below), and their incursion into neritic waters can be favored both by coastal advective processes (NEUMANN-LEITÃO; SANT'ANNA, et al., 2008), and by the reduced size of the continental shelf, observed mainly along the northeast Brazilian region (NEUMANN-LEITÃO; SILVA TDA, et al., 1999; NEUMANN-LEITÃO; SANT'ANNA, et al., 2008). The occurrence of *P. draco* and *S. bipunctata* on the Alagoas and Sergipe shelf, for example, has already been related to the presence of oceanic water masses in the area, such as the Tropical Water (ARAÚJO, H. M. P.; RIBEIRO, V. A., 2005). In a later study, the profiles of salinity and temperature showed that oceanic waters in fact spread on the Sergipe shelf, possibly because it is narrow and interrupted by two large submarine canyons, which can still guide processes of local resurgence (ARAÚJO, H. M. P.; RIBEIRO, V. A., 2005). The reduced size of the continental shelf also may favor the general dispersion of the neritic zooplankton towards the ocean (DADON; BOLTOVSKOY, 1982; NEUMANN-LEITÃO; SILVA TDA, et al., 1999; NEUMANN-LEITÃO; SANT'ANNA, et al., 2008), which makes it an important means of interaction and biological connectivity between these environments and their communities. According to Neumann-Leitão, Sant'anna, et al. (2008), advective processes and geomorphological characteristics of the shelf as mentioned above, condition a significant homogeneity of the zooplankton assembly along the Brazilian Tropical Atlantic.

Such homogeneity can be observed through some studies involving open and oceanic neritic areas of the northeast region, since they report the occurrence of the same species previously mentioned (*F. enflata, P. friderici, P. tenuis, F. hispida, S. serratodentata, S. bipunctata, P. draco, K. pacifica*and *F. hexaptera*, with only two additional records of the species *Krohnitta subtilis*and *Sagitta helenae* to the composition of Chaetognatha (PARANAGUÁ, 1966; NASCIMENTO-VIEIRA; SANT'ANNA, et al., 1990; NEUMANN-LEITÃO; MATSUMURA-TUNDISI, 1998; NEUMANN-LEITÃO; SILVA TDA, et al., 1999; LIANG, T. H.; VEGA-PÉREZ, 2001; NEUMANN-LEITÃO; SANT'ANNA, et al., 2008). *K. subtilis* has been described as neritic-oceanic, while *S. helenae* as a typically oceanic species (BONE; KAPP; PIERROT-BULTS, A. C., 1991; PIERROT-BULTS, A. C.; SUAREZ; GASCA, 1996; CASANOVA, 1999; ÁVILA; ARRUDA; BONECKER, S. L. C., 2006). However, as most of the studies do not describe the species-specific distribution of the group, there is no way to ensure that these two taxa have occurred only, or preferably in some range of the evaluated gradient (neritic or oceanic). The distribution of these species was better investigated in areas comprised of higher Brazilian latitudes (RESGALLA-JUNIOR; MONTÚ, 1995; BONECKER, S. L. C.; ARAUJO, A. V. de, et al., 2014), where *K. subtilis* appears to be mainly related to the cooler waters (see Distribution Vertical section).

In general, the north Brazil presents a significant deficiency of publications addressing the identification of Chaetognatha. Of the few studies available, most were developed in coastal systems of the region (KRUMME; LIANG, T.-H., 2004; COSTA, K. G.; PEREIRA; COSTA, R. M., 2008; LEITE, N. D. R.; PEREIRA; COSTA, R. M. D., 2009; COSTA, R. M. et al., 2011; COSTA, K. G.; BEZERRA, et al., 2013), while only two investigated a more extensive horizontal gradient (ALVARIÑO, 1968; NEUMANN-LEITÃO;

MELO, P. A. M. C., et al., 2018). The study by Neumann-Leitão, Pedro A. M. C. Melo, et al. (2018), for example, comprised estuarine areas and reef formations to oceanic waters adjacent to the Amazon River. In this area, a relatively low richness of Chaetognatha was observed (*S. serratodentata, F. enflata, P. tenuis, F. hispida, K. pacifica, P. draco*), with the first two species having been reported as the most important. Quantitative data for each species were not provided. However, it is cited that the evaluated ecosystem presented a mixture of coastal and oceanic zooplankton communities, with a gradual separation between them along the area in question. The relative homogeneity was related to the large extent of the estuarine plume of Amazonas, which seems to favor the dispersion of many zooplankton organisms towards the ocean (since coastal species occurred in stations distant from the mouth of the Amazonas), at the same time that the oceanic circulation also contributes with several species to the coastal reef system. Specific information of Chaetognatha would be important to confirm this general pattern observed for zooplankton.

The second publication available on a larger horizontal scale in the north region describes a richer community towards higher geographic latitudes (ALVARIÑO, 1968). The distribution of Chaetognatha has been investigated from the mouth of the Amazon River, in Amapá (far north of Brazil) to the latitude of Porto Rico, in oceanic waters (Table S3.1). Although only a small part of Brazil was included in this study, 10 of the 12 species recorded were equivalent to previously described taxa (*F. enflata, P. tenuis, F. hispida, S. serratodentata, K. pacifica, K. subtilis, S. bipunctata, S. helenae, P. draco, F. hexaptera*). The two additional species corresponded to *Decipisagitta decipiens* and *Pseudosagitta lyra*. These taxa are considered typical of oceanic environments, characteristic of higher depths (CASANOVA, 1999; PIERROT-BULTS, A. C.; SUAREZ; GASCA, 1996; ÁVILA; ARRUDA; BONECKER, S. L. C., 2006). In the surface (0-200 m), their record usually occurs in association with the outcropping of deeper waters (ALVARIÑO, 1968; SOUZA, C. S. D.; LUZ; MAFALDA JR., 2014) (see Vertical Distribution section).

Some of these species were also recorded between the south of the state of Bahia (northeast region) and the state of Rio de Janeiro (Cabo de São Tomé, southeast region), including *Decipisagitta sibogae* (ÁVILA; ARRUDA; BONECKER, S. L. C., 2006). Agreeing with its ecology, most of these taxa showed preference for oceanic waters: M. minima and *D. decipiens* were distributed mainly from the 200 m isobath, while *D. sibogae* occurred beyond this isobath. Only *P. lyra* seemed did not demonstrate a preferential range of occurrence (ÁVILA; ARRUDA; BONECKER, S. L. C., 2006). This study comprised from coastal systems to oceanic waters, and was based on the use of various methodologies (different types of hauls performed between 0-200 m, different mesh sizes selected for sampling), with a large number of samples analyzed, which may have significantly favored the high richness of Chaetognatha along the study area (from Salvador, Bahia to Cabo de São Tomé, Rio de Janeiro; including the Vitória-Trindade Chain), with a total of 17 registered species.

As described in the next section, the southeast region of Brazil gathers important general publications that investigated the distribution of zooplankton in neritic waters on the shelf and slope of the Campos basin, located between the states of Espírito Santo and Rio de Janeiro (BONECKER, S. L. C.; ARAUJO, A. V. de, et al., 2014; BONECKER, A. C. T.; ARAÚJO, A. V., et al., 2017). Of the 16 species of Chaetognatha recorded, 12 occurred along the horizontal gradient evaluated (*P. friderici, F. enflata, F. hexaptera, K. pacifica, K. subtilis, M. minima, P. lyra, P. draco, S. serratodentata, D. sibogae*). These species composed homogeneous communities in the two seasonal periods studied (rainy and dry), however, a greater richness was obtained on the continental shelf (10 species-rainy; 9 species-dry season) and not in the area of the slope (8 species recorded in the two periods). This observation disagrees with the general tendency to find a greater number of species in points farther from the coast, as it was reported for other planktonic groups such as Copepoda, Siphonophora and Euphasiacea in the same studies (BONECKER, A. C. T.; ARAÚJO, A. V., et al., 2017; BONECKER, S. L. C.; ARAUJO, A. V. de, et al., 2014). The superficial sampling, considering only the first meter of depth of the Tropical Water, may have influenced directly in obtaining this result.

The south portion of the Campos Basin still gathers some publications that approached Chaetognatha in the system of upwelling in Cabo Frio. Due to this phenomenon, the area has been studied mainly as to its circulation processes and nutrient dynamics, as well as in relation the composition of epipelagic micro and mesozooplankton (BONECKER, S. L. C.; ARAUJO, A. V. de, et al., 2014). The Chaetognatha communities described in the area comprise the species *P. tenuis, F. enflata, P. friderici, F. hispida, S. serratodentata, M. minima, P. draco* and *K. subtilis* (VALENTIN; MONTEIRO-RIBAS, et al., 1987; MONTEIRO RIBAS; MUREB, 1989; LIANG, T. H.; VEGA-PÉREZ, 2001), with an average of five taxa recorded per study. The smallest richness observed comprised a community formed by *P. tenuis, F. enflata, P. friderici and F. hispida* (LIANG, T. H.; VEGA-PÉREZ, 2001). According this study, environments characterized by a greater instability in the thermohaline structure are favorable to the development of a smaller number of species, which usually occur in high abundance. A typical and stable oceanic zone, on the other hand, would support more complex trophic relationships, favoring a consequent increase in the richness and local biological diversity (LIANG, T. H.; VEGA-PÉREZ, 2001; BONECKER, A. C. T.; ARAÚJO, A. V., et al., 2017). In Cabo Frio, the most abundant species of Chaetognatha are F. enflata (VALENTIN; MONTEIRO-RIBAS, et al., 1987; MONTEIRO RIBAS; MUREB, 1989) and *P. friderici* (LIANG, T. H.; VEGA-PÉREZ, 2001), this latter already having been registered in high representativeness during local upwelling events (> 90% of the total Chaetognatha) (Valentin, 1984).

Further south of the southeast region, the horizontal distribution of Chaetognatha from coastal to oceanic waters was investigated more deeply in the localities of Ubatuba (LIANG, T. H.; VEGA-PÉREZ, 1994) and São Sebastião (LIANG, T.-H.; VEGA-PEREZ, 2002), state of São Paulo. In this last study, for example, a community consisting of seven species (Table S3.1) was structured in two main areas: i) a coastal zone, characterized by few species; and, ii) a oceanic zone, where many species occurred. In agreement with previously discussed data, the most coastal zone was dominated by the species *P. friderici* and *P. tenuis*, while in the oceanic zone there was a predominance of *F. enflata*. According to the cluster analysis, the species *P. friderici*, *P. tenuis* and *S. bipunctata* were characterized as neritic. The other species (*F. enflata*, *F. hispida*, *K. pacifica* and *M. minima*) were then classified as semi-neritic, because although they have occurred mainly in the oceanic area, were also distributed on the continental shelf. This study still brings other relevant information, and up to the present, scarce on the group in Brazilian waters. It was observed that along the coast-ocean gradient, the density and biomass parameters of Chaetognatha increased to the extent that shore clearance occurred, behavior also observed for this group in a previous study, which comprised from the area of Cabo Frio (southeast region) to the ASPSP (northeast region) (LIANG, T. H.; VEGA-PÉREZ, 2001). On the other hand, an opposite gradient of biomass (of to decrease from the coast to the ocean) was verified by Neumann-Leitão, Silva TDA, et al. (1999) for the zooplankton community, registered between the states of Ceará and Pernambuco (northeast region). In this case, the reported pattern occurred for the general zooplankton, which did not necessarily correspond to the specific behavior of Chaetognatha in the area. Some authors suggest that increasing the abundance of the group towards the ocean is something expected, since, as well as the richness, this tendency would also be linked to the preference of most species by oceanic waters (HOSSFELD, 1996; LIANG, T.-H.; VEGA-PEREZ, 2002).

Horizontal distribution data of some of the species cited by Tsui-Hua Liang and Vega-Perez (2002) are confirmed through publications previously discussed, and also by the study of Almeida-Prado (1968), conducted further south of the state of São Paulo, in points along the continental shelf (Table S3.1). The species *F. enflata* and *M. minima*, for example, have shown preference for more oceanic and saline waters than *P. friderici*. The taxa *K. pacifica* and *F. hispida*, on the other hand, were more related to Shelf Water. Almeida-Prado (1968) still cited the occurrence in lower concentrations of the species *K. subtilis*, *S. serratodentata* and *P. draco*, with the last two species in narrow association with the oceanic Tropical Water. In way general, the distribution data reported by this author are in agreement with that described by Tsui Hua Liang and Vega-Pérez (1994) to Ubatuba (São Paulo); and, by Almeida-Prado (1961b), which investigated the distribution of Chaetognatha from Cabo Frio to Montevideo (Uruguay)

(Table S3.1).

In addition to the previous publication which involves a larger spatial scale considering Chaetognatha (VEGA-PERÉZ, 1993), the south region of the country counts with only two publications on the detailed distribution of the group, having been developed on the continental shelf (internal and external) and slope of Rio Grande do Sul, state located in the extreme south of Brazil (RESGALLA-JUNIOR; MONTÚ, 1995; RESGALLA-JUNIOR, 2008). Both publications are discussed in the Vertical Distribution section of the species, however, since it also contains important information about its horizontal distribution, it becomes pertinent to mention them. The study by Resgalla-Junior and Montú (1995), for example, registered 18 species, one of the highest richness reported by the publications gathered by this review (see Vertical Distribution section; Table S3.1). Most species followed a clear patterns of distribution: i) Those found only or preferably on the external shelf or slope in the two study periods (summer and winter) showed close association with oceanic waters (*P. draco*, *S. serratodentata*, *F. hexaptera*, *P. lyra*, *K. subtilis*, *M. minima*, *Serratosagitta tasmanica*, *Eukrohnia hamata*); ii) species restricted to the slope in both seasons, occurring typically at higher depths (*D. decipiens* and *S. planctonis*); and, iii) species recorded only in winter, also typical of higher depths, and that occurred in small concentrations restricted to the slope (M. maxima, *E. bathypelagica* and *P. gazellae* - only 1 species). The species *P. tenuis* (= *P. friderici* in this study), *F. enflata* and *F. hispida* occurred throughout the entire gradient evaluated in at least one of the periods. The first was considered the most frequent and abundant species during the winter, gathering the highest densities of Chaetognatha on the internal shelf; while *F. enflata* was the dominant taxon throughout the summer period.

The distribution of species recorded by Resgalla-Junior and Montú (1995) was also associated with regional water masses. *P. tenuis* was related to Coastal Water; *F. enflata* and *F. hispida* to Shelf Water; *P. draco* and *K. pacifica* were associated with oceanic Tropical Water; *D. decipiens*, *P. lyra* and *K. subtilis* to SubTropical Water; and *S. tasmanica* to the Subantarctic Water. The taxa *S. serratodentata* and *M. minima*, in turn, were related to mixed waters between the areas of Tropical Water and Subantarctic Water. In general, the association of Chaetognatha with these water masses was confirmed by a later study in the same area (RESGALLA-JUNIOR, 2008); and, by studies conducted in the northeast and southeast regions, with respect to the species *F. enflata*, *P. draco* and *S. serratodentata* (ALMEIDA-PRADO, 1963, 1968; LIANG, T. H.; VEGA-PÉREZ, 1994; LIANG, T. H.; VEGA-PÉREZ, 2001). Additional studies developed on a larger scale would be valid to investigate the distribution of species along the Brazilian south oceanic zone.

Oceanic Islands and Seamounts

Brazil has a significant set of oceanic topographies along its extension (ASPSP, North Chain, Fernando de Noronha Chain), some directly from the coast towards the ocean (Vitória-Trindade Chain). From the decade of 50 to present, Chaetognatha was the object of specific study in some of these areas (VANNUCCI; HOSOE, 1952; HOSOE, 1956; COSTA, P. F., 1971; LIANG, T. H.; VEGA-PÉREZ, 2001; SOUZA, C. S. D.; LUZ; MAFALDA JR., 2014), in addition to general publications of zooplankton that still approached the species in the northeast islands (PARANAGUÁ, 1966; PINTO; MAFALDA; SANTOS, A. T., 1997; MELO, P. A. M. D. C. et al., 2012; CAMPELO et al., 2018) and southeast Brazil (ÁVILA; ARRUDA; BONECKER, S. L. C., 2006). The communities described in these publications consist of Chaetognatha typically registered in neritic and oceanic environments of Tropical waters (e.g. NEUMANN-LEITÃO; SILVA TDA, et al., 1999; NEUMANN-LEITÃO; SANT'ANNA, et al., 2008) and subtropical in South Atlantic (ALMEIDA-PRADO, 1963; RESGALLA-JUNIOR, 2010).

An average of eight species is estimated when considering the island areas and seamounts within the available data on Chaetognatha, excluding those publications where the richness of the group was clearly underestimated (PINTO; MAFALDA; SANTOS, A. T., 1997; CAMPELO et al., 2018). The registered species include *F. enflata*, *P. tenuis*, *P. friderici*, *F. hispida*, *S. serratodentata*, *M. minima*, *S. bipunctata*, *K. pacifica*, *K. subtilis*, *P. draco*, *F. hexaptera*, *P. lyra*, *D. decipiens*, *D. sibogae* and *Caecosagitta macrocephala* (VANNUCCI; HOSOE, 1952; HOSOE, 1956; PARANAGUÁ,

1966; LIANG, T. H.; VEGA-PÉREZ, 2001; ÁVILA; ARRUDA; BONECKER, S. L. C., 2006; MELO, P. A. M. D. C. et al., 2012; SOUZA, C. S. D.; LUZ; MAFALDA JR., 2014). Among these studies, the community with lower richness and diversity (4-6 species) was reported by T. H. Liang and Vega-Pérez (2001) in the region known as Intertropical Zone (between the ASPSP and Fernando de Noronha Archipelagos), a result like that recorded in the locality of Cabo Frio (see above) and in the area of the seamounts of Vitória, also evaluated in this work. The areas in question would be prone to the development of a small number of species due to the relative hydrodynamic instability caused by advective processes; however, these species would also be subject to reach a high representativity (LIANG, T. H.; VEGA-PÉREZ, 2001). Indeed, the highest values of abundance in this study were recorded in the Intertropical Zone and in the seamounts of Vitória, with emphasis on Chaetognatha *S. serratodentata* and *F. enflata*. The authors mention that this result may be related to the influence of SACW on shallower layers in these regions: since this water mass is cooler and nutrient-rich, the increase in primary productivity would be favored, positively affecting other trophic levels, such as Chaetognatha. This information agrees with previous reports mentioning that the SACW can occupy smaller depths in proximity to banks and islands, because of the regime of winds and local circulation (TAKAHASHI; BARTH, 1968), providing the so-called ”island effect” (DOTY; OGURI, 1956). Similar data regarding the richness of Chaetognatha were also obtained by other authors, such as in Fernando de Noronha (5 species HOSOE, 1956); and, considering jointly the seamounts and oceanic islands of northeast Brazil (6 species SOUZA, C. S. D.; LUZ; MAFALDA JR., 2014).

Although the above studies have described lower richness in island environments, it is important to mention that this is not a pattern for Chaetognatha. A community consisting of 10 species, for example, was described by Pedro Augusto Mendes De Castro Melo et al. (2012) in the vicinity of the SPSPA. The causes for the observation of this result are unclear, since the methodology used did not present any particularity (subsurface sampling at dawn, performed in the same seasonal period of the study of T. H. Liang and Vega-Pérez (2001)). However, changes in the hydrodynamic structure of the area, such as variations in current intensity and cyclonic vortices productions (ARAÚJO, M.; CINTRA, 2009), may be linked to the differences in the richness of Chaetognatha observed at different times. Pedro Augusto Mendes De Castro Melo et al. (2012) cited that physical forcing in general can act as significant structuring of the zooplankton community, modifying patterns of diversity, migration and distribution of the species evaluated.

Higher richness were still recorded in the vicinity of Trindade Island (VANNUCCI; HOSOE, 1952; COSTA, P. F., 1971; ÁVILA; ARRUDA; BONECKER, S. L. C., 2006) (Table S3.1). These studies present relevant information on the ecology of the species, as well as provide an overview of its distribution in Brazil (COSTA, P. F., 1971) and its worldwide geographic distribution (VANNUCCI; HOSOE, 1952; ÁVILA; ARRUDA; BONECKER, S. L. C., 2006). Among these publications, Vannucci and Hosoe (1952) offer detailed data on the morphology and anatomy of the species registered, which led this study to be the pioneer in presents the taxonomic bases about Chaetognatha in Brazil. Up to the present, this research has been function as a of the most widely used guides for the phylum identification, together with the studies developed in the decade of 60 (ALMEIDA-PRADO, 1961, 1963).

At the end of this session, it is important to mention that all the holoplanktonic species described above are also reported in the compilation of data presented by Casanova (1999) for the South Atlantic. This author also mentions the occurrence of *Eukrohnia fowleri*, a common oceanic species in the bathypelagic zone, recently discovered as the second chaetognath to produce bioluminescence, besides to *C. macrocephala* (THUESEN; GOETZ; HADDOCK, 2010). *Serratosagitta pacifica*, in turn, is the only species cited just in the check-list developed by Vega-Pérez and Schinke (2011), not having been registered by any of the other studies included in the present survey. Below, follows specific information about the main chaetognaths registered along the coast-ocean gradient in Brazilian waters.

MOST FREQUENT SPECIES RECORDED IN THE COAST-OCEAN GRADIENT

Parasagitta Genus

Figure 2 – Exemplars of the species *Parasagitta tenuis* (a) and *P. friderici* (b), photographed from samples collected in the north region of Brazil. The scale is based on 1 mm in length. **Source**: Xiomara Díaz (a) and Christianne Sampaio (b)

The species of the genus *Parasagitta* (Figures 2a and 2b) can be observed in coastal systems with wide variations in temperature and salinity (LEITE, N. D. R.; PEREIRA; COSTA, R. M. D., 2009; MIYASHITA et al., 2012; NOGUEIRA-JUNIOR et al., 2018), and in environments where only salinity varied widely, with similar temperature values between seasons or sampling periods (MELO-MAGALHÃES et al., 1996; FERNANDES; STERZA; NEVES, K. O., 2005; CAVALCANTI; NEUMANN-LEITÃO; VIEIRA, 2008; SANTOS, T. G. et al., 2009). Due to its eurithermic and eurihaline character, *P. tenuis* and *P. friderici* still tend to occur in open waters on the shelf (NEUMANN-LEITÃO et al., 1991; RESGALLA-JUNIOR; MONTÚ, 1995; ARAÚJO, H. M. P.; RIBEIRO, V. A., 2005), slope (RESGALLA-JUNIOR; MONTÚ, 1995; ARAÚJO, H. M. P.; RIBEIRO, V. A., 2005; BONECKER, S. L. C.; ARAUJO, A. V. de, et al., 2014; BONECKER, A. C. T.; ARAÚJO, A. V., et al., 2017; BONECKER, S. L. C.; ARAÚJO, A. V., et al., 2017; BONECKER, A. C. T.; DIAS, C. D. O., et al., 2018) and oceanic zone (VANNUCCI;

HOSOE, 1952; LIANG, T.-H.; VEGA-PEREZ, 2002; MELO, P. A. M. D. C. et al., 2012), generally presenting lower population concentrations with shore distance. In neritic environments, *P. tenuis* already been associated with to Coastal Water (RESGALLA-JUNIOR; MONTÚ, 1995; NEUMANN-LEITÃO; SILVA TDA, et al., 1999; NEUMANN-LEITÃO; SANT'ANNA, et al., 2008), and to Shelf Water (LIANG, T. H.; VEGA-PÉREZ, 1994; LIANG, T. H.; VEGA-PÉREZ, 2001); while *P. friderici* has been reported as an indicator of colder waters, especially of the SACW in the southeast Brazilian region (ALMEIDA-PRADO, 1963; VALENTIN, 1984; VALENTIN; MONTEIRO-RIBAS, et al., 1987; MONTEIRO RIBAS; MUREB, 1989; VEGA-PÉREZ; LIANG, T. H., 1992; LIANG, T. H.; VEGA-PÉREZ, 1994).

Flaccisagitta enflata

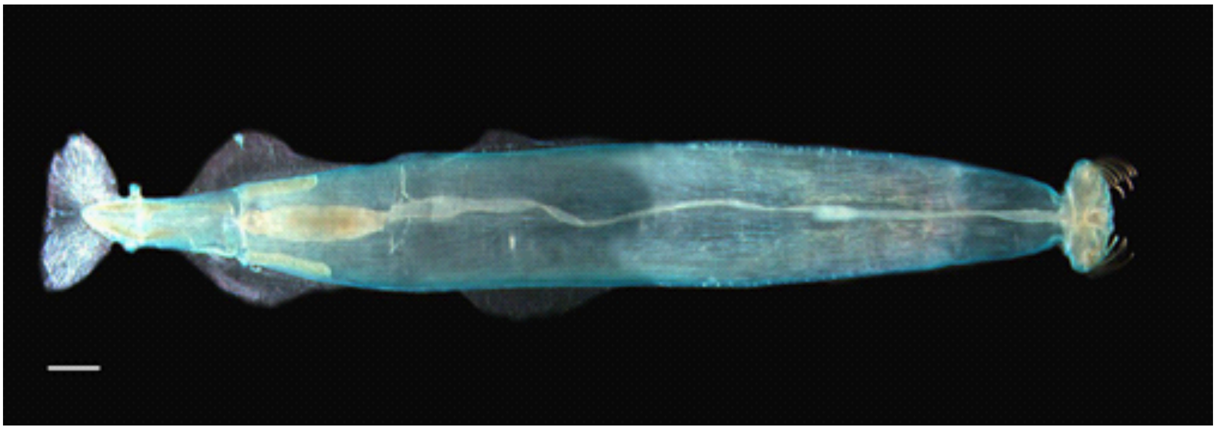


Figure 3 – Exemplary of the species *Flaccisagitta enflata*, photographed from samples collected in the north region of Brazil. The scale is based on 1 mm in length. **Source**: Xiomara Díaz

The other species most commonly recorded in coastal systems of Brazil is also cited as the most abundant and/or frequent in several other environments, along the continental shelf (ALMEIDA-PRADO, 1963; VALENTIN; MONTEIRO-RIBAS, et al., 1987) or comprising neritic and oceanic areas (NASCIMENTO-VIEIRA; SANT'ANNA, et al., 1990; VALENTIN; MONTEIRO-RIBAS, 1993; NEUMANN-LEITÃO; SILVA TDA, et al., 1999; LIANG, T. H.; VEGA-PÉREZ, 2001; NEUMANN-LEITÃO; SANT'ANNA, et al., 2008; BONECKER, S. L. C.; ARAUJO, A. V. de, et al., 2014; NEUMANN-LEITÃO;

MELO, P. A. M. C., et al., 2018); including islands and seamounts of the northeast (SOUZA, C. S. D.; LUZ; MAFALDA JR., 2014) and southeast Brazil (VANNUCCI; HOSOE, 1952). *F. enflata* (Figure 3) is a cosmopolitan species of the Indian, Pacific and Atlantic Oceans (PIERROT-BULTS, A. C.; NAIR, 1991), considered eurithermic and eurihaline by many authors (ALMEIDA-PRADO, 1963; MONTEIRO RIBAS; MUREB, 1989; MARAZZO; NOGUEIRA, C. S. R., 1996; MELO-MAGALHÃES et al., 1996; BOLTOVSKOY, 2005; NOBLEZADA, M. M. P.; CAMPOS, 2012), and often associated with Shelf Water (ALMEIDA-PRADO, 1963; MONTEIRO RIBAS; MUREB, 1989; LIANG, T. H.; VEGA-PÉREZ, 2001) or to Tropical Water (RESGALLA-JUNIOR; MONTÚ, 1995; NEUMANN-LEITÃO; SILVA TDA, et al., 1999; RESGALLA-JUNIOR, 2009) between the northeast and south regions of the country. Although it presents a wide distribution, it is observed that, in general, its higher concentrations are related to higher salinities, such as those that typically occur along the continental shelf (35-36) (ALMEIDA-PRADO, 1963; MONTEIRO RIBAS; MUREB, 1989; MARAZZO; NOGUEIRA, C. S. R., 1996). In oceanic areas, its abundance can also be very elevated, reaching 50%-70% of the total composition of Chaetognatha (LIANG, T. H.; VEGA-PÉREZ, 2001; LIANG, T.-H.; VEGA-PEREZ, 2002). Some studies thus consider *F. enflata* as a species semi-neritic (MARAZZO; NOGUEIRA, C. S. R., 1996; LIANG, T.-H.; VEGA-PEREZ, 2002), while others report it as preferably oceanic (CASANOVA, 1999; NEUMANN-LEITÃO; SILVA TDA, et al., 1999; STERZA; FERNANDES, 2006; DIAS, C. O.; CARVALHO, et al., 2018), especially in more diverse zooplankton communities (FURNESTIN, 1957; VALENTIN; MONTEIRO-RIBAS, et al., 1987; ALMEIDA-PRADO, 1968). Due to its extensive horizontal distribution, *F. enflata* is the main species registered in Brazilian waters (Figure 3).

Ferosagitta hispida

F. hispida (Figure 4) is a neritic species described by some authors with preference for Shelf Water (ALMEIDA-PRADO, 1968; LIANG, T. H.; VEGA-PÉREZ, 1994; MARAZZO; NOGUEIRA, C. S. R., 1996; MARAZZO; MACHADO; NOGUEIRA, C. S. R., 1997), but that due to its eurihaline characteristic, it is able to survive from more coastal environments (COSTA, P. F., 1971) to environments with more oceanic characteristics, subject to the predominant influence of Tropical Water (ALMEIDA-PRADO, 1963, 1968; RESGALLA-JUNIOR; MONTÚ, 1995). According to Tsui Hua Liang and Vega-Pérez (1994), the eurythermic nature of *F. hispida* (as well as of *P. tenuis* and *K. pacifica*) would also contribute to its occurrence in oceanic waters, usually at low concentrations. This fact was recorded by Pedro Augusto Mendes De Castro Melo et al. (2012), when reporting this taxon as little abundant in ASPSP.

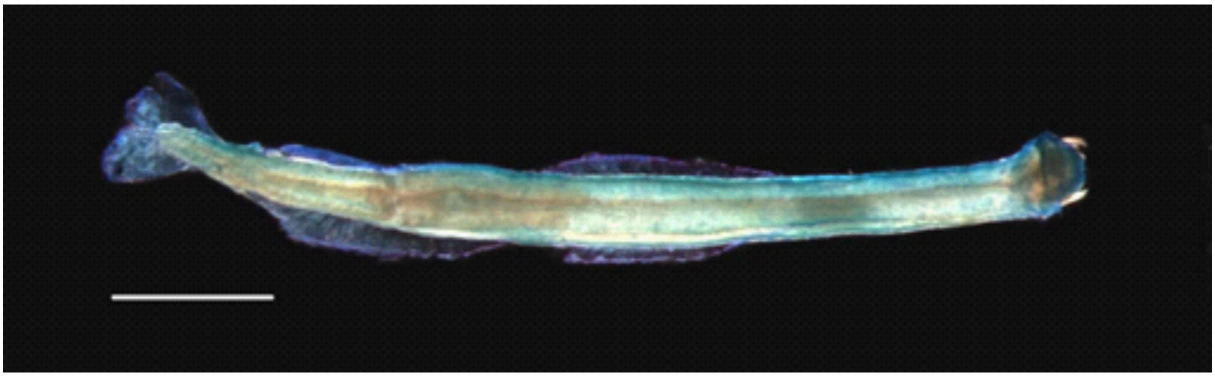


Figure 4 – Exemplary of the species *Ferosagitta hispida*, photographed from samples collected in the north region of Brazil. The scale is based on 1 mm in length. **Source**: Xiomara Díaz

Serratosagitta serratodentata

Like *F. enflata*, *S. serratodentata* (Figure 5) is a cosmopolitan species of the Indian, Pacific and Atlantic Oceans (FURNESTIN, 1953), characterized as eurithermic and stenohaline of high salinity ranges (preference 36) (VANNUCCI; HOSOE, 1952; ALMEIDA-PRADO, 1963; PARANAGUÁ, 1966; COSTA, P. F., 1971). This characteristic leads most of the authors to treat the species as oceanic, usually associated with the flow of Tropical Water (VANNUCCI; HOSOE, 1952; ALMEIDA-PRADO, 1963, 1968; PARANAGUÁ, 1966; RESGALLA-JUNIOR; MONTÚ, 1995; LIANG, T. H.; VEGA-PÉREZ, 1994; NEUMANN-LEITÃO; SILVA TDA, et al., 1999; LIANG, T. H.; VEGA-PÉREZ, 2001; NEUMANN-LEITÃO; SANT'ANNA, et al., 2008). Almeida-Prado (1963), for example, observed a strong connection of the species to this water mass, along the latitude of Cabo Frio (southeast Brazil) to Montevideo (Uruguay). Was reported that a gradual predominance of *S. serratodentata* towards the south occurred simultaneously to a quantitative decrease of most other registered chaetognaths. According to the author, the Tropical Water loses temperature and becomes poorer in salts as it moves to the south, conditioning the predominance of the species in higher latitudes, since it would be more resistant to these conditions. To support this idea, Almeida-Prado (1963) considered the species as stenohaline of a not very strict nature.

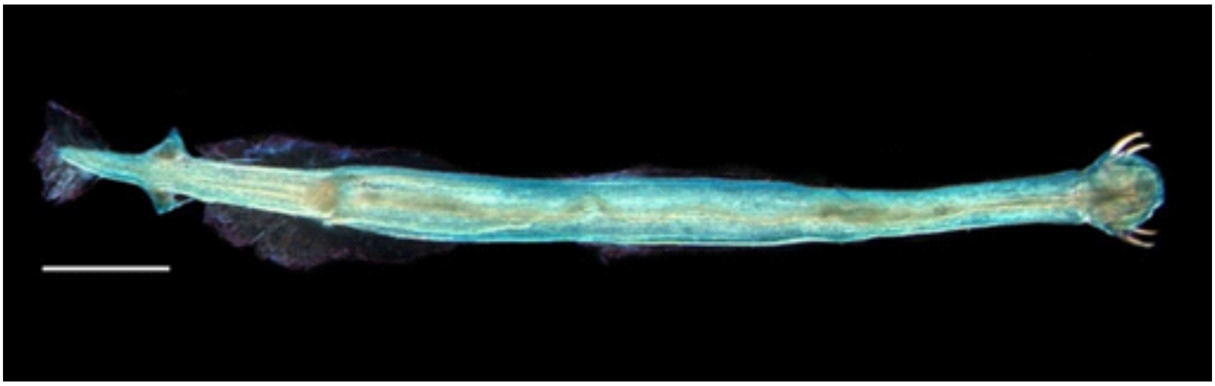


Figure 5 – Exemplary of the species *Serratosagitta serratodentata*, photographed from samples collected in the north region of Brazil. The scale is based on 1 mm in length. **Source**: Xiomara Díaz

In island regions, *S. serratodentata* already demonstrated be the most abundant species in Fernando de Noronha (HOSOE, 1956) and in the ASPSP (MELO, P. A. M. D. C. et al., 2012); as well as the second most abundant and frequent when considered together, the seamounts and oceanic islands of northeast Brazil. These data support the typically oceanic characteristic of the species.

Pterosagitta draco

Some chaetognaths registered in Brazilian waters are generally reported as oceanic of wide distribution, such as *P. draco*, *S. bipunctata* and *F. hexaptera* (VANNUCCI; HOSOE, 1952; HOSOE, 1956; ALMEIDA-PRADO, 1963; ALVARIÑO, 1980; BOLTOVSKOY, 1981; COSTA, P. F., 1971; RESGALLA-JUNIOR; MONTÚ, 1995; ARAÚJO, H. M. P.; RIBEIRO, V. A., 2005). *P. draco* (Figure 6) occurs in Tropical and subtropical waters, demonstrating preference for higher temperatures and salinities in the Atlantic (CASANOVA, 1999). These characteristics were confirmed by some authors when evaluating neritic and oceanic areas of northeast Brazil, including Fernando de Noronha (PARANAGUÁ, 1966); as well as when considering only island areas of the same region (SOUZA, C. S. D.; LUZ; MAFALDA JR., 2014), where greater abundances of *P. draco* were observed. Almeida-Prado (1963) considers it as a typical species of Tropical Water, however, is observed that in higher latitudes (from Cabo Frio to Montevideo), this species presents in lower population concentrations, possibly due to the gradual reduction of the temperature of the water mass in question. Reduced concentrations of *P. draco* in the south Brazil shelf were also observed by Resgalla-Junior (2008).

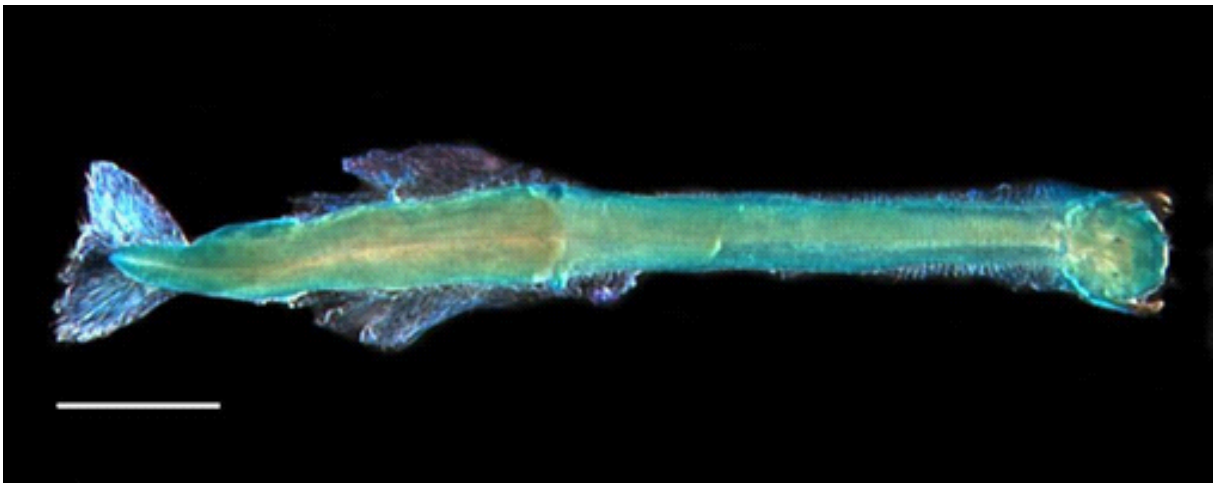


Figure 6 – Exemplary of the species *Pterosagitta draco*, photographed from samples collected in the north region of Brazil. The scale is based on 1 mm in length. **Source**: Xiomara Díaz

Krohnitta pacifica

This is the only species of Chaetognatha to be frequently described in Brazilian waters and not to belong to the Sagittidae family (Table 1). The distribution of *K. pacifica* (Figure 7) is in general related to high temperatures, occurring commonly in association with the Shelf Water (ALMEIDA-PRADO, 1968; LIANG, T. H.; VEGA-PÉREZ, 1994; LIANG, T. H.; VEGA-PÉREZ, 2001) or to Tropical Water in ocean environments (RESGALLA-JUNIOR; MONTÚ, 1995; BONECKER, A. C. T.; DIAS, C. D. O., et al., 2018). Some authors have also described low concentrations of this species in surface waters around of islands of the northeast region (HOSOE, 1956; MELO, P. A. M. D. C. et al., 2012). In coastal systems, the record of *K. pacifica* is reported as sporadic (NOGUEIRA-JUNIOR et al., 2018), and its occurrence appears to be limited to collection points or seasonal periods characterized by higher values of salinity (DIAS, C. O.; BONECKER, S. L. C.; NOGUEIRA, C. R., 1999; DIAS, C. O.; BONECKER, S. L. C., 2008).

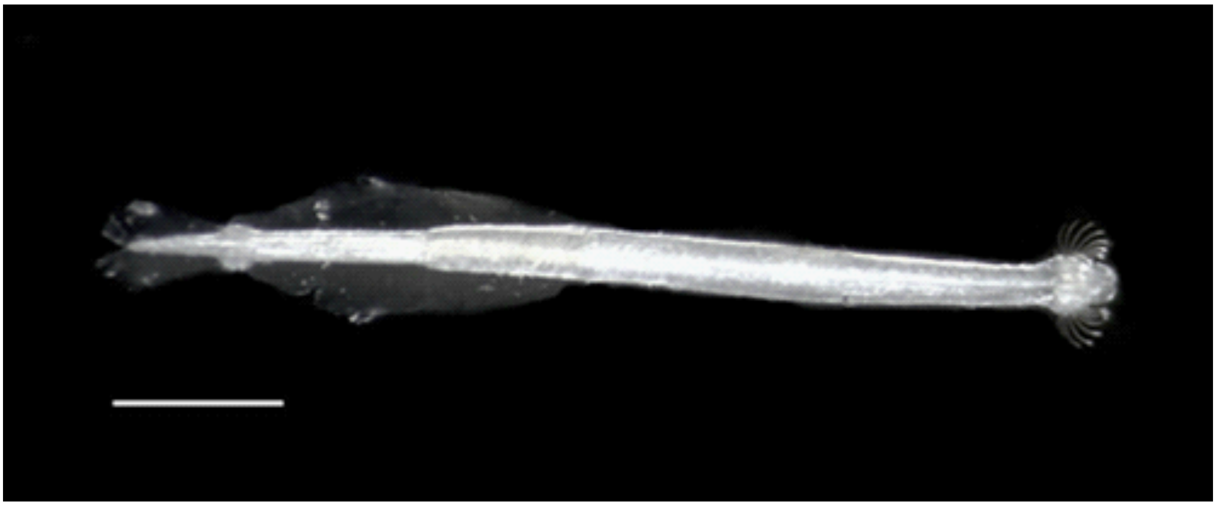


Figure 7 – Exemplary of the species *Krohnitta pacifica*, photographed from samples collected in the north region of Brazil. The scale is based on 1 mm in length. **Source**: Christianne Sampaio

VERTICAL DISTRIBUTION AND NOTES OF SEASONAL DISTRIBUTION

The region that borders the west coast of the Atlantic Ocean presents few publications involving deep water masses. These types of studies usually require greater financial investment in their planning and execution, becoming less common to be accomplished.

Since the increase in depth conditions a reduction of food resources starting with phytoplankton, it is expected that parameters such as density, biomass and diversity of superior taxa are also reduced (WEIKERT, 1982; ROBISON, 2004). Following this pattern, higher densities of Chaetognatha are usually recorded along the epipelagic zone (PIERROT-BULTS, A. C., 1983; TERAZAKI, 1996; OZAWA et al., 2007; PIERROT-BULTS, A. C.; NAIR, 2010; BONECKER, S. L. C.; ARAUJO, A. V. de, et al., 2014; BONECKER, A. C. T.; DIAS, C. D. O., et al., 2018). Richer communities, however, are found around 300 m and in the stratum from 800 to 1000 m (PIERROT-BULTS, A. C.; SUAREZ; GASCA, 1996; ÁVILA; ARRUDA; BONECKER, S. L. C., 2006; VEGA-PÉREZ; SCHINKE, 2011), when there is an increment of characteristic species of greater depths.

According to Valentin, Monteiro-Ribas, et al. (1987), the vertical distribution of zooplankton depends on the hydrological structure of the evaluated region, should be considered the nature of the dominant water body and/or the degree of mixing between different waters. Lower-scale oceanographic characteristics also affect habitat and batimetric distribution of zooplanktonic species (FERNÁNDEZ-ÁLAMO; FÄRBER-LORDA, 2006). Following these premises, chaetognaths are usually affected by the oceanographic conditions of their environment, developing frequent ecological associations with water masses to which are better adapted (see previous section). The species, when demonstrating significant levels of abundance or density, may be considered hydrological indicators of specific vertical strata, and related, for example, to warm, cold or mixed waters (BIERI, 1959; MCLELLAND, 1984; TERAZAKI, 1992; ULLOA; PALMA, S.; SILVA, N., 2000; RESGALLA-JUNIOR, 2008; SOUZA, C. S. D.; LUZ; MAFALDA JR., 2014). Studies using Chaetognatha as indicators can thus constitute important tools to monitor the dynamics of water masses and regional oceanographic processes on a vertical scale (OMORI; IKEDA, 1984; RESGALLA-JUNIOR, 2008).

In Brazil, knowledge about the group's vertical distribution can be considered incipient. Studies of this scope had began with Almeida-Prado (1968), on the southeast shelf of the country (Table S3.1). In this study, are described seven species of Chaetognatha occurring in the range of 0-45 m of depth were described, collected in two series of samples representing the dry and rainy seasons in region. Thermocline apparently did not constitute an important barrier to the distribution of most species, which, according to the authors, may be partly explained by the eurythermic characteristic of the registered chaetognaths, especially *F. enflata* and *K. pacifica*. For these two species, as well as for *F. hispida* and *S. serratodentata*, indications of vertical migration are also reported along the evaluated stratum.

This is a phenomenon commonly observed in chaetognaths (OWRE, 1960; KOLOSOVA, 1972; ROE, 1974; PIERROT-BULTS, A. C., 1983; LOUGH; TRITES, 1989; TERAZAKI, 1996; GIESECKE; GONZALEZ, 2008), something that can be associated to biological factors, such as obtaining metabolic advantages in greater depth (SULLIVAN, 1980; PREVIATELLI; SANTOS-SILVA; DARWICH, 2005); or behavioral, such as it keeping in layers with greater availability of food (ALVARIÑO, 1968; RESGALLA-JUNIOR; MONTÚ, 1995), avoid ecological relations of competition and cannibalism (MATSUDA; TANIGUCHI, 2001; KEHAYIAS; KOUROUVAKALIS, 2010) and/or to escape from predators in general (ZARET; SUFFERN, 1976; SULLIVAN, 1980; HAYS, 2003; LIE; TSE; WONG, 2012). Environmental parameters such as light and temperature also seem to constitute important stimulus to the migration of species in the marine ecosystems (OWRE, 1960). Unfortunately, detailed studies on this phenomenon in the group lack in Brazilian waters, which makes it difficult the understanding how local processes and factors can affect their bathymetric distribution.

Subsequently to the study by Almeida-Prado (1968), the data presented by Tsui Hua Liang and Vega-Pérez (1994) deserves to be highlighted for demonstrating important correlations between the population composition of Chaetognatha with seasonal changes observed in the vertical structure, identified through a temporal analysis in the region of Ubatuba (southeast Brazil). A community of 10 species collected in 50 and 100m isobaths was described (Table S3.1). Summer was notably marked by lower values in the abundance of chaetognaths, which was associated with the characteristic intrusion of the SACW during the period in the region, leading to a pronounced thermal stratification of the water column with the presence of a thermocline. Greater body lengths were also recorded, with the predominance of mature stages for chaetognaths *P. friderici* and *F. enflata*, something that was related to lower temperatures of the water mass in question (< 18ºC). On the other hand, in the samples collected during the winter, populations formed by young individuals with shorter lengths were dominant. The abundance of the whole community was also superior during this period. According to the authors, this would be a direct result of the vertical mixture and homogeneity of the thermal structure, observed characteristically during winter. The highest temperature of the Shelf Water (20°C-27ºC, LIANG, T. H.; VEGA-PÉREZ, 2001), formed by this vertical mixture of distinct water masses (Coastal Water, Tropical Water and SACW), would also condition in this period a population composition formed essentially by younger stages of Chaetognatha. The results of this study confirm, therefore, that aspects such as abundance and population structure of the group are influenced by the hydrodynamic structure of the area in which they occur.

Still in the decade of 90, the study developed by Resgalla-Junior and Montú (1995) in south Brazil can be considered the most complete available until today. A total of 18 species were recorded along five sampling strata, from the surface down to 500 m deep, involving the areas of the shelf (internal and external) and continental slope in a space-temporal approach (Table S3.1). The high richness of Chaetognatha in the region can be related to three factors: larger vertical scale sampled, circulation pattern in the region and methodology used. In addition to Tropical Water, circulation in the region is characterized by the presence of Subantarctic Water (25-100 m); and, of the SubTropical Convergence, an zone formed from the mixing processes between these two water masses. The AAIW was also detected in the winter period at lower depths. According to the authors, this water mass associated with the strong influence of the Subantarctic Water and the cold waters from the SubTropical Convergence, would have allowed the appearing of bathypelagic species, as *E. hamata* and *E. bathypelagica* in upper strata of depth. *S. tasmanica*, a species not commonly collected in Brazilian waters, but typical of the Argentine coast (Kapp, 1980), was also recorded in this study, occurring in association with the core of the Malvinas Current (Subantarctic Water). The methodology used was still decisive for the high species richness observed in the region (Table S3.1). The Bongo net (300 µm) sampled more efficiently the species that occurred at low densities (eg., *S. bipunctata*), while that the closing net used in vertical collection (150 µm) was more effective in capturing meso and bathypelagic species (eg., *S. planctonis*, *E. hamata*, *E. bathypelagica*). As for the bathymetric amplitude, the species followed two general patterns: i) those that remained restricted to specific strata of the epipelagic zone or with homogeneous distribution along the same (0-200 m): *P. tenuis* (= *P. friderici* in this study), *F. enflata*, *F. hexaptera*, *F. hispida*, *K. pacifica*, *K. subtilis* and *P. draco*; and, ii) those that occurred in wide vertical range (depths relative to the epipelagic zone up to 500 m): *S. serratodentata*, *S. tasmanica*, *D. decipiens*, *P. lyra*, M. minimum, M. maxima, *E. hamata* and *E. bathypelagica*. The species *S. planctonis* was limited to depths greater than 200 m, while for the species *S. bipunctata* and *P. gazellae* no specific information was presented on their vertical distribution. This study represents a great contribution to the group's research in Brazil, and demonstrated how the combination of methodologies can cooperate satisfactorily in the investigation of Chaetognatha along a larger vertical scale.

Ecological associations with water masses using the most frequent species of Pteropoda, Cladocera and Chaetognatha were further evaluated by Resgalla-Junior (2008) in the same layers sampled from the previous study (Table S3.1). It is important to mention that the chaetognaths *D. decipiens* and *K. subtilis* were related to SubTropical Waters in both collection periods, water mass characteristic of upwelling processes, common in the breakdown of the south shelf of Brazil during the summer. According to the authors, it was possible to observe in this period a tendency of substitution of the shelf Tropical fauna (including *F. enflata*) by the subtropical fauna, which pointed the species *D. decipiens* and *K. subtilis* as indicators of the seasonal upwelling occurring in the region. Both species are common in deeper layers of the water column (> 200m) (PIERROT-BULTS, A. C.; SUAREZ; GASCA, 1996; CASANOVA, 1999; ÁVILA; ARRUDA; BONECKER, S. L. C., 2006).

The association of meso and bathypelagic chaetognaths with thermohaline disturbances observed on the surface was also described in the north region near the mouth of the Amazon River (*D. decipiens* - ALVARIÑO, 1968), in the zone of divergence of the Brazilian Current (*Solidosagitta zetesios* - ALVARIÑO, 1980), and in the insular region of Brazilian northeast (MELO, P. A. M. D. C. et al., 2012; SOUZA, C. S. D.; LUZ; MAFALDA JR., 2014). In SPSPA, for example, the presence of the mesopelagic species *F. hexaptexa* and of the Copepoda *Phaena spinifera* in superficial waters was considered indicative of possible upwelling processes occurring in its surroundings (MELO, P. A. M. D. C. et al., 2012). Similarly, the chaetognath *P. lyra*, typically recorded at higher depths, presented high abundance in the stratum of 0-200 m in the area of the seamounts and oceanic islands, especially in stations close to the SPSPA (SOUZA, C. S. D.; LUZ; MAFALDA JR., 2014). This occurred during 1997, when the flow-topography interaction was more pronounced, causing the formation of a cold dome in the superficial layer of the water column. According to the authors, this phenomenon would have allowed the presence of *P. lyra* at the surface. A positive correlation of the species with chlorophyll-a was also explained as a probable consequence of upwelling events that appeared in 1997. This study still highlights the presence of *F. enflata* as the most frequent and abundant species in the region, representing approximately 40% of the total community. Unlike *P. lyra*, higher abundances of *F. enflata* were related to the greater stability of the water column. The mentioned study is to the present, the most complete available on Chaetognatha in the seamounts and oceanic islands of northeast Brazil (Table S3.1), having demonstrated that the composition and abundance of the species agree with data recorded for Tropical waters, and that the observed distribution patterns were well related to the hydrology of the evaluated area.

In the context of general publications, some studies deserve to be highlighted by addressing the distribution of Chaetognatha on wide vertical scale (depths > 1000 m). These were developed in the Campos basin (southeast Brazil), for the investigation of the spatial-temporal distribution of zooplankton along the continental shelf and slope (BONECKER, S. L. C.; ARAUJO, A. V. de, et al., 2014; BONECKER, A. C. T.; ARAÚJO, A. V., et al., 2017); and at a fixed point in the slope, in order to describe the vertical variation of the group in short temporal scale (eight days) (BONECKER, S. L. C.; ARAÚJO, A. V., et al., 2017; BONECKER, A. C. T.; DIAS, C. D. O., et al., 2018). Although none of these studies present quantitative information of density or abundance for each species of Chaetognatha registered, their data are pioneers in the knowledge of deep-water mass fauna in Brazil, becoming an important comparative basis for future studies carried out in the Atlantic.

The data generated by Sérgio L. C. Bonecker, Adriana V. de Araujo, et al. (2014), for example, report the vertical occurrence of 16 chaetognaths species in the Campos Basin: *F. hispida*, *P. friderici*, *F. enflata*, *F. hexaptera*, *S. serratodentata*, *S. helenae*, *S. bipunctata*, *P. lyra*, *M. minima*, *D. sibogae*, *D. decipiens*, *P. draco*, *K. mutabbii* (synonym of *K. pacifica*), *K. subtilis*, *E. bathypelagica* and *C. macrocephala*. These species were recorded in different strata between the surface and a depth superior to 2000 m, a vertical extension that comprised the totality of water masses identified in the region (TW- sampling at 1m, SACW - 250 m; AAIW - 800 m; UCDW [Upper Circumpolar Deep Water] - 1200 m; and NADW - 2300 m). The highest richness was observed in the UCDW during the rainy season, when this water gathered 15 species, corroborating the premise of greater richness of the group close to 1000 m deep. The most frequent species also was *F. enflata*, which occurred in all sampling stations (100% OF) and curiously in all water masses, when they were evaluated during the rainy season. Although it is characterized as epipelagic, the occurrence of this species seems not to be restricted to superficial waters, since it was again documented at depths related to UCDW in the same region, in a later study (BONECKER, A. C. T.; ARAÚJO, A. V., et al., 2017); and at depths exceeding 200 m in the Sargasso Sea - North Atlantic (PIERROT-BULTS, A. C.; NAIR, 2010).

(BONECKER, S. L. C.; ARAUJO, A. V. de, et al., 2014) also reported a vertical pattern equivalent to that of *F. enflata* for other epipelagic chaetognaths, as *P. friderici* and *P. draco*; and to *S. serratodentata*, characterized as a epi-mesopelagic transition species (ÁVILA; ARRUDA; BONECKER, S. L. C., 2006). As the methodology of this work was based on the use of nets with automatic closure, the contamination of samples collected in different layers becomes unlikely. Thus, the occurrence in deep and cold water masses may be indicative of the increase of the distribution range of these species, usually associated with warmer and superficial waters (e.g.

DADON; BOLTOVSKOY, 1982; CASANOVA, 1999; BOLTOVSKOY, 2005; ÁVILA; ARRUDA; BONECKER, S. L. C., 2006). The same inference would also be possible for *M. minima* (epipelagic), *K. pacifica* and *K. subtilis* (epi-mesopelagic), and *F. hexaptera* (mesopelagic), which occurred from surface to UCDW also in the rainy season. Although that only occurrence data have been presented, the extent of the vertical distribution of these chaetognaths may be consistent, in consequence of the little knowledge available on deep habitats in Southwest Atlantic. This hypothesis is briefly considered by the authors as a probable explanation for zooplankton species registered atypically in deeper layers (BONECKER, S. L. C.; ARAUJO, A. V. de, et al., 2014). Still, special attention should be given to those species characteristic of the bathypelagic zone that were not restricted to great depths, as in the case of *E. bathypelagica* (SACW, AAIW and UCDW) and of the chaetognath *C. macrocephala* (AAIW and UCDW), recorded in the respective water masses in the two collection periods (BONECKER, S. L. C.; ARAUJO, A. V. de, et al., 2014). The association of the group with the hydrodynamic structure of the region was not treated in this study.

In way general, the composition of the community above described is similar to other areas of the Atlantic, as in its northwest portion near Bermuda, North America (PIERROT-BULTS, A. C., 1983); and, in its eastern portion in Namibia, South Africa (DURÒ; GILI; ANDREU, 1994), both studies performed on smaller vertical scale. Still in the Atlantic, it is common the phenomenon known as Tropical submergence, when cosmopolitan chaetognaths are found in depths relative to the meso and/or bathypelagic zones; while in polar and sub-polar regions are usually registered in the surface (Casanova, 1999). Some known examples refer to the species *P. maxima* (KULAGIN; NERETINA, 2017) and *E. hamata* (MIYAMOTO; MACHIDA; NISHIDA, 2012), established in Atlantic as meso and bathypelagic chaetognaths, respectively.

From the approached in this section, it becomes clear the need of which new studies can investigate aspects until then poorly explored in relation to the bathymetric distribution of Chaetognatha in Brazil. Methodologies that allow effective samplings along wider vertical ranges can be applied in other areas of the West Atlantic, in order to discuss the data obtained with the already existing. It would be possible, in this way, to evaluate and establish more safely zoogeographic boundaries, relating the tolerance of the species to the physical parameters that form the different water masses. Through this review it was possible to infer that of the 26 species of Chaetognatha cataloged for Brazil, only 11 have been registered with high frequency in the studies performed (Figures 8a and 8b), the equivalent to 42% of the total species recorded. This issue reflects certain factors, such as greater availability of publications directed to coastal systems, in which there is the predominance of the same few species (saved exceptions); and, the relative unavailability of investigations comprising strata greater than 200 m deep, from which species typical of the meso and bathypelagic zones could be, according to their ecology in the Atlantic, more commonly recorded. The high frequency of some species (eg. *F. enflata*), is mainly due to its wide distribution in the pelagic domain.

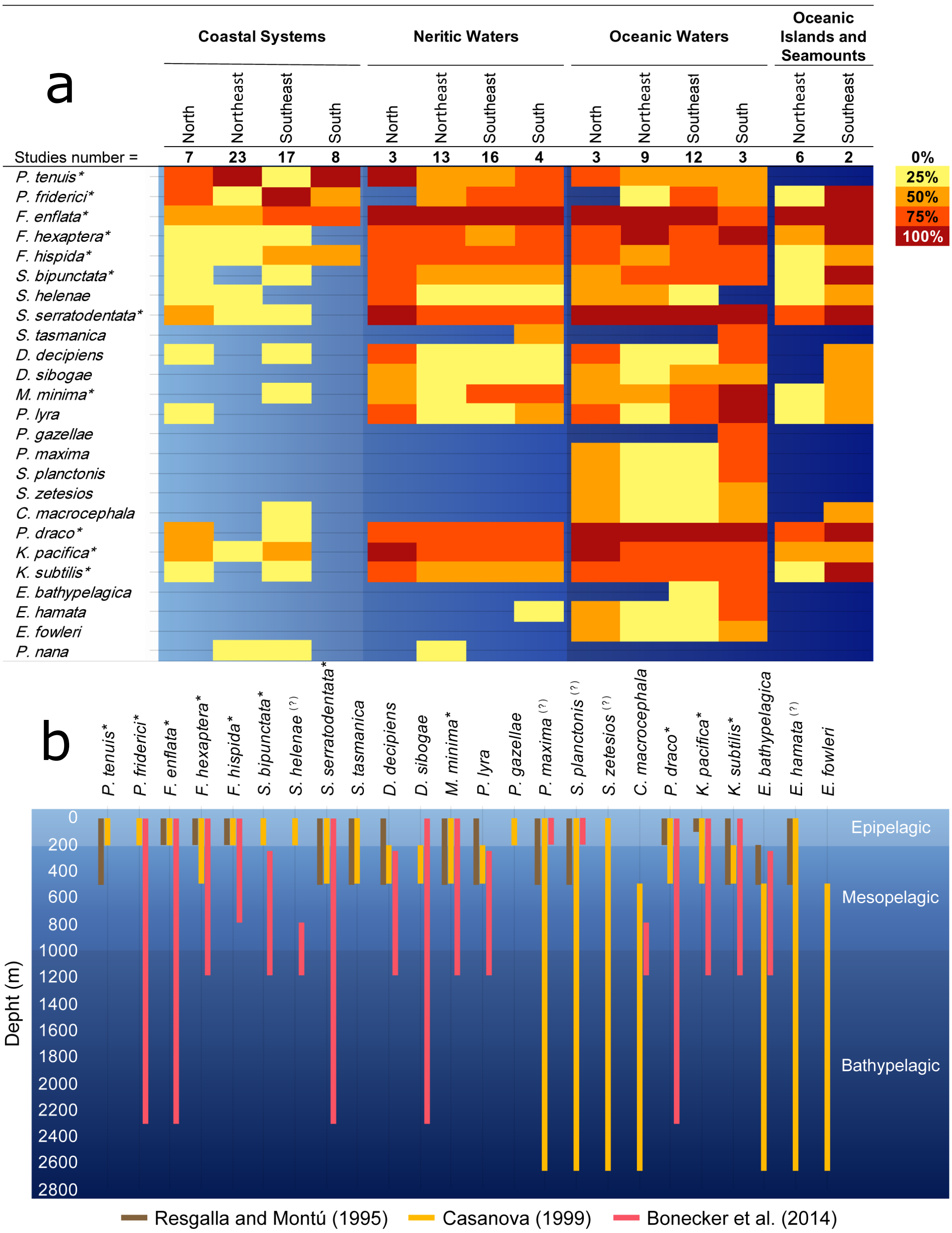


Figure 8 – Schemes demonstrating the horizontal (a) and vertical (b) distribution of the species registered in Brazil, elaborated from published studies between 1950 and August 2018. Asterisks indicate the species most frequently cited in publications (> 28 citations). For the vertical distribution, were used three studies containing information on a larger vertical scale (> 200 m). The interrogations indicate dubious distribution patterns. Publications containing information already considered by other studies (BOLTOVSKOY, 1981; DADON; BOLTOVSKOY, 1982; NEUMANN-LEITÃO; SILVA TDA, et al., 1999; MARAZZO; VALENTIN, 2004; RESGALLA-JUNIOR, 2008; BONECKER, A. C. T.; ARAÚJO, A. V., et al., 2017; BONECKER, S. L. C.; ARAÚJO, A. V., et al., 2017) were not included. **Source**: Alef Silva

Perspectives for the study of Chaetognatha in Brazil

Vega-Pérez and Schinke (2011) highlighted three questions related to the progress of the study of Chaetognatha in the state of São Paulo: (i) the importance of encouraging the training of specialists in order to deepen the knowledge about the general biodiversity of the communities; (ii) the need to create and maintain scientific collections, which would provide access and make simpler the work of researchers dedicated to the investigation of the species; and, (iii) the importance of studies aimed at aspects still little known, such as the fauna of benthic chaetognaths and those inhabitants of greater depths.

Issues like these are also valid for Brazil as a whole. The increase in the number of qualified specialists can constitute an important advancement not only in the registration of new species, but also in the greater knowledge about the distribution of those already reported. The incentive to scientific collections is another key point. They can act as multidisciplinary tools, allowing researchers to deposit reference specimens, send specimens for confirmation, and consult databases on the biota of cataloged regions. These banks should bring together the specialized and regional literature available, making it accessible to the consultation of researchers interested parties and thus facilitate information exchange (MIGOTTO; TIAGO, 1999). Unfortunately, there are no records of complete reference collections formed by chaetognaths in Brazil, since the preservation of marine invertebrates in traditional museums involves several limitations (MIGOTTO; TIAGO, 1999; MAGALHÃES et al., 2005). The preservation of the species in the humid environment, the requirement for adequate spaces and qualified technicians to perform the curatorship of the material are only some of the concerns (MIGOTTO; TIAGO, 1999). The need, therefore, is that financial support can be provided to museums or other institutions, regarding the qualification of professionals and provision of apparatus to development of scientific collections in Brazil.

Lastly, and as already commented briefly in the previous sections, the investigation of the Chaetognatha species in still little known environments is relevant for all of Brazil. The review developed by Nogueira-Júnior et al. (2018), for example, mentions that the spatial distribution of the group in estuaries has not been evaluated in details until today; and that the methodology described by many works may have compromised the registration of rare species in these environments, since only small fractions of the samples were analyzed (NOGUEIRA-JÚNIOR et al., 2018). The fauna of benthic chaetognaths is also poorly known, and the only species recorded so far (*P. nana*) has no a distribution pattern identified. Vertical studies involving greater depths are equally rare, and data on Chaetognatha are still superficial. Furthermore, stands out the expressive gap of specific publications for the north region of the country.

It is expected that such panorama can be modified with financial incentives to research projects and improvement of methodologies, something that even in the long term, could yield significant advances to the study of this taxon of high importance in the marine environment.

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MATERIAL SUPLEMENTAR

Table S3.1: Information on specific Chaetognatha studies, published between 1950 and August 2018.

Study locality	**Brazilian Latitude Comprised**	**Brazilian Longitude Comprised**	**Brazilian Correspondent Region**	**Objective (s) of the work**	**Haul type**	**Net mesh size**	**Species registered/worked in Brazilian waters**	**Reference**
Jaseur seamount and Trindade Island (state of Espírito Santo).	Seamount Jaseur - 20°31' S Trindade Island - 20°30'0"S	Seamount Jaseur - 35°52'W Trindade Island - 29°22'0"W	Southeast	To launch the taxonomic bases of the Chaetognatha study in order to be able, in the future, to relate biological data with those of the environment in which live the organisms.	**NI**	**NI**	*Flaccisagitta enflata; Parasagitta friderici; Sagitta. bipunctata; Serratosagitta serratodentata; Pterosagitta draco; Krohnitta subtilis; Flaccisagitta hexaptera; P. besnardi**	Vannucci and Hosoe, 1952
Jaseur seamount and Trindade Island (state of Espírito Santo).	Seamount Jaseur - 20°31' S Trindade Island - 20°30'0"S	Seamount Jaseur - 35°52'W Trindade Island - 29°22'0"W	Southeast	Correction of species previously considered as new (*Pterosagitta besnardi*), synonimized in this work with *Pterosagitta draco*.	**NI**	**NI**	*P. besnardi = P. draco*	Vannucci and Hosoe, 1956
Fernando de Noronha (state of Pernambuco).	3°51' S -	32°25' W	Northeast	To contribute to the knowledge about the phylum Chaetognatha collected in an insular area of the Tropical South Atlantic.	Surface and subsurface Horizontal	**NI**	*F. enflata; F. hexaptera; S. serratodentata; P. draco; K. pacifica*	Hosoe, 1956
Continental shelf of Cabo Frio (Rio de Janeiro State) to Montevideo (Uruguay)	23°04'S to ~ 33°40'S	41°31'W to 51°45'W	Southeast and south	Continue the systematic studies of the chaetognaths found in Brazilian waters, initiated by Vannucci and Hosoe (1952).	Surface Horizontal	**NI**	*P. friderici; Parasagitta tenuis; Ferosagitta hispida; Mesosagitta minima*	Prado, 1961a
Continental shelf of Cabo Frio (Rio de Janeiro State) to Montevideo (Uruguay)	22°S to ~ 33°40'S	41°W to 52°W	Southeast and south	To study the geographic distribution of Chaetognatha and its relationship with the different water masses.	**NI**	**NI**	*F. enflata, P. friderici; F. hispida; S. bipunctata; M. minima; S. serratodentata; P. draco; Krohnitta pacifica; F. hexaptera; Sagitta gloriae**	Prado, 1961b

Amazonian River Estuarine system (from the state of Amapá) to the Samaller Antilles Arch.	**NI**	**NI**	North	To characterize, in general way, the distribution of Chaetognatha along the evaluated area.	Oblique	**NI**	*F. enflata; P. tenuis; F. hispida; S. bipunctata; S. serratodentata; P. draco; K. subtilis; K. pacifica; F. hexaptera; Sagitta helenae; Decipisagitta decipiens; Pseudosagitta lyra*	Alvariño, 1968
Continental shelf of Cananéia and Santos (State of São Paulo), also involving estuarine waters in Cananéia.	24°04.8'S - 24°10.0' S - 24° 16.8' S - 24°24.0'S - 25°07.9' S - 25°08.4'S - 25°09.5'S -	46°13.7' W 46°08.0 'W 46° 00 .4'W 45°52 .9'W 47°48.4'W 47°44. 2'W 47°35.7'W	Southeast	To know the species of Chaetognatha and the indicators of water masses and their vertical and spatial distribution.	Vertical	58 µm	*F. enflata; P. friderici; F. hispida; M. minima; S. serratodentata; P. draco; K. pacifica*	Prado, 1968
Guanabara Bay (State of Rio de Janeiro).	22°52'50'' S -	43°10'02'' W	Southeast	Preliminar note on the knowledge of Chaetognatha in Guanabara Bay.	Surface Horizontal	120 and 130 µm	*F. enflata; P. friderici*	Costa, 1970
Continental shelf and Oceanic zone between Vitória and Trindade Island (Espírito Santo State)	19°24'S to 19°25'S	31°W to 39°W	Southeast	To identify the species that occurred in the area, observe its distribution and associate them with the water masses.	Surface Horizontal	125 µm	*F.enflata; P. friderici; F. hispida; P. draco; S. serratodentata; M. minima; K.subtilis; F.hexaptera; P. lyra.*	Costa, 1971
Continental shelf and oceanic zone of Brazil, Uruguay and Argentina.	32°04'S to 53°10'8S	42°58'W	Southeast and south of Brazil	To expand the knowledge about Chaetognatha as to its ecological characteristics in the South Atlantic Ocean.	Surface and subsurface sampling	139 µm	*F. enflata; P. tenuis; S. serratodentata; S. bipunctata; K. subtilis; K. pacifica; P. draco; M. minima; F. hexaptera; P. lyra.*	Boltovskoy, 1975

Focus on the Southwestern Atlantic (South America - from Brazil to Argentina).	0°N to 33°S	**NI**	North, northeast, southeast and south	Identification Guide and Bibliographic Review. It provides information mainly on the biology, distribution and ecological importance of the species recorded in the Southwest Atlantic Ocean. Also provided are literature data on the distribution of species in the Pacific, Indian and North Atlantic.	**-**	**-**	*F. enflata; P. tenuis; F. hispida; S. serratodentata; S. bipunctata; S. helenae; K. subtilis; K. pacifica; P. draco; M. minima; F. hexaptera; Solidosagitta planctonis; Serratosagitta tasmanica; Pseudosagitta maxima; Pseudosagitta gazellae; Eukrohnia hamata; Caecosagitta macrocephala.* Some data are presented as uncertain by the authors *D. decipiens; P. lyra; Eukrhonia bathypelagica* e *Eukrhonia fowleri*).	Boltovskoy, 1981
Southwesten Atlantic (South America - from Brazil to Argentina).	0°N to 33°S	25° to 70°W	North, northeast, southeast and south	Bibliographic Review. It presents the associations between planktonic groups of Pteropoda, Euphasiacea and Chaetognatha in the Southwest Atlantic.	**-**	**-**	*F. enflata; P. tenuis; F. hispida; S. serratodentata; S. bipunctata; K. subtilis; K. pacifica; P. draco; M. minima; F. hexaptera; S. planctonis; S. tasmanica; P. lyra; Pseudosagitta maxima; E. hamata*	Dadon and Boltovskoy, 1982
Potengi River Estuary (state of Rio Grande do Norte)	~ 05°47'S -	~ 35°12'W	Northeast	To study the variations in the distribution and reproduction of Chaetognatha in the estuarine system of Potengi River during 1979-1981.	Vertical	120 µm	*F. enflata; P. tenuis; S. helenae*	Nair and Sankarankuty, 1988
Continental shelf of Cabo Frio (state of Rio de Janeiro)	**NI**	**NI**	Southeast	To identify the species that occurs in the researched area, as well as its abundance, distribution and relationship with the different water masses.	Vertical	500 µm	*F. enflata; P. friderici; F. hipida; S. serratodentata; M. minima; K. subtilis.*	Monteiro-Ribas and Mureb, 1989
Continental shelf of Ubatuba (state of São Paulo)	23°35'S -	44°49'W	Southeast	To study the dietary composition of *P. friderici* and determine the existence of selective feeding.	Vertical	200 µm	Focus in *P. friderici*	Vega-Pérez and Liang, 1992

Continental shelf and oceanic zone of Ubatuba (state of São Paulo)	24° 10'S - to 23° 30'S -	44°30'W to 45°20 ' W	Southeast	To evaluate the population structure, distribution and abundance of Chaetognatha through surveys in periodic and regular stations.	Oblique	200 and 303 µm	*F. enflata; P. friderici; P. tenuis; F. hispida; S. serratodentata; P. draco; M. minima; S. bipunctata; K. pacifica; F. hexaptera*	Liang and Vega-Pérez, 1994
Continental shelf and oceanic zone of Ubatuba (state of São Paulo)	24° 10'S - to 23° 30'S -	44°30'W to 45°20 ' W	Southeast	To analyze the qualitative and quantitative dietary composition of the species of Chaetognatha collected in the region of Ubatuba.	Oblique	200 and 303 µm	*F. enflata; P. friderici; P. tenui; F. hispida*	Liang and Vega-Pérez, 1995
Continental shelf and slope of the state of Rio Grande do Sul	31° 40'S to 33° 45'S	50°W to 54°W	South	To study the horizontal and vertical distribution of Chaetognatha and relate the species registered to the water masses of the region.	Oblique and Vertical	300 µm / 150 µm	*F. enflata; P. tenuis; F. hispida; S. bipunctata; S. serratodentata; K. subtilis; K. pacifica; P. draco; D. decipiens; S. tasmanica; S. planctonis; M. minima; F. hexaptera; P. lyra; P. maxima; P. gazellae; E. hamata; E. bathypelagica*	Resgalla Junior and Montú, 1995
Estuarine complex Lagunar Mundaú Manguaba (state of Alagoas)	09°35'S to 09°45''S	35°42'30''W to 35°57'30'' W	Northeast	To identify the species, estimate the relative abundance of the developmental stages and the frequency of occurrence of Chaetognatha in region of study. Also, determine the spatial-temporal distribution of the group.	Surface Horizontal	140 µm	*F. enflata; P. tenuis; F. hispida*	Melo-Magalhães et al. 1996
Guanabara Bay (state of Rio de Janeiro)	23°41' to 23°56'S	43°02' to 43°18'W	Southeast	To evaluate the composition of Chaetognatha, its spatial and temporal distribution, the physicochemical parameters that influence these organisms; and, the relationship between the distribution and abundance of species and Copepoda.	Surface Horizontal	200 µm	*F. enflata; P. friderici; F. hispida*	Marazzo and Nogueira, 1996

Potengi River Estuary (state of Rio Grande do Norte)	**NI**	**NI**	Northeast	To present data referring to an unusual concentration of *P. tenuis* observed on December 8, 1992 in the estuary of the River Potengi (Natal-Brazil).	Vertical	125 µm	*F. enflata, P. tenuis; S. helenae*	Sankarankuty et al., 1996
Guanabara Bay (state of Rio de Janeiro)	23° 41'S to 23° 56'S	43°02' to 43° 18'W	Southeast	To perform a preliminary diet analysis of the most abundant species of Chaetognatha occurring in Guanabara Bay.	Vertical	200 µm	*F. enflata; P. friderici; F. hispida*	Marazzo et al., 1997
South Atlantic, comprised the continental shelf of South America to the shelf of Africa.	0°N to 33°S	~50°W to 30°W	North, northeast, southeast and south	Identification Guide and Bibliographic Review. This work provides a documentation of the Chaetognatha species present in the South Atlantic based on several studies, mainly in the developed by Alvariño (1969).	-	-	*F. enflata; P. tenuis; P. friderici; F. hispida; S. serratodentata; S. tasmanica; S. bipunctata; S. helenae; K. subtilis; K. pacifica; D. decipiens; D. sibogae; P. draco; M. minima; F. hexaptera; S. planctonis; P. maxima; P. lyra; P. gazellae; E. hamata; E. bathypelagica; Solidosagitta zetesios; Eukrohnia fowleri; Caecosagitta macrocephala*	Casanova, 1999
Continental shelf and oceanic zone, from the Cabo Frio (state of Rio de Janeiro) to the de Saint Peter and Saint Paul's Archipelago.	01°N to 23°S	29°W to 42°W	Northeast and southeast	To describe the diversity, abundance and biomass of Chaetognatha, departing from the southeastern Brazilian platform (Cabo Frio) to the Saint Peter and Saint Paul's Archipelago (Northeast region). The distribution of the species is also related to the water masses described in the literature.	Oblique	333 and 505 µm	*F. enflata; P. friderici; P. tenuis; F. hispida; S. serratodentata; K. subtilis; K. pacifica; P. daco; M. minima; F. hexaptera; P. maxima.*	Liang and Vega-Pérez, 2001
Continental shelf and oceanic zone of São Sebastião (state of São Paulo).	23°30'S to 24°15'S	45°W to 45°45'W	Southeast	To describe the abundance, distribution, biomass, population structure and dietary habits of Chaetognatha.	Oblique	333 and 505 µm	*F. enflata; P. friderici; P. tenuis, F. hispida, S. bipunctata; K. pacifica; M. minima.*	Liang and Vega-Perez, 2002

Cananéia Estuary (São Paulo State)	25° 01 '11' 'S -	47° 55' 43 '' W	Southeast	To describe the distribution of *P. friderici* throughout the year and relate it to the tidal movement. Information on population dynamics, biomass, daily production and habits is also provided the food of the species.	Vertical	150 µm	Focus in *P. friderici*	Liang et al., 2003
Vitória Bay Estuary/ Passagem Channel (State of Espírito Santo).	20°23'S -	40°20'W	Southeast	To study the distribution and abundance of Chaetognatha in the estuarine system of Vitória Bay/Passagem Channel.	Subsurface Horizontal	200 µm	*F. enflata; P. friderici; F. hispida; M. minima; D. decipiens*	Fernandes et al., 2005
Continental shelf (states of Sergipe and Alagoas).	10°20' to 11°40'S	36°0' to 37°40'W	Northeast	To study the composition and distribution of the species of Chaetognatha on the continental shelf of the states of Sergipe and Alagoas.	Oblique	200 µm	*F. enflata, P. tenuis; F. hispida; S. bipunctata; K. pacifica; P. draco*	Araújo and Ribeiro, 2005
Continental shelf and oceanic zone of the following area: Rio Real (coastal system - state of Bahia) to Cape São Tomé (state of Rio de Janeiro). Also included were the seamounts and oceanic islands of Trindade and Martin Vaz.	12°S to 22°S	**NI**	Northeast and southeast	To characterize the pelagic environment to evaluate the fishing potential of the continental shelf and slope of the Brazilian ZEE.	Vertical and Oblique	200 µm / 300 and 500µm	*F. enflata, P. friderici, P. tenuis, F. hispida, S. bipunctata, K. subtilis, K. pacifica, S. helenae, S. serratodentata, P. draco, M. minima, D. decipiens, D. sibogae, F. hexaptera, P. lyra, C. macrocephala*	Ávila et al., 2006
Continental shelf and slope (state of Rio Grande do Sul).	31°40'S to 34°45'S	**NI**	South	To analyze the associations of species of Pteropoda, Cladocera and Chaetognatha on the south coast of Brazil, to present a biological diagnosis of the oceanographic conditions.	Vertical	150 µm	*F. enflata; P. tenuis; F. hispida; K. pacifica; K. subtilis; P. draco; D. decipiens; M. minima; S. serratodentata; S. tasmanica*	Resgalla Junior, 2008

Paranaguá Bay (State of Paraná).	25°30'S -	48°31'W	South	To describe the presence of progenetic metacercariae of *Parahemiurus merus* found parasitizing *Parasagitta friderici* in the bay of Paranaguá.	**NI**	**NI**	Focus in *P. friderici*	Almeida et al., 2009
Coastal zone of the municipality of Aracruz (Espírito Santo)	18°23'30"S -	39°27'30" W	Southeast	To describe a new occurrence of *Paraspadella nana*.	Surface Horizontal	200 µm	*Paraspadella nana*	Arruda et al., 2010
Cassino Beach (state of Rio Grande do Sul)	32°9'S -	52°18'W	South	To know some parameters of *P. friderici*. The morphological variations, maturation stages and frequency distribution of the length classes in the Cassino Beach, were studied for comparisons with populations of other regions.	Surface Horizontal	300 µm	Focus in *P. friderici*	Resgalla Junior, 2010
Shelf, slope and oceanic zone of the state of São Paulo (São Paulo)	-	-	Southeast	To present the list of species of Chaetognatha registered in the state of São Paulo in comparison to those registered in Brazil, describe the main research groups and gaps in the knowledge of this phylum; as well as presenting the study prospects for the next 10 years. The article also addresses historical notes of the phylum Chaetognatha.	-	-	-	Vega-Pérez and Schinke, 2011
Guanabara Bay (State of Rio de Janeiro)	22°54'04'' S -	43°08'53'' W	Southeast	To describe the density, reproduction period and structure of the population of *P. friderici* in terms of developmental stages.	Vertical	200 µm	Focus in *P. friderici*	Mendes et al., 2012

Area 1 - Saint Peter and Saint Paul's Archipelago; Area 2 - Fernando de Noronha Chain; Area 3 - North Brazilian Chain; Area 4 - Oceanic area	0° 56.2' N - 3° S to 5° °S - 1ºS to 3° S - 0° S to 2° S -	29° 20.6' W 32° W to 38° W 37° W to 39° W 30° W to 34° W	Northeast	To describe the spatial distribution of Chaetognatha around of the seamounts and islands of northeast of Brazil and provide information about its variability in relation to the water masses.	Oblique	500 µm	*F. enflata; S. helenae; S. serratodentata; P. draco; F. hexaptera; P. lyra.*	Souza et al., 2014
Atlantic, Artic and Antartic oceanic zone	10.30° S - 22.72° S - 26.64° S - 29.45° S -	26.61° W 32.08° W 33.97° W 39.25° W	Northeast, southeast and south	To investigate genetic diversity of the cosmopolitan chaetognath *Eukrohnia hamata* in order to identify its spatial structure.	**NI**	**NI**	Focus in *E. hamata*	Kulagin et al, 2014
Atlantic and Artic oceanic zone	7.02° S - 29.28° S - 32.18° S -	26.07° W 36.93° W 46.44° W	Northeast and south	To define population subdivision of *P. maxima*, to elucidate their geographic boundaries and to discuss the possible mechanism that forms the present genetic structure of this species. Some morphological characters of *P. maxima* also were examined to reveal some differences between populations.	**NI**	**NI**	Focus in *P. maxima; P. lyra; P. gazellae*	Kulagin and Neretina, 2017
Coastal system of Tamandaré (State of Pernambuco); and Abrolhos Bank (State of Bahia)	Tamandaré Bay - 8˚ 45'' S; Abrolhos Bank - 38˚ 42' W;	Tamandaré Bay - 35˚ 05'' W; Abrolhos Bank - 38˚ 42' W;	Northeast	To describe two new occurrences of *P. nana.*	Traps for demersal plankton collection.	200 µm	*P. nana*	Figueirêdo et al., 2018

Source: Danielle Melo

4 ARTIGO 2 - GENETIC DIVERSITY AND CONNECTIVITY OF *FLACCISAGITTA ENFLATA* (CHAETOGNATHA: SAGITTIDAE) IN THE TROPICAL ATLANTIC OCEAN (NORTHEASTERN BRAZIL)

Espécime adulto de *Flaccisagitta enflata*. **Fonte**: Xiomara García-Diaz

ABSTRACT

The phylogeography of the holoplanktonic chaetognath *Flaccisagitta enflata* was investigated for the first time in the Tropical Western Atlantic (TWA). The study areas included neritic (Port of Recife and Tamandaré) and oceanic (Fernando de Noronha Archipelago - FN, Rocas Atoll, Guará seamount and Saint Peter and Saint Paul's Archipelago - SPSPA) locations of the Brazilian Blue Amazon. We used the mitochondrial cytochrome c oxidase subunit I gene (COI) as molecular marker. Partial sequences (425 bp) were obtained for 116 specimens and employed to reconstruct the phylogeny, build an haplotype network, evaluate the best gene flow (migration) model, and estimate diversity indexes, population structuring and demographic history. High levels of haplotype diversity (mean: 0.98) and moderate to high levels of nucleotide diversity (mean: 0.023) were observed. The phylogeny and the haplotype network topologies show weak geographic clustering, indicating a general scenario of a panmitic population. This finding was supported by the Migrate-n, which indicated the model of one population as the best for to represent the genetic flow of *F. enflata* in the region (98.9%). However, subtle differences were detected by the general AMOVA and some pairwise Φst comparisons, suggesting lower levels of connectivity among some locations. Significant Φst values were observed when Guará seamount population was compared to those of FN and SPSPA; as well as when Tamandaré was compared to FN. These results might be related to the oceanic dynamics which rules the TWA, sustaining such dissimilarities. Small structuring were also observed between the Port of Recife and all oceanic locations. We hypothesize that the topography of the port inlet, enclosured by a reef barrier, may constrain the water turnover ratio and thus migration rates of *F. enflata* in region. A brief demographic evaluation of the species still demonstrated that the neutral hypothesis of stable populations may not be rejected for most of the locations evaluated. This work is the start point to broaden the knowledge on the phylogeography and population genetic structure of a numerically dominant species in the Western Atlantic, with key role in the marine trophic web.

Keywords: Holoplankton. Phylogeography. Blue Amazon. Oceanic Islands. Seamounts.

COI.

INTRODUCTION

The phylum Chaetognatha constitutes a group of small marine carnivores (2 to 120 mm) with broad distribution in coastal and oceanic regions of the world (Casanova, 1999), occurring from the surface of the water column to depths into the abyssopelagic zone (OZAWA et al., 2007). Chaetognatha play an important ecological role in the food web as assiduous zooplankton predators, food items of multiple taxa and producers of particulate organic matter (PEARRE JR., 1980; BONE; KAPP; PIERROT-BULTS, A. C., 1991). Some species are also closely associated with specific water masses, which makes them good environmental indicators (ALVARIÑO, 1969; MCLELLAND, 1984; JOHNSON, W. S.; ALLEN, 2005). The life cycle of a large part of the group is holoplanktonic and the development is direct (CASANOVA, 1999; VEGA-PÉREZ; SCHINKE, 2011), where from the hatching of the eggs emerge individuals very similar to adults with regard to body organization. All species described until the present are protandrous hermaphrodites (VEGA-PÉREZ; SCHINKE, 2011). The lifetime is variable and known for a few members of the phylum, with a maximum estimate of approximately 15 months for a species investigated in shelf waters of the Atlantic ocean (DAPONTE et al., 2004).

Holoplanktonic species are generally characterized by large population sizes, high fecundity rates and broad dissemination by marine currents (PALUMBI, 1992). These aspects can also be applied to Chaetognatha (e.g. DAPONTE et al., 2004; REEVE, 1970; PEIJNENBURG; BREEUWER, et al., 2004) making them an interesting study model to understand dispersal processes and genetic connectivity of plankton among geographically distant environments. Recent researches based on molecular genetics have demonstrated, for example, important connections between the ranges of occurrence of species and the gene flow in the pelagic zone (PEIJNENBURG; BREEUWER, et al., 2004; PEIJNENBURG; FAUVELOT, et al., 2006; KULAGIN; STUPNIKOVA, et al., 2013), as well as the existence of cryptic complexes in different oceanic regions (PEIJNENBURG; BREEUWER, et al., 2004; PEIJNENBURG; FAUVELOT, et al., 2006; MIYAMOTO; MACHIDA; NISHIDA, 2010).

Among the cosmopolitan species of Chaetognatha, *Flaccisagitta enflata* (Grassi, 1881) was selected as model for this study due to its extensive horizontal distribution and high abundance in marine plankton. This species can reach lengths of up to 25 mm in the adult stage and presents a typical occurrence in epipelagic waters of the Tropical and subtropical regions throughout the world (VANNUCCI; HOSOE, 1952; ALMEIDA-PRADO, 1961; TERAZAKI, 1996; OZAWA et al., 2007; COTA-MEZA; FERNANDEZ-ALAMO; FUNES-RODRIGUEZ, 2015), including neritic and oceanic areas of north-eastern Brazil, where it is usually related as the most abundant species of the phylum (NEUMANN-LEITÃO; SILVA TDA, et al., 1999; NEUMANN-LEITÃO; SANT'ANNA, et al., 2008; SOUZA, C. S. D.; LUZ; MAFALDA JR., 2014). Its distribution based on conventional taxonomic identification is, therefore, well documented in the literature. However, specific data on the genetic diversity and connectivity of *F. enflata* remains scarce (JENNINGS; BUCKLIN; PIERROT-BULTS, A., 2010), since most molecular studies involving this species are directed at investigating the phylogenetic position or evolutionary history of Chaetognatha (PAPILLON et al., 2006; TELFORD; HOLLAND, 1997; MATUS; HALANYCH; MARTINDALE, 2007; PAPS; BAGUNA; RIUTORT, 2009; GASMI et al., 2014).

Previous studies conducted with different molecular markers demonstrated that species with broad distribution and at least one planktonic larval stage form a single population between the Brazilian coast and oceanic islands of the Tropical Western Atlantic (TWA), characterized by high levels of gene flow among the studied sites – Echinodermata (LESSIOS; KANE; ROBERTSON, 2003); Polychaeta (BARROSO et al., 2009); and reef fish (SOUZA, A. S. et al., 2015). Marine currents often favor this scenario type, providing an effective transportation for such organisms during their plankton period and contributing to their long-range dispersal (PALUMBI, 1994; EDWARDS; LUBBOCK, 2009; RUDORFF et al., 2009a). Moreover, biological factors as species ecology and behavior, in association with their interactions with the oceanographic environment, are important determinants of connectivity (GOETZE, 2005) or genetic isolation among populations (e.g. BUCKLIN; ASTTHORSSON, et al., 2000). Although the gene flow is suggestively high among holoplankton even at global scales (e.g. NORRIS, 2000; NORRIS; VARGAS, 2000; DARLING et al., 2000), some studies have reported varied levels of genetic structure for widely distributed zooplanktonic species, investigated from macro to meso geographical scales (BUCKLIN; LAJEUNESSE, et al., 1996; LEE, 2000; PEIJNENBURG; BREEUWER, et al., 2004; GOETZE, 2005; KIRBY; LINDLEY; BATTEN, 2006; CHEN; HARE, 2011).

Issues of this type are often clarified by the analysis of mitochondrial DNA (mtDNA) in population studies. Using mtDNA provides a series of advantages, such as maternal inheritance, a faster evolutionary rate compared to the nuclear genome and the presence of genes considered highly informative for the diagnosis of eukaryotes (WILSON et al., 1985; AVISE; ARNOLD, et al., 1987). Its cytochrome c oxidase subunit I gene (COI), for example, has been proposed as the universal molecular system (*barcode*) for animal identification (HEBERT; RATNASINGHAM; WAARD, 2003), being already successful in investigating the phylogeography of Chaetognatha (MIYAMOTO; MACHIDA; NISHIDA, 2010; KULAGIN; STUPNIKOVA, et al., 2013; KULAGIN; NERETINA, 2017).

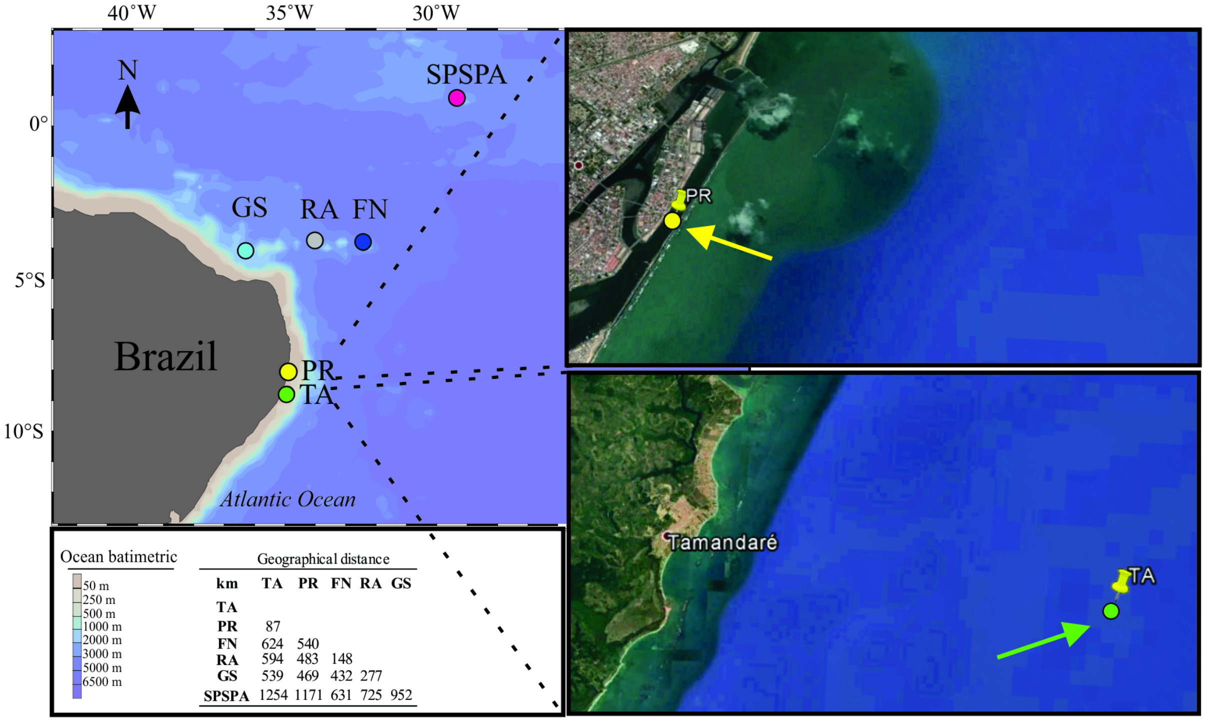
Based on these considerations, we aimed at (i) determine the level of genetic diversity of *F. enflata*; (ii) describe the genetic connectivity pattern exhibited by this species between the neritic and oceanic region of northeastern Brazil (TWA), and (iii) provide an overview of its demographic history; employing COI gene sequences analysis. Considering the broad geographic range in which this species occurs and the fact that it presents its entire life cycle in the plankton, the central hypothesis of this study is that *F. enflata* exhibits connectivity due to its high dispersal capacity, forming a panmictic population among the study sites; here comprised in a geographic meso- (tens to hundreds of Km) to macro-scale (thousands of Km) approach. This hypothesis can also be sustained by virtue of low mutation rates observed for Chaetognatha along an extensive evolutionary history, probably originated at the Cambrian onset ($\sim$540-520

Myr ago) (VANNIER et al., 2007).

This work provides original data on a species that is both highly abundant and frequent in the holoplankton in Brazilian waters. Our results can thus contribute to the understanding of issues still barely explored when considering the great ecological importance of this group in the marine environment.

MATERIALS AND METHODS

STUDY AREAS



Geographical distance

km	TA	PR	FN	RA	GS
TA					
PR	87				
FN	624	540			
RA	594	483	148		
GS	539	469	432	277	
SPSPA	1254	1171	631	725	952

Figure 9 – Sampling locations. The colored circles represent the areas included in the present study. Green: Tamandaré (TA); yellow: Port of Recife (PR); light blue: Guará seamount (GS); grey: Rocas Atoll (RA); dark blue: Fernando de Noronha Archipelago (FN); pink: Saint Peter and Saint Paul’s Archipelago (SPSPA). The sampling points in PR and TA were highlighted for better visualization. Below are the geographical distances between the locations evaluated. **Source**: Simone Lira

The study areas included neritic (Port of Recife - PR, and Tamandaré continental shelf - TA) and oceanic (Fernando de Noronha Archipelago - FN, Saint Peter and Saint

Paul’s Archipelago - SPSPA, Rocas Atoll- RA and Guará seamount - GS) locations in northeastern Brazil (TWA) (Figure 9).

PR (08º03.4’S; 34º52.1’W) and TA (8°47’20”S; 35°06’45”W) are respectively part of the central and southern neritic zones of the state of Pernambuco. PR is highly impacted by human activities, such as the discharge of domestic and industrial waste (CORDEIRO, I. A. et al., 2014). On the other hand, TA integrates the Coral Coast Preservation Area, one of the largest marine conservation units of Brazil. Evidence of eutrophication have not been reported for this site (FERREIRA; MAIDA, 2006).

The volcanic islands of FN (03º51’S; 32º25’W) and RA (03º50’S; 33º49’W) integrate the Fernando de Noronha Mountain Chain, which extends from the Brazilian continental shelf to the FN Archipelago, and also includes several seamounts, as Guará (4°5’24.79’’S; 36°18’03.42’’W) (Becker, 2001). FN is instituted as National Marine Park and State Environmental Protection Area, located 345 km off the coast of Brazil and 148 km apart from RA. This latter is located 260 km off the coast of Rio Grande do Norte state and recognized as the first biological reserve in Brazil (SERAFINI; FRANÇA; ANDRIGUETTO-FILHO, 2010). North of the Equator (0°55’06”N; 29°20’48” W), the SPSPA comprises a group of rocky islands on top of Mid Atlantic Ridge tectonic fault, where the depth range is 4-5000 meters (MABESOONE; COUTINHO, 1970). This archipelago is located 1010 km off the coast of Brazil and 610 km distant from FN (ARAÚJO, M.; CINTRA, 2009), comprising the FN - RA - SPSPA Environmental Protection Area (SERAFINI; FRANÇA; ANDRIGUETTO-FILHO, 2010).

SAMPLING

Plankton samples were collected from six sites in the TWA (Figure 9 and Table S4.1), using a bongô plankton net with 300 and a 500 µm mesh sizes. In the neritic area, horizontal hauls were used to sample the surface layer. Oceanic sites were sampled during two expeditions, through of research vessels Transmar I (FN and ASPSP), in the scope of the project “Plankton community in the Saint Peter and Saint Paul’s Archipelago and its association with physical mechanisms: vertical distribution of diversity and productivity"; and Antea (Rocas Atoll and Guará seamount), in the scope of the project "Acoustics along the Brazilian Coast 2". In these locations, superficial horizontal hauls were performed, as well as oblique hauls out in the depth-layer of 0-200 meters, whenever possible.

In the field, samples were washed in sterile 3% saline solution and subsequently fixed in 100% ethanol. In the laboratory, the chaetognaths were quickly separated from the material obtained and the species *F. enflata* was identified based on specialized literature (Casanova, 1999). Tissue samples (up to 25 mm^3) were then removed from the best-preserved individuals and with no apparent stomach contents, through dissection with previously sterilized disposable blades. In total, tissue samples from 36 individuals from the PR, 16 from TA, 19 from FN, 12 from the GS, seven from RA and 26 from SPSPA were conserved in 100% ethanol and at a temperature of 4°C, where its remained until DNA extraction step.

SAMPLING PERMIT

The biological material collected and evaluated in this study was obtained under the licenses of Ministério do Meio Ambiente (MMA): Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio - Number 17689) and to the Sistema de Autorização e Informação de Biodiversidade (SISBio - Number 47270-5).

DNA *BARCODING* AND PHYLOGENY

Total DNA was obtained using the Blood and Tissue extraction kit from Qiagen, following the manufacturer's protocol. The universal primers for COI amplification: LCO1490 (5'- GGT CAA CAA ATC ATA AAG ATA TTG G - 3') and HCO2198 (5'- TAA ACT TCA GGG TGA CCA AAA AAT CA - 3') were used (Folmer, 1994). PCRs were performed in 20 µl, consisting of 10 µl of Master Mix Go Taq G2 C (Promega), 5 pmol of each primer, and 20 to 50 ng of extracted DNA. The reaction protocol involved an initial denaturation step at 95°C for 1 minute; followed by 35 cycles of denaturation at 94ºC for 30 seconds, annealing at 52ºC for 40 seconds and extension at 72ºC for 1 minute; with a final extension step at 72ºC for 5 minutes performed at the end of the last cycle (modified from Folmer, 1994). Products were purified, sequenced and edited to generate consensus sequences, which were compared to the Genbank database, as described in (MOREIRA et al., 2013).

The consensus sequences were obtained by overlapping the raw sequences from each primer and manual editing using the software Chromas Pro v. 1.5 (Technelysium Pty Ltd). Edited sequences were exported to AliView v. 1.18.1 (LARSSON, 2014) and translated to inferred amino acids to verify that they translated correctly. The set of aminoacid sequences were then aligned using the Multiple Sequence Comparison by Log-Expectation (MUSCLE) tool (EDGAR, 2004) in AliView and returned later to DNA format. The alignment was manually edited and primer sequences were removed. Sequences generated in this work were deposited under the BARCODE section of GenBank along with metadata (Accession Numbers MH244934- MH245013) (Table S4.1). For reference, 15 COI sequences were added from GenBank (Table S4.2). To investigate the evolutionary history of COI, a model of DNA sequence evolution was selected using the Smart Model Selection (SMS) (LEFORT; LONGUEVILLE; GASCUEL, 2017) under Akaike's Information Criterion (AIC). The General Time Reversible (GTR) model was selected, with an estimated proportion of DNA sites invariant (I; 0.465 sites), and mutation rates among sites following a gamma distribution (G) (GRT +I +G) (NEI; KUMAR, 2000). A Maximum Likelihood (ML) tree was generated with PhyML 3.1 (GUINDON et al., 2010) starting from a neighbor-joining tree. The support for the nodes was assessed using the approximate likelihood ratio test for branches (aLRT) (ANISIMOVA; GASCUEL, 2006) and the *bootstrap* test (1000 repetitions). The tree was visualized using iTOL v.3 (LETUNIC; BORK, 2006) and included 131 sequences with 425 nucleotide positions.

POPULATION GENETICS

The following genetic diversity indexes: number of haplotypes (H), haplotype diversity (Hd), number of polymorphic sites (Nps), mean number of nucleotide differences (MnNd) and nucleotide diversity (π) were obtained from the Arlequin v.3.5 (EXCOFFIER; LISCHER, 2010) and DnaSP v. 5.0 (LIBRADO; ROZAS, 2009) programs.

A haplotype network was also constructed to observe the general genealogy patterns at the intraspecific level. For such, the PopArt v.1.7 program (`www.popart.otago.ac.nz/index.shtml`) was used, employing the median-joining criterion.

Population genetic structuring was investigated with the Bayesian Analysis of Population Structure (BAPS) 5.0 program (CORANDER; MARTTINEN, 2006), which identifies and groups genetically similar individuals in panmictic groups, henceforth denominated haplogroups. For this test, the parameters considered were "analysis of genetic mixture with linked loci or sequences" and "population mixture" estimated at each 10,000 generations per individual.

Within-population and between-population structuring values were calculated through the Analysis of Molecular Variance (AMOVA) (EXCOFFIER; SMOUSE; QUATTRO, 1992) and genetic pairwise differentiation from the fixation index (ΦST) (WRIGHT, 1949), both based on the F statistic and using 10,000 permutations in Arlequin v.3.5 (EXCOFFIER; LISCHER, 2010). Due to the significant structuring values demonstrated by general AMOVA and some pairwise comparisons, new AMOVA tests were performed considering different groupings scenarios.

In order to find the migration model (MM) most appropriate to the flow of the species in the region, different tests were performed in the Migrate-n v.4.4 software (BEERLI, 2005; BEERLI; PALCZEWSKI, 2010). For each model tested were conducted three independent Markov Chain Monte Carlo (MCMC) runs, sampling each 100th generation to a total of 500,000 generations. The parameters were estimated after a burn-in of 10,000 generations. The probability of each model was calculated following Migrate-N tutorial, and using the best log marginal likelihood found as base for these three independent runs. First, all MM log marginal likelihoods were subtracted from the highest individual MM log marginal likelihood, generating a list of values. Each element of this list was then exponentiated and their individual results were summed to obtain the equivalent denominator. Finally, the probability of each MM was obtained dividing each exponential by their respective denominator.

The demographic history of *F. enflata* in each study location still was inferred using (i) the Tajima's D, a statistical method for testing the neutral mutation hypothesis by DNA polymorphism (TAJIMA, 1989); and, (ii) the Fu's Fs, a method that tests the neutrality of mutations against population growth, hitchhiking and background selection (FU, 1997). These two indexes are based on the hypothesis of stable population sizes to detect deviations from neutrality within a set of mitochondrial gene sequences. The indexes were obtained through the Arlequin v.3.5 (EXCOFFIER; LISCHER, 2010) and applying 10,000 permutations.

CIRCULATION MODEL

To complement the results and provide a better basis for discussing connectivity aspects, the outputs of an oceanic dynamic model approach was implemented . The model was provided by Mercator Ocean NEMO configuration with a 1/12° high resolution centered over the Atlantic (`https://www.mercator-ocean.fr/`). The numerical velocity fields data corresponded to the same periods of the Acoustics along the Brazilian Coast survey, and were used to associate the large-scale circulation with the biological observations that span a relatively limited area.

RESULTS

DIVERSITY AND PHYLOGENY

Fragments with 425 bp long of the COI mitochondrial gene were obtained from 116 selected specimens of *F. enflata*. The genetic indexes demonstrated high and uniform haplotype diversity values; whereas more heterogeneous values, and moderate to high, were found for nucleotide diversity (Table 2). Mean haplotype diversity was 0.97, encompassing a minimum of 0.90 for PR to a maximum of 0.99 for TA and GS.

Nucleotide diversity ranged from 0.018 (at three of the six locations: PR, FN and GS) to 0.035 (RA), with an overall mean of 0.023 including all the six areas. In total, 61 COI haplotypes were detected (Table 2). Among the 425 sites, 87 were polymorphic

(20.47%), with the range of polymorphic sites varying from 32 (FN) to 43 (TA). The mean number of nucleotide differences comprised a minimum of 7.39 (PR) to 14.67 (RA) (Table 2).

Table 2 – Molecular diversity indexes for the COI region of mtDNA of *Flaccisagitta enflata*, from neritic and oceanic locations in Tropical Western Atlantic

GENETIC INDEXES	All samples	SAMPLING LOCATIONS					
		TA	PR	SPSPA	FN	GS	RA
N	116	16	36	26	19	12	7
H	61	15	20	18	12	11	6
Hd	0.97	0.99	0.9	0.95	0.94	0.99	0.95
Nps	87	43	41	41	32	34	37
MnNd	9.57	8.21	7.39	11.85	7.6	7.55	14.67
π	0.023	0.019	0.018	0.028	0.018	0.018	0.035

Source: Danielle Melo

The optimal gene tree presented short branches within each species, whereas longer branches determined the separation of the species (Figure 10). The monophyletic *F. enflata* group bifurcated into one branch comprising a single sequence from the Sargasso Sea (GQ368400.1), and another with all the remainders. The multiple branch further bifurcated clustering 19 sequences from the present study apart from all the others, including one from the Sargasso Sea and another from the Mid-Atlantic Bight (North Atlantic). These 19-sequences harbored only one haplotype from GS, and PR haplotypes appeared somewhat clustered. The six locations sampled in this study were represented in both branches stemming from this bifurcation (Figure 10).

Overall, the patterns and the mild clustering trends were replicated in the haplotype network (Figures 10 and 11A). The network topology exhibited two subgroups separated by ten mutational steps (Figure 11A). Among the 61 haplotypes recorded, 14 were shared among different study areas, the most frequent of which was H11 (12.07%

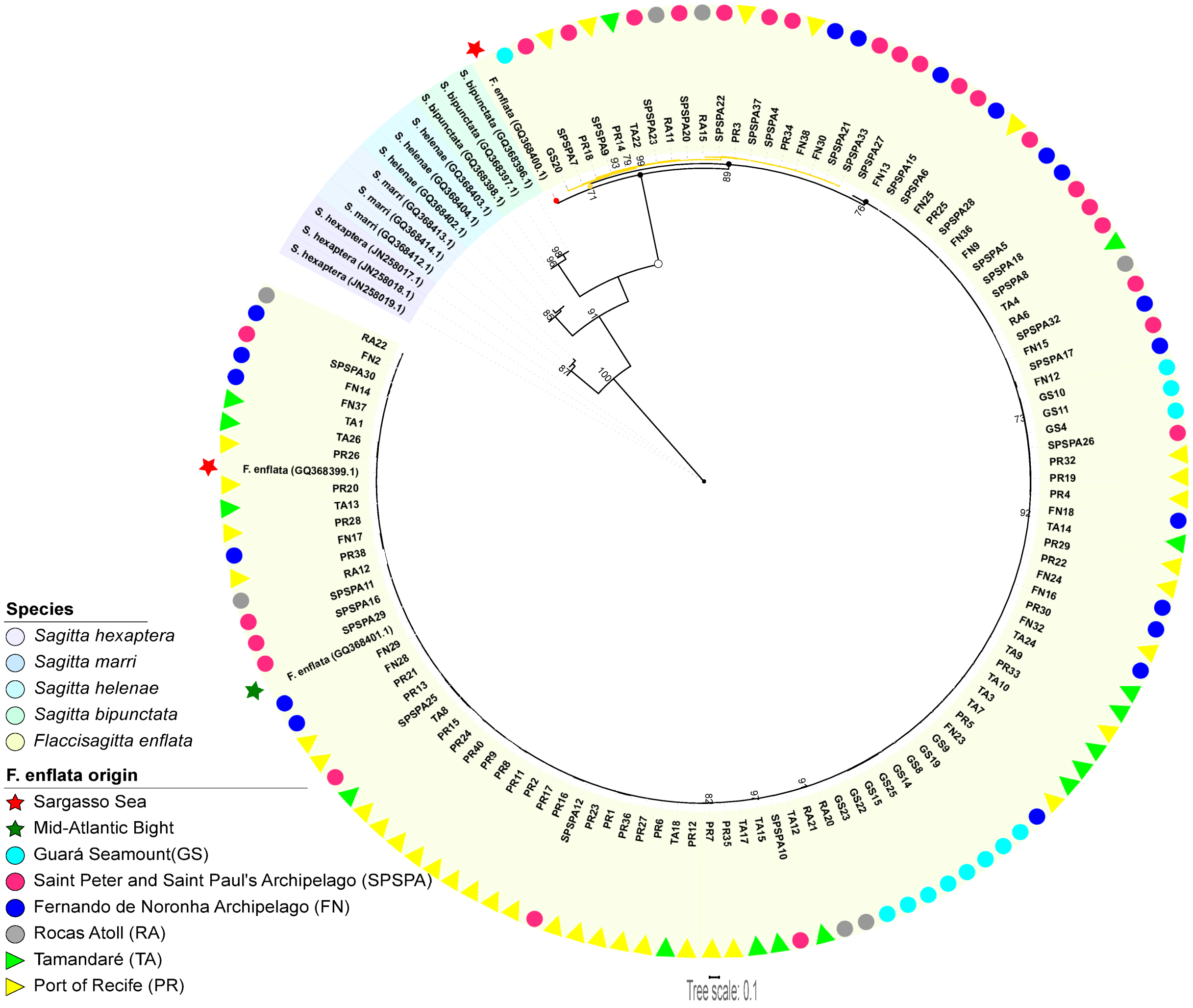


Figure 10 – Gene tree for COI showing topology based on Maximum-Likelihood (ML) criterion. Node support values are indicated by whole numbers > 70 and represent percentages. Scale bar denotes distance along branches. Sequences retrieved from GenBank are identified by the accession numbers. Sequences from this study are identified by location abbreviations and sample number (Table S4.1). The main nodes of the *Flaccisagitta enflata* branch are depicted with circles: *F. enflata* species branch, empty; single-haplotype branch, red filled; 19-haplotypes branch, yellow filled; others, black filled. Branches of the 19-haplotypes cluster are colored yellow. **Source**: Ana Paula Moreira

- 1 individual from TA, 11 from PR and 2 from SPSPA); followed by H25 (8.62% - 1 individual from PR, 5 from SPSPA and 4 from FN) and H23 (7.76% - 2 individuals from PR, 03 from SPSPA and 2 from FN). Subgroup 1 (smaller) was formed by 3 shared haplotypes (H13, H27 and H25) and 11 single-frequency haplotypes, representatives of the clustering 19 sequences of *F. enflata* in the smaller branch of the tree. Subgroup

2, in its turn, joined the 47 remaining haplotypes, including 11 shared haplotypes and 36 single-frequency from the analyzed neritic and oceanic locations (Figure 11A).

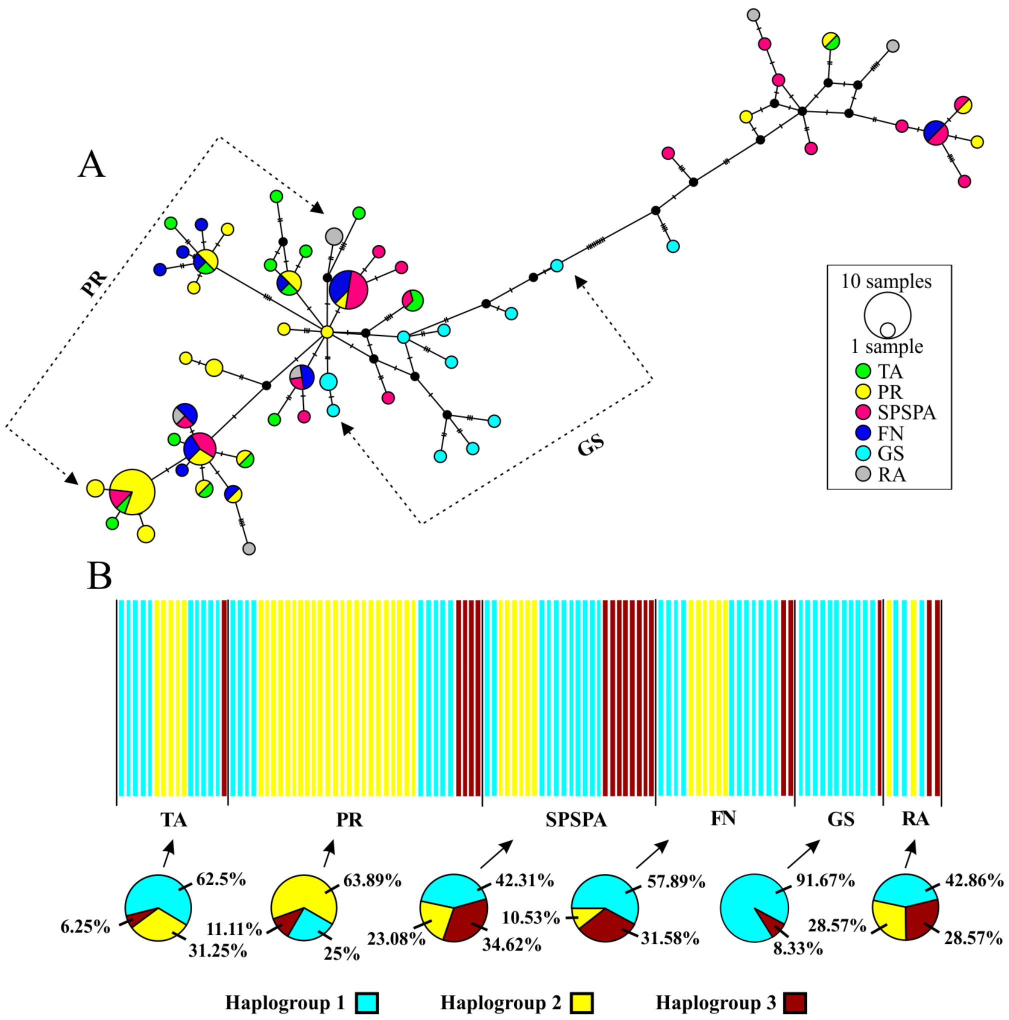


Figure 11 – Haplotype network and Bayesian Analysis of Population Structure (BAPS) based on the COI region of mtDNA from *Flaccisagitta enflata* from neritic and oceanic locations in Tropical Western Atlantic. **A**. Haplotype network generated for 61 haplotypes from 116 sequences of the species. The numbers below white circles indicate haplotype frequency and the area of each circle is proportional to the number of individuals exhibiting that haplotype. The colors indicate individuals of the different location. **B**. BAPS. The colors represent different haplogroups and the circular graphs represent the distribution of the haplogroups per location. Abbreviations: TA - Tamandaré; PR - Port of Recife; SPSPA - Saint Peter and Saint Paul's Archipelago; FN - Fernando de Noronha Archipelago; GS - Guará seamount; and RA - Rocas Atoll. **Source**: Danielle Melo and Simone Lira

The BAPS analysis detected three haplogroups (k = 3), which were present in five of the six evaluated locations. GS was the only area to exhibit two haplogroups, with > 90% of the individuals affiliated to haplogroup 1 (Figure 11B). This was dominant in all locations, with the notable exception of the PR, where the haplogroup 2 was the most numerous (63.89%). These two haplogroups (1 and 2) were mainly represented within subgroup 2 in the haplotype network (Figures 11A and 11B). All individuals were correctly assigned to their respective haplogroups ($p > 0.05$) .

POPULATION STRUCTURE

The AMOVA general test (Table 3) revealed a low level of genetic structuring when testing all locations as a panmictic group (Φst = 0.033; $p < 0.001$), with a much higher percentage of molecular variation within populations (96.66%) than between them (3.34%). In some of the secondary tests performed,significant values were only recorded within populations (Φst) and among populations within groups (Φsc). Significant structuring between groups (Φct) was not observed, whatever scenarios evaluated.

Among most of the locations, the pairwise Φst comparisons did not detect statistically significant genetic differentiation (Table 4). Some of the exceptions ($p < 0.05$) were observed between PR and all oceanic locations: SPSPA (Φst = 0.038), FN (Φst = 0.061), GS (Φst = 0.060) and RA (Φst = 0.076). Subtle differences also were recorded between GS and both SPSPA (Φst = 0.032) and FN (Φst = 0.038), and when TA was compared with FN (Φst = 0.027; $p < 0.05$ - Table 4). These results corroborating the low level of structuring detected by the AMOVA general test.

Table 3 – Analyses of molecular variance (AMOVA) based on the COI region of mtDNA *Flaccisagitta enflata*, from neritic and oceanic locations in Tropical Western Atlantic. (Abbreviations: d.f - degrees of freedom; TA - Tamandaré; PR - Port of Recife; SPSPA - Saint Peter and Saint Paul’s Archipelago; FN - Fernando de Noronha Archipelago; GS - Guará seamount; and RA - Rocas Atoll. * p < 0.001)

COMPARISONS/SOURCE OF VARIATION	d.f.	Percentage of Variation	Φ Statistic
All Locations			
Among populations	5	3.34	Φst = 0.033*
Within populations	110	96.66	
Neritic (TA, PR) vs. InSular (FN, RA, GS, SPSPA) Locations			
Among groups	1	2.36	Φct = 0.023
Among populations within groups	4	1.86	Φsc = 0.020*
Within populations	110	95.78	Φst = 0.042*
PR vs. All Other Locations (TA, FN, RA, GS, SPSPA)			
Among groups	1	2.62	Φct = 0.026
Among populations within groups	4	1.91	Φsc = 0.020*
Within populations	110	95.47	Φst = 0.045*

TA vs. All Other Locations (PR, FN, RA, GS, SPSPA)			
Among groups	1	-1.56	Φct = -0.015
Among populations within groups	4	3.87	Φsc = 0.038*
Within populations	110	97.69	Φst = 0.023*
GS vs. All Other Locations (TA, PR, FN, RA, SPSPA)			
Among groups	1	0.88	Φct = 0.033
Among populations within groups	4	3.13	Φsc = 0.001
Within populations	110	95.98	Φst = 0.034
GS vs. Other Oceanic Locations (FN, RA, SPSPA)			
Among groups	1	3.3	Φct = 0.033
Among populations within groups	2	0.14	Φsc = 0.001
Within populations	60	96.56	Φst = 0.034
GS vs. FN, SPSPA			
Among groups	1	5.17	Φct = 0.052
Among populations within groups	1	-1.71	Φsc = -0.018
Within populations	54	96.54	Φst = 0.035

Source: Danielle Melo

Table 4 – Pairwise fixation indexes (Φst) based on the COI region of mtDNA between individuals of *Flaccisagitta enflata*, from neritic and oceanic locations in Tropical Western Atlantic

LOCATION	TA	PR	SPSPA	FN	GS	RA
TA	-					
PR	0.024	-				
SPSPA	0.018	0.038*	-			
FN	0.027*	0.061*	-0.018	-		
GS	0.012	0.060*	0.032*	0.038*	-	
RA	0.026	0.076*	0.036	0.024	0.03	-

Abbreviations: TA - Tamandaré;PR - Port of Recife; SPSPA - Saint Peter and Saint Paul’s Archipelago; FN - Fernando de Noronha Archipelago; GS - Guará sea mount; and RA - Rocas Atoll.
p 0.05
Source: Danielle Melo

Migrate-n results were consistent with the AMOVA secondary tests and most of the pairwise Φst comparisons. The best fit migration model indicated high levels of gene flow with expressive probability (98.9%) for one population (MM1). The marginal log likelihoods for all tested models in distinct runs are shown in Table S4.3.

DEMOGRAPHIC HISTORY

Tajima's D and Fu's Fs estimates demonstrated negative values in most cases, however statistical significance was only detected for Fu's value of TA ($p < 0.02$) (Table 5). Exceptions were found for the SPSPA and RA, which presented, respectively, non-significant positive values for Tajima's index ($D = 0.39$, $p > 0.05$) and Fu's index ($Fs = 0.81$; $p > 0.02$) (Table 5).

Table 5 – Demographic indexes based on the COI region of mtDNA *Flaccisagitta enflata*, from neritic and oceanic locations in Tropical Western Atlantic

DEMOGRAPHIC INDEXES	TA	PR	SPSPA	FN	GS	RA	Mean
Tajima index (D)	-1.54	-0.91	0.39	-0.68	-1.49	-0.16	-0.7
p of D	0.05	0.18	0,71	0.26	0.06	0.45	0.28
Fu index (Fs)	-6.89	-4.37	-2,53	-1.33	-3.82	0.81	-3
p of Fs	0.003*	0.07	0,16	0.03	0.03	0.57	0.18

Abbreviations: TA - Tamandaré; PR -Port of Recife; SPSPA - Saint Peter and Saint Paul's Archipelago; FN - Fernando de Noronha Archipelago; GS - Guará seamount; and RA - Rocas Atoll.
p 0.02
Source: Danielle Melo

CIRCULATION MODEL

Currents dynamic of the TWA is dominated by the North Brazil Current/North Brazil Undercurrent (NBC/NBUC) system, which is mainly controlled by the different branches of the South Equatorial Current (SEC) (Figure 12). Currents characteristics of the region can be observed in the water circulation obtained from the Mercator model. In the 50 first meters of the water column (Figure 12A), we observe the presence of a continuous northwestward flow near and along the shelf break corresponding to the NBC/NBUC system. Between 5-6° S this flow intensifies, with mean velocity reaching a maximum of 1 m.s-1 around the GS. At the same depth, the influence of the central branch of the SEC (cSEC) was registered, with an average velocity of 0.3 m.s-1, transporting waters from Eastern Tropical Atlantic to the oceanic region around RA and FN. The model also indicates the presence of westward flows associated with the north branch of the SEC (nSEC), which are located in the same region of the SPSPA. Likewise, the model results at 150 m depth (Figure 12B) depict the northwestward transport provided by the NBC/NBUC along the shelf break (parallel to the Northeast Brazilian shelf), associated with relatively high velocity (0.6-1.0 m.s-1). The model also records the presence of the South Equatorial Undercurrent (SEUC), transporting waters eastward from the near shelf break, reaching the regions around RA and FN. These results suggest the presence of the Equatorial Undercurrent (EUC) around SPSPA, which is in good agreement with an eastward deviation of the waters coming from Western Tropical Atlantic, off the coast of Brazil.

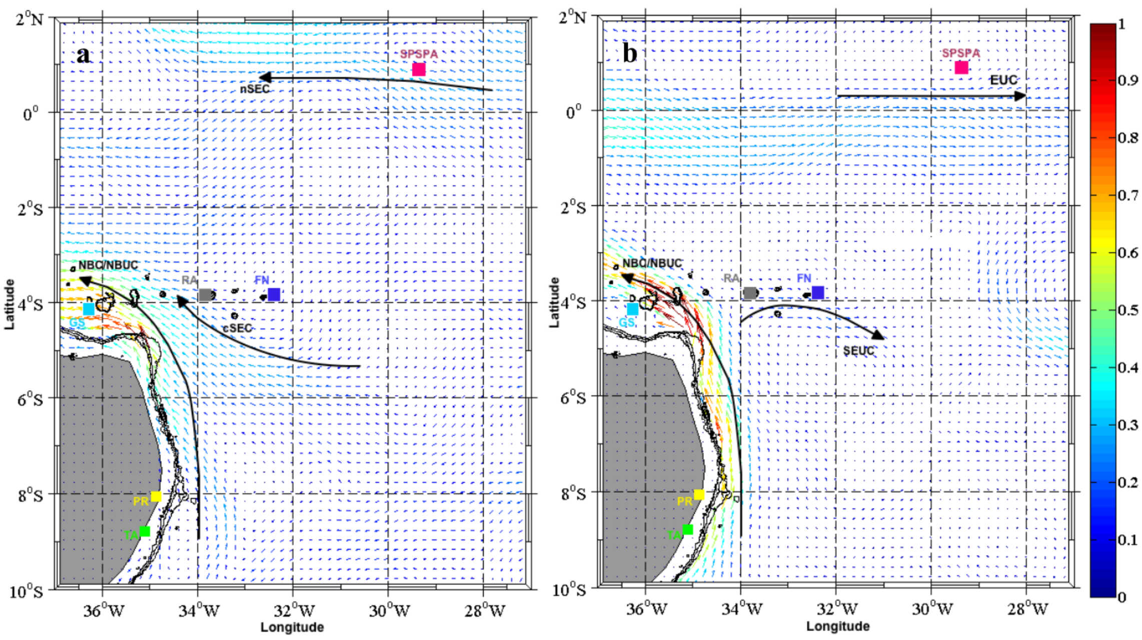


Figure 12 – Horizontal distribution of current velocity from Mercator model results along 0-50 m (A) and 150 m (B). Chaetognaths sampling locations are indicated by colored squares - green: Tamandaré (TA); yellow: Port of Recife (PR); light blue: Guará seamount (GS); gray: Rocas Atoll (RA); dark blue: Fernando de Noronha Archipelago (FN); pink: Saint Peter and Saint Paul's Archipelago (SPSPA). Main currents that surround in the areas: cSEC = central South Equatorial Current; nSEC north South Equatorial Current; NBC/NBUC = North Brazil Current/North Brazil Undercurrent system; EUC = Equatorial Undercurrent; SEUC = South Equatorial Undercurrent. The black lines represent the isobaths 50 m, 500 m and 1000 m. **Source**: Alex Costa

DISCUSSION

GENETIC DIVERSITY AND CONNECTIVITY

In the present investigation, the COI molecular marker satisfactorily confirmed the identity and evaluated the diversity and phylogeographic aspects of the species *Flaccisagitta enflata*. This is the first study to offer data of this scope for a numerically dominant taxon, encompassing the neritic region and oceanic islands of the northeastern Brazil (TWA). Its high frequency of occurrence in both space and time (e.g. SOUZA, C. S. D.; LUZ; MAFALDA JR., 2014) also make this chaetognath a key species in the marine trophic chain, exerting a relevant influence on the zoo- and ichthyoplanktonic communities. Our results suggest that even an holoplanktonic and cosmopolitan species may deviate from genetic homogeneity expected in a regional approach.

In general *F. enflata* displayed high levels of genetic diversity, which is frequently associated with large population sizes of zooplankton (NORRIS, 2000) and stable environmental conditions for a long evolutionary period (HELLBERG, 2009). Similar nucleotide diversity data using the COI gene were described for populations of the harpacticoid copepod *Macrosetella gracilis* in the Pacific and Atlantic oceans ($\pi = 0.010$ and 0.044, respectively) (EBERL et al., 2007) and for the rotifer *Brachionus calyciflorus* in a lake in China ($\pi = 0.011$ to 0.042) (Li et al., 2010). However, haplotype diversity for these species comprised lower values in comparison to that found in the present study (Hd copepod = 0.69 [Atlantic] to 0.96 [Pacific]; Hd rotifer = 0.61 to 0.88, respectively). Other chaetognaths also presented lower diversity based on COI, such as *Eukrohnia fowleri* in the Atlantic ($\pi = 0.00$ and Hd = 0.12) (MIYAMOTO; MACHIDA; NISHIDA, 2012) and *E. hamata* in three oceans (Atlantic: $\pi = 0.005$ and Hd = 0.833; Arctic: $\pi = 0.010$ and Hd = 0.844; Antarctic: $\pi = 0.004$ and Hd = 0.542) (KULAGIN; STUPNIKOVA, et al., 2013). The high genetic diversity of *F. enflata* in the TWA suggests that this species displays no apparent risk regarding diversity loss.

In the global ocean, it is common that widely distributed planktonic species exhibit a high dispersion capacity (WAPLES, 1998; NORRIS, 2000). This aspect was here confirmed through of the phylogeny and haplotype network topologies, which identified a weak geographic clustering. The separation between the haplotypes defined by a few mutational steps was also indicative that the dispersion occurred over long distances, which may explain the presence of shared haplotypes among very distant locations (up to 1000 km). Together, these results portray a general picture of genetic connectivity for the species in the TWA. Similar patterns were described for the reef fish *Cephalopholis fulva* in the same area (SOUZA, A. S. et al., 2015), and for Chaetognatha species in the North Atlantic, including three specimens of *F. enflata* from the Sargasso Sea (two individuals) and the Mid Atlantic Bight (one individual) (JENNINGS; BUCKLIN; PIERROT-BULTS, A., 2010). In this latter study, the lack of association between diversity and geographic location was attributed to the high chaetognaths' potential for genetic mixing and/or to a relatively short evolutionary time for the populations to split into genetically distinct lineages (JENNINGS; BUCKLIN; PIERROT-BULTS, A., 2010). In the present investigation, non-significant pairwise Φst comparisons and the MM of one population selected by Migrate-n were also indicative of a high degree of gene flow, reflecting in the observed populational homogeneity for *F. enflata* (Table 4; Table S4.3).

The flow of this connectivity may be related to the surface and subsurface currents dynamics that circulate in the basin of the Tropical Atlantic, and which remained relatively stable since the closure of the Panama Isthmus (MAIER-REIMER; MIKOLAJEWICZ; CROWLEY, 1990; HAUG; TIEDEMANN, 1998). The western portion of the Atlantic is mainly controlled by three branches (south, central and north) of the SEC at the surface (EKAU; KNOPPERS, 1999). The sSEC carries subtropical waters towards the Brazil shelf region, where around 14°S, it bifurcates into the NBUC to the north and in the Brazil Current (BC) to the south (STRAMMA, 1991). On its course from east to west, the cSEC and nSEC exert strong influence on the region of oceanic seamounts and islands of northeastern Brazil, passing through the SPSPA and FN Chain, flowing later towards the Brazilian coast (STRAMMA; SCHOTT, 1999). Moreover, the SEUC and EUC are superficial systems which contribute with the marine flow in the opposite direction to that of the SEC (west to east). The EUC is located a depth of 50 to

200 m (BOURLÈS et al., 1999), and is fed by the NBC/NBUC system that crosses the Equator (STRAMMA; SCHOTT, 1999). Studies developed in the area report that the currents may effectively contribute to the dispersal of pelagic larvae in several directions, both in neritic and oceanic sites of the TWA, resulting in genetic connectivity patterns among populations (SCHELTEMA, 1986; LEITE, T. S. et al., 2008; SOUZA, A. S. et al., 2015). Thus, marine circulation may be favoring *F. enflata* gene flow in both directions of the currents, since this species is vertically distributed throughout the entire epipelagic layer.

Available data correlating connectivity to current systems in the TWA are based on species with different life cycles, and investigated by distinct molecular markers. For instance, the existence of a single population of the fish *C. fulva* was described among the northeastern and southeastern coasts of Brazil (states of Ceará, Rio Grande do Norte, Bahia and Espírito Santo) and the FN and RA oceanic islands (SOUZA, A. S. et al., 2015). Similar lineages of the Cephalopoda *Octopus insularis* were also recorded between the northeastern coast (states of Rio Grande do Norte and Pernambuco) and the same oceanic islands evaluated in this study (SPSPA, FN and RA) (LEITE, T. S. et al., 2008). In addition, even semi-terrestrial species as the crabs *Johngarthia lagostoma* (RODRÍGUEZ-REY; HARTNOLL; SOLÉ-CAVA, 2016) and *Grapsus grapsus* (TESCHIMA et al., 2016) constitute genetically homogeneous populations between FN and RA; and between SPSPA, FN and RA, respectively. All these organisms have in common a planktonic phase in their life cycle, during which they disperse throughout long distances and seem to establish viable populations in the different locations. On wider spatial scales, species of Euphasiacea (ZANE; OSTELLARI, et al., 1998; ZANE; PATARNELLO, 2000) and Copepoda (BUCKLIN; ASTTHORSSON, et al., 2000) constitute examples of holoplanktonic populations connected by high levels of gene flow, exhibiting little evidence of genetic structure along the evaluated geographic range.

Up to now there is no consensus on the lifetime of Chaetognatha. The available investigations based in different methodologies demonstrate that temperature is an important parameter influencing the body size and sexual maturity, reflecting in life cycles with different duration of time. Ocean temperature varies according to season, latitude and depth, therefore, it would be expected that the lifetime of holoplanktonic species is also influenced by these factors. Shorter life-cycles (18-50 d) were observed for *Ferosagitta hispida* under controlled laboratory conditions (temperature range of 17-31 °C) (Reeve and Walter, 1972), while a 15-month estimate was proposed for *Parasagitta friderici* in shelf waters of Argentine (temperature range of 10.1-21.1ºC) (DAPONTE et al., 2004). The life-cycle of *F. enflata* was estimated in 47d in Chile's neritic waters, in a study that correlated their reproductive phase with the abundance of Copepoda, the main food item of Chaetognatha (GIESECKE; GONZALEZ, 2008). It is unknown if this estimate resembles the lifetime of the species in Tropical environments as those uncovered in the present study. However, an approximate time may be sufficient for *F. enflata* to transit between oceanic waters and the Brazilian coast, establishing similar genetic profiles in the TWA. The observation of continuous reproductive cycles over of the whole year, a common to characteristic to Chaetognatha species (VEGA-PÉREZ; SCHINKE, 2011), would further contribute to its dispersion in the here evaluated areas.

GUARÁ SEAMOUNT

Individuals from GS did not share haplotypes with those from any other location, which resulted in one of the highest haplotype diversity indexes found (Table 2). Low levels of differentiation were also recorded for this location compared to SPSPA and FN (Table 4). Besides, GS was the only area where the haplogroup 2 was not detected, and where there was a dominance > 90% of haplogroup 1 composing its individuals (Figure 11B). Interestingly, *F. enflata* from the seamount presented higher similarity with those collected off TA continental shelf (distant 539 km), than with those from FN (430 km), or from SPSPA. Such pattern might result from the current circulation among sites. Between TA and GS both surface and subsurface currents flow consistently from the first to the second site (NBC/NBUC system; Figure 12). A water flow also occurs between GS and FN, but in a lesser degree, since a retroflection of the surface currents exists in FN area. This also might explain the lower genetic similarity observed between

GS and SPSPA, as well as between TA and FN. Subsurface currents still present a divergence at 4ºS - 34ºW, with a part flowing eastwards and diverging from the NBUC-NBC system, which contributes to feeding the SEUC (Figure 12). Together, these particularities of the oceanic circulation could originate the subtle differences observed (Table 4), even if no overall structuring has been detected by the AMOVA (Table 3).

Re-sampling and the application of multiple molecular marker systems should be suited to assess a clearer populational picture of *F. enflata* between GS and other locations of the TWA.

PORT OF RECIFE

PR presented higher pairwise Φst values when compared to all the other oceanic locations (Table 4), besides being the only area where the haplogroup 2 was dominant (Figure 11B). In general way, differentiation in marine species is characteristically defined by lower values for fixation indexes (WARD, R., 1994; WAPLES, 1998).) R. Ward (1994) proposed that differentiation rose from 0.062 in marine fishes. Waples (1998) used this data to highlight that, despite the average to be 0.062, the median was much lower (0.020). This author discussed that R. Ward (1994) values indicative of differentiation were < 0.03. In association, the results here observed might reflect regional characteristics limiting the connectivity of the species in PR.

The sampling point in question is inserted in a semi-closed basin, influenced by the coastal dynamics and bounded by a reef line that occurs in parallel to the littoral (Figure 9) (OTSUKA et al., 2018). It has been previously mentioned that this reef limits the flow of planktonic organisms outward of port basin (PARANAGUÁ et al., 1990), meaning it functions as a physical barrier capable of constraining the local water turnover ratio. Additionally, currents as the NBC and NBUC flow along the external shelf of the region, making PR an area isolated from the ocean circulation. These factors might be acting synergistic, impairing the migration of *F. enflata* to the outside and/or inside of the location. If so, PR might be developing a discrete differentiation, herein early detected by COI. This hypothesis deserves further investigation, increasing sample size and including sites outside the reef line.

Marine populations in general were once seen as demographically opens, with genetic isolation over the long term hard to develop. Accumulating evidence suggests otherwise (WARD, R., 1994; WAPLES, 1998; SWEARER et al., 2002; HELLBERG, 2009), since that varied levels geographic structuring in holoplanktonic cosmopolitan species challenge the idea of their unrestrained dispersal (BUCKLIN; LAJEUNESSE, et al., 1996; LEE, 2000; PEIJNENBURG; BREEUWER, et al., 2004; GOETZE, 2005; KIRBY; LINDLEY; BATTEN, 2006; CHEN; HARE, 2011). Currently there is a pressing need for reevaluation of populations designated as demographically opens (SWEARER et al., 2002).

DEMOGRAPHIC HISTORY

The Tajima's D and Fu's Fs estimates were negative for most of the locations. Among these, only TA showed a significant value for Fu's index ($p < 0.02$ - Table 5). Significant negative values are usually associated with demographic expansion events (FU, 1997; GOETZE, 2005; OLIVEIRA-NETO et al., 2008), especially in face of high haplotype diversity (FARHADI et al., 2013; FERNÁNDEZ et al., 2013). However, results of this type may also be indicative of purifying sweeps (TEMPLETON, 2006; HAMILTON, 2009) or directional selection (TAJIMA, 1989).

When considering the demographic factors, the hypothesis of stable population sizes could not be rejected for five out of the six evaluated locations (PR, FN, GS, RA and SPSPA) ($p> 0.05$ - Table 5), since these showed only non-significant values for both estimates.

CONCLUSIONS

The use of the COI *barcode* allowed to successfully (i) confirm the morphology-based identification of *F. enflata*; and, (ii) evaluate the diversity and phylogeographic aspects of this species. We demonstrated that *F. enflata* presented the high dispersal potential expected for an holoplanktonic organism, exhibiting a general connectivity scenario in the TWA. Our results characterize a panmitic population, with little evidence of genetic structure. This may be the expected standard for a hermaphrodite species with this life cycle, and that presents a long evolutionary history of 540 Myr. However, future studies should increase the representativity of the samples in different locations of the TWA, in order to fully elucidate the phylogeography of *F. enflata* in the region.

The present work represents an advance in the understanding of dispersal scenarios and connectivity of a dominant holoplanktonic species in the Atlantic. The complexity and relevance biological of this group merit larger scale phylogeographic studies, in order to precisely determine the physical and/or ecological barriers to its dispersal, and if there are structuring processes in ongoing.

ACKNOWLEDGMENTS

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SUPPORTING INFORMATION

Table S4.1 - Identification, geographic location, sampling date and GenBank accession numbers of *Flaccisagitta enflata* analyzed in the present study.

Identification	Geographic Location	Date	Latitude Longitude	Accession Number
TA1	Tamandaré	10-Mar-16	08° 46’ 22” S 34° 55’ 53” W	MH244934
TA3	Tamandaré	10-Mar-16	08° 46’ 22” S 34° 55’ 53” W	MH244935
TA4	Tamandaré	10-Mar-16	08° 46’ 22” S 34° 55’ 53” W	MH244936
TA7	Tamandaré	10-Mar-16	08° 46’ 22” S 34° 55’ 53” W	MH244937
TA8	Tamandaré	10-Mar-16	08° 46’ 22” S 34° 55’ 53” W	MH244938
TA9	Tamandaré	10-Mar-16	08° 46’ 22” S 34° 55’ 53” W	MH244939
TA10	Tamandaré	10-Mar-16	08° 46’ 22” S 34° 55’ 53” W	MH244940
TA12	Tamandaré	10-Mar-16	08° 46’ 22” S 34° 55’ 53” W	MH244941
TA13	Tamandaré	10-Mar-16	08° 46’ 22” S 34° 55’ 53” W	MH244942
TA14	Tamandaré	10-Mar-16	08° 46’ 22” S 34° 55’ 53” W	MH244943
TA15	Tamandaré	10-Mar-16	08° 46’ 22” S 34° 55’ 53” W	MH244944
TA17	Tamandaré	10-Mar-16	08° 46’ 22” S 34° 55’ 53” W	MH244945
TA18	Tamandaré	10-Mar-16	08° 46’ 22” S 34° 55’ 53” W	MH244946
TA22	Tamandaré	10-Mar-16	08° 46’ 22” S 34° 55’ 53” W	MH244947

TA24	Tamandaré	10-Mar-16	08° 46’ 22” S 34° 55’ 53” W	MH244948
TA26	Tamandaré	10-Mar-16	08° 46’ 22” S 34° 55’ 53” W	MH244949
PR1	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244950
PR2	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244951
PR3	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244952
PR4	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244953
PR5	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244954
PR6	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244955
PR7	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244956
PR8	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244957
PR9	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244958
PR11	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244959
PR12	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244960
PR13	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244961
PR14	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244962
PR15	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244963
PR16	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244964
PR17	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244965
PR18	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244966

PR19	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244967
PR20	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244968
PR21	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244969
PR22	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244970
PR23	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244971
PR24	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244972
PR25	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244973
PR26	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244974
PR27	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244975
PR28	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244976
PR29	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244977
PR30	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244978
PR32	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244979
PR33	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244980
PR34	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244981
PR35	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244982
PR36	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244983
PR38	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244984
PR40	Port of Recife	21-Jun-16	08° 3’ 49.42” S 34°52’11.69” W	MH244985

SPSPA4	Saint Peter and Saint Paul’s Archipelago	11-Jan-17	00° 55’ N 29° 21.17’ W	MH244986
SPSPA5	Saint Peter and Saint Paul’s Archipelago	11-Jan-17	00° 54’ N 29° 20.55’ W	MH244987
SPSPA6	Saint Peter and Saint Paul’s Archipelago	11-Jan-17	00° 55’ N 29° 21.17’ W	MH244988
SPSPA7	Saint Peter and Saint Paul’s Archipelago	11-Jan-17	00° 55’ N 29° 21.17’ W	MH244989
SPSPA8	Saint Peter and Saint Paul’s Archipelago	11-Jan-17	00° 55’ N 29° 21.17’ W	MH244990
SPSPA9	Saint Peter and Saint Paul’s Archipelago	11-Jan-17	00° 55’ N 29° 21.17’ W	MH244991
SPSPA10	Saint Peter and Saint Paul’s Archipelago	11-Jan-17	00° 55’ N 29° 21.17’ W	MH244992
SPSPA11	Saint Peter and Saint Paul’s Archipelago	11-Jan-17	00° 56.99’ N 29° 20.44’ W	MH244993
SPSPA12	Saint Peter and Saint Paul’s Archipelago	11-Jan-17	00° 54’ N 29° 20.55’ W	MH244994
SPSPA15	Saint Peter and Saint Paul’s Archipelago	11-Jan-17	00° 54’ N 29° 20.55’ W	MH244995
SPSPA16	Saint Peter and Saint Paul’s Archipelago	11-Jan-17	00° 54’ N 29° 20.55’ W	MH244996
SPSPA17	Saint Peter and Saint Paul’s Archipelago	11-Jan-17	00° 54’ N 29° 20.55’ W	MH244997
SPSPA18	Saint Peter and Saint Paul’s Archipelago	11-Jan-17	00° 54’ N 29° 20.55’ W	MH244998
SPSPA20	Saint Peter and Saint Paul’s Archipelago	11-Jan-17	00° 55’ N 29° 21.17’ W	MH244999
SPSPA21	Saint Peter and Saint Paul’s Archipelago	11-Jan-17	00° 55’ N 29° 21.17’ W	MH245000
SPSPA22	Saint Peter and Saint Paul’s Archipelago	11-Jan-17	00° 55’ N 29° 21.17’ W	MH245001
SPSPA23	Saint Peter and Saint Paul’s Archipelago	11-Jan-17	00° 55’ N 29° 21.17’ W	MH245002
SPSPA25	Saint Peter and Saint Paul’s Archipelago	11-Jan-17	00° 55’ N 29° 21.17’ W	MH245003
SPSPA26	Saint Peter and Saint Paul’s Archipelago	11-Jan-17	00° 55’ N 29° 21.17’ W	MH245004

SPSPA27	Saint Peter and Saint Paul’s Archipelago	11-Jan-17	00° 55’ N 29° 21.17’ W	MH245005
SPSPA28	Saint Peter and Saint Paul’s Archipelago	11-Jan-17	00° 55’ N 29° 21.17’ W	MH245006
SPSPA29	Saint Peter and Saint Paul’s Archipelago	11-Jan-17	00° 55’ N 29° 21.17’ W	MH245007
SPSPA30	Saint Peter and Saint Paul’s Archipelago	11-Jan-17	00° 55’ N 29° 21.17’ W	MH245008
SPSPA32	Saint Peter and Saint Paul’s Archipelago	11-Jan-17	00° 55’ N 29° 21.17’ W	MH245009
SPSPA33	Saint Peter and Saint Paul’s Archipelago	11-Jan-17	00° 55’ N 29° 21.17’ W	MH245010
SPSPA37	Saint Peter and Saint Paul’s Archipelago	11-Jan-17	00° 55’ N 29° 21.17’ W	MH245011
FN2	Fernando de Noronha Archipelago	7-Jan-17	03° 49.43’ S 32° 24.78’ W	MH245012
FN9	Fernando de Noronha Archipelago	7-Jan-17	03° 49.43’ S 32° 24.78’ W	MH245013
FN12	Fernando de Noronha Archipelago	7-Jan-17	03° 49.43’ S 32° 24.78’ W	MH245014
FN13	Fernando de Noronha Archipelago	7-Jan-17	03° 49.43’ S 32° 24.78’ W	MH245015
FN14	Fernando de Noronha Archipelago	7-Jan-17	03° 49.43’ S 32° 24.78’ W	MH245016
FN15	Fernando de Noronha Archipelago	7-Jan-17	03° 49.43’ S 32° 24.78’ W	MH245017
FN16	Fernando de Noronha Archipelago	7-Jan-17	03° 49.43’ S 32° 24.78’ W	MH245018
FN17	Fernando de Noronha Archipelago	7-Jan-17	03° 49.43’ S 32° 24.78’ W	MH245019
FN18	Fernando de Noronha Archipelago	7-Jan-17	03° 49.43’ S 32° 24.78’ W	MH245020
FN23	Fernando de Noronha Archipelago	7-Jan-17	03° 49.43’ S 32° 24.78’ W	MH245021
FN24	Fernando de Noronha Archipelago	26-Jan-17	03° 48.45’ S 32° 24.20’ W	MH245022
FN25	Fernando de Noronha Archipelago	26-Jan-17	03° 48.45’ S 32° 24.20’ W	MH245023

FN28	Fernando de Noronha Archipelago	26-Jan-17	03° 47.29’ S 32° 23.9’ W	MH245024
FN29	Fernando de Noronha Archipelago	26-Jan-17	03° 47.29’ S 32° 23.9’ W	MH245025
FN30	Fernando de Noronha Archipelago	26-Jan-17	03° 47.36’ S 32° 23.25’ W	MH245026
FN32	Fernando de Noronha Archipelago	26-Jan-17	03° 48.45’ S 32° 24.20’ W	MH245027
FN36	Fernando de Noronha Archipelago	26-Jan-17	03° 47.29’ S 32° 23.9’ W	MH245028
FN37	Fernando de Noronha Archipelago	26-Jan-17	03° 47.29’ S 32° 23.9’ W	MH245029
FN38	Fernando de Noronha Archipelago	26-Jan-17	03° 47.29’ S 32° 23.9’ W	MH245030
GS4	Guará seamount	6-May-17	04° 5’ 24.79” S 36° 18’ 03.42” W	MH245031
GS8	Guará seamount	6-May-17	04° 5’ 24.79” S 36° 18’ 03.42” W	MH245032
GS9	Guará seamount	6-May-17	04° 5’ 24.79” S 36° 18’ 03.42” W	MH245033
GS10	Guará seamount	6-May-17	04° 5’ 24.79” S 36° 18’ 03.42” W	MH245034
GS11	Guará seamount	6-May-17	04° 5’ 24.79” S 36° 18’ 03.42” W	MH245035
GS14	Guará seamount	6-May-17	04° 5’ 24.79” S 36° 18’ 03.42” W	MH245036
GS15	Guará seamount	6-May-17	04° 5’ 24.79” S 36° 18’ 03.42” W	MH245037
GS19	Guará seamount	6-May-17	04° 5’ 24.79” S 36° 18’ 03.42” W	MH245038
GS20	Guará seamount	6-May-17	04° 5’ 24.79” S 36° 18’ 03.42” W	MH245039
GS22	Guará seamount	6-May-17	04° 5’ 24.79” S 36° 18’ 03.42” W	MH245040
GS23	Guará seamount	6-May-17	04° 5’ 24.79” S 36° 18’ 03.42” W	MH245041
GS25	Guará seamount	6-May-17	04° 5’ 24.79” S 36° 18’ 03.42” W	MH245042

RA6	Rocas Atoll	2-May-17	03° 45’ 30.84” S 34° 00’ 5.42” W	MH245043
RA11	Rocas Atoll	2-May-17	03° 45’ 30.84” S 34° 00’ 5.42” W	MH245044
RA12	Rocas Atoll	2-May-17	03° 45’ 30.84” S 34° 00’ 5.42” W	MH245045
RA15	Rocas Atoll	2-May-17	03° 45’ 30.84” S 34° 00’ 5.42” W	MH245046
RA20	Rocas Atoll	2-May-17	03° 45’ 30.84” S 34° 00’ 5.42” W	MH245047
RA21	Rocas Atoll	2-May-17	03° 45’ 30.84” S 34° 00’ 5.42” W	MH245048
RA22	Rocas Atoll	2-May-17	03° 45’ 30.84” S 34° 00’ 5.42” W	MH245049

Source: Danielle Melo

Table S4.2 - Informations on the COI sequences used as a reference for the investigation of the evolutionary history of *Flaccisagitta enflata* analyzed in the present study.

Identification	Deposited as	Current Taxonomy	Accession Number	Authors
UCONN:Ch15.1.1	*Sagitta enflata*	*Flaccisagitta enflata*	GQ368399.1	Jennings RM, Bucklin A, Pierrot-Bults A, 2010
UCONN:Ch15.1.2	*Sagitta enflata*	*Flaccisagitta enflata*	GQ368400.1	Jennings RM, Bucklin A, Pierrot-Bults A, 2010
UCONN:Ch15.2.1	*Sagitta enflata*	*Flaccisagitta enflata*	GQ368401.1	Jennings RM, Bucklin A, Pierrot-Bults A, 2010
NIOBZC17	*Sagitta hexaptera*	*Flaccisagitta hexaptera*	JN258017.1	Nair VR, et al., 2015
NIOBZC18	*Sagitta hexaptera*	*Flaccisagitta hexaptera*	JN258018.1	Nair VR, et al., 2015
NIOBZC19	*Sagitta hexaptera*	*Flaccisagitta hexaptera*	JN258019.1	Nair VR, et al., 2015
UCONN:Ch18.1.1	*Sagitta marri*	*Solidosagitta marri*	GQ368412.1	Jennings RM, Bucklin A, Pierrot-Bults A, 2010
UCONN:Ch18.1.2	*Sagitta marri*	*Solidosagitta marri*	GQ368413.1	Jennings RM, Bucklin A, Pierrot-Bults A, 2010
UCONN:Ch18.1.3	*Sagitta marri*	*Solidosagitta marri*	GQ368414.1	Jennings RM, Bucklin A, Pierrot-Bults A, 2010
UCONN:Ch16.1.1	*Sagitta helenae*	*Sagitta helenae*	GQ368402.1	Jennings RM, Bucklin A, Pierrot-Bults A, 2010
UCONN:Ch16.2.1	*Sagitta helenae*	*Sagitta helenae*	GQ368403.1	Jennings RM, Bucklin A, Pierrot-Bults A, 2010
UCONN:Ch16.3.1	*Sagitta helenae*	*Sagitta helenae*	GQ368404.1	Jennings RM, Bucklin A, Pierrot-Bults A, 2010
UCONN:Ch22.1.1	*Sagitta bipunctata*	*Sagitta bipunctata*	GQ368396.1	Jennings RM, Bucklin A, Pierrot-Bults A, 2010
UCONN:Ch22.1.2	*Sagitta bipunctata*	*Sagitta bipunctata*	GQ368397.1	Jennings RM, Bucklin A, Pierrot-Bults A, 2010
UCONN:Ch22.2.1	*Sagitta bipunctata*	*Sagitta bipunctata*	*GQ368398.1*	*Jennings RM, Bucklin A, Pierrot-Bults A, 2010*

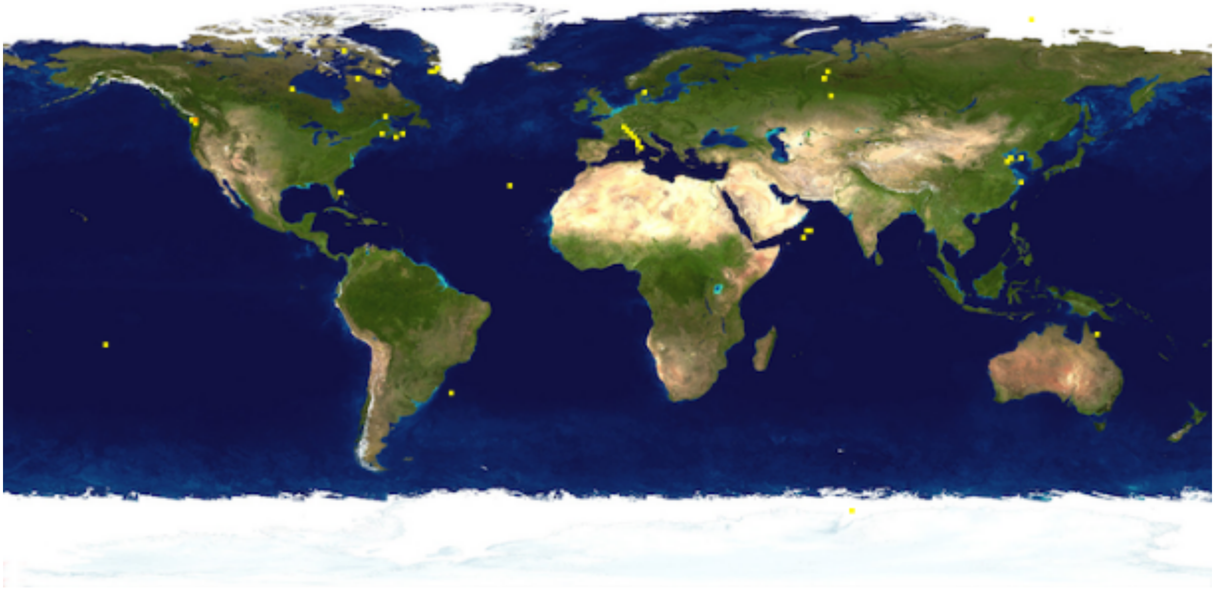
Source: Danielle Melo

Table S4.3 - Log marginal likelihood for distinct runs and migration models (MM), based on the COI region of mtDNA of *Flaccisagitta enflata* analyzed in the present study. In bold are the best likelihood used to calculate the model probability.

MODEL	POPULATIONS	LOG MARGINAL LIKELIHOOD			MODEL PROBABILITY (%)
		Run 1	Run 2	Run 3	
MM1	TA+PR+SPSPA+FN+RA+GS	-188,870,484	-18,633,774	-187,680,573	98.9
MM2_GS	GS ⇆ TA+PR+SPSPA+FN+RA	-18,782,859	-19,064,498	-1,891,481	0
MM2_PR	PR ⇆ TA+SPSPA+FN+RA+GS	-18,997,555	-18,829,525	-18,996,597	0
MM3	TA+PR ⇆ SPSPA ⇆ FN+RA+GS	-1,880,371,882	-1,896,032,281	-1,879,789,129	0
MM4	TA+PR ⇆ SPSPA ⇆ FN+RA ⇆ GS	-188,245,856	-1,901,166,567	-1,886,962,248	0
MM5	TA ⇆ PR ⇆ SPSPA ⇆ FN+RA ⇆ GS	-18,899,462	-1,894,993,041	-1,890,342,595	0
MM6	TA ⇆ PR ⇆ SPSPA ⇆ FN ⇆ RA ⇆ GS	-186,788,529	-1,889,111,263	-1,875,006,122	1.1

Source: Danielle Melo

5 ARTIGO 3 - DIVERSIDADE DE CHAETOGNATHA NA AMAZÔNIA AZUL (BRASIL, ATLÂNTICO TROPICAL) BASEADA EM DNA BARCODE (COI)



Pontos geográficos catalogados para o COI *barcode* de Chaetognatha - maio de 2019.
Fonte: `http://planktonchronicles.org`

RESUMO

O gene COI (subunidade I da citocromo c oxidase mitocondrial) é atualmente reconhecido como o código de barras universal para identificação animal (DNA *barcode*). Com intuito de ampliar os dados disponíveis sobre o filo Chaetognatha, o presente trabalho analisou a variabilidade molecular intra e interespecífica de espécies do filo, incluindo sequências COI de *Parasagitta friderici* oriundas do Atlântico Sudoeste. Esta região, assim como o Atlântico Equatorial, ainda são pobremente representadas quanto ao *barcode* de Chaetognatha. Neste sentido, amostras de plâncton foram coletadas em agosto de 2018, na baía de Tamandaré (Brasil, Atlântico Sudoeste Tropical). A espécie *P. friderici* foi obtida deste material, identificada pela morfologia, e posteriormente sequenciada. Os fragmentos de *barcode* gerados foram analisados em conjunto a sete táxons da família Sagittidae, incluindo sequências de *Flaccisagitta enflata* oriundas de localidades do Atlântico Sudoeste e Equatorial (n =165). A média K2P das diferenças intraespecíficas foi de 0,017 (±0.009), enquanto o valor médio obtido para as diferenças interespecíficas foi de 0,333 (±0,038). De maneira geral, estes valores foram superiores à diversidade observada para outros grupos marinhos, e podem estar associados aos grandes tamanhos populacionais alcançados por espécies do zooplâncton. Com relação à filogenia, a árvore gerada pelo método de Máxima Verossimilhança (MV) apresentou ramos longos ao determinar a separação das espécies, com altos valores de suporte (79-100%). As seis sequências de *P. friderici* partiram de uma bifurcação que também originou o ramo com as sequências de *Parasagitta setosa* (Suíça, Atlântico Norte). A vizinhança filogenética entre essas espécies havia sido observada anteriormente com base em sequências ribossomais (gene 28S). Por sua vez, o agrupamento das sequências de *F. enflata* (n=119) apresentou os mesmos ramos internos gerados por estudos anteriores, empregando tanto Análise Bayesiana quanto MV. Este trabalho apresenta o primeiro relato molecular de *P. friderici* no Atlântico Sudoeste, e representa um esforço geral em avaliar a diversidade genética por meio de *barcoding*, utilizando quetognatos numericamente abundantes no oceano Atlântico Tropical.

Palavras-chave: DNA mitocondrial. Sagittidae. *Parasagitta*. Distância K2P.

INTRODUÇÃO

utilização do DNA *barcode* na investigação de aspectos populacionais tem sido aplicada a uma vasta diversidade de táxons marinhos (LESSIOS; KANE; ROBERTSON, 2003; DURAN; PASCUAL; TURON, 2004; LIND et al., 2007; AZUMA et al., 2007; SANNA et al., 2009). A vantagem de empregá-lo resulta de sua taxa de evolução superar aquelas dos genes ribossomais na maioria dos grupos, o que permite discriminar com precisão espécies intimamente relacionadas. Além disso, este gene frequentemente permite identificar níveis significativos de variação intraespecífica associada à estruturação geográfica, detectada desde meso (dezenas a centenas de km) a macro escalas espaciais (centenas a milhares de km) (BUCKLIN; STEINKE; BLANCO-BERCIAL, 2011). Resultados satisfatórios envolvendo o DNA *barcode* têm sido especialmente registrados em grupos holoplanctônicos de ampla distribuição, que podem exibir altos níveis de diversidade genética em reflexo aos seus grandes tamanhos populacionais (ex. GOETZE, 2005; DEAGLE et al., 2015; NOBLEZADA, M. M. et al., 2016). Alguns estudos também têm evidenciado a presença de complexos crípticos dentro de espécies taxonomicamente reconhecidas, reforçando a premissa de que a biodiversidade marinha ainda é fortemente subestimada (LEE, 2000; GOETZE, 2005; CHEN; HARE, 2008, 2011; VIÑAS et al., 2015; KORDBACHEH; GARBALENA; WALSH, 2017).

Dentre os grupos zooplanctônicos amplamente distribuídos, Chaetognatha ocorre desde sistemas costeiros a oceânicos, bem como em extensa faixa vertical na coluna d’água (CASANOVA, 1999; BOLTOVSKOY, 2005; OZAWA et al., 2007; PIERROT-BULTS, A. C.; NAIR, 2010). As espécies apresentam diversos aspectos ecológicos importantes, destacando-se sua atuação como predadores-chave de Copepoda e indicadores hidrológicos de massas d’água específicas (BONE; KAPP; PIERROT-BULTS, A. C., 1991; VEGA-PÉREZ; SCHINKE, 2011). Diante de sua importância e elevada frequência e abundância no plâncton marinho, estudos baseados em DNA *barcode* vêm sendo desenvolvidos na última década, a fim de conhecer a diversidade genética deste grupo (JENNINGS; BUCKLIN; PIERROT-BULTS, A., 2010; MELO,

D. C. M. M. et al., 2019, *in press*) e investigar a existência de possíveis complexos crípticos (MIYAMOTO; MACHIDA; NISHIDA, 2010, 2012; KULAGIN; STUPNIKOVA et al., 2013).

O presente trabalho foi desenvolvido em complemento a estes estudos, buscando analisar a variabilidade molecular intra e interespecífica de espécies holoplanctônicas de Chaetognatha, através da utilização de sequências parciais do gene mitocondrial COI (subunidade I da citocromo c oxidase - DNA *barcode*). Em especial, esta investigação representa um avanço no sentido de preencher a lacuna existente em relação ao sistema *barcode* de quetognatos no oceano Atlântico Tropical. A avaliação de aspectos filogeográficos do grupo em ambientes pouco ou ainda não explorados é recomendada para melhor compreensão de seus padrões de distribuição no domínio pelágico.

MATERIAL E MÉTODOS

AMOSTRAGEM

Amostras de plâncton foram coletadas em agosto de 2018 na baía de Tamandaré (Brasil, Atlântico Sudoeste Tropical) (8º45’53.4”S 35º05’56.7”W) (Figura 13). A amostragem foi realizada mediante arrastos horizontais superficiais, utilizando rede de plâncton com 500 µm de abertura de malha. Em campo, as amostras foram lavadas com solução salina estéril a 3% e posteriormente fixadas em etanol a 100%.

Em laboratório, os quetognatos foram rapidamente separados do material obtido e a espécie *Parasagitta friderici* foi identificada com base em literatura especializada (CASANOVA, 1999). Após a fixação, foram retiradas amostras de tecido (até 25 mm^3) dos espécimes mais conservados e sem conteúdo estomacal aparente, através de dissecção com lâminas descartáveis previamente esterilizadas. As amostras teciduais foram então conservadas em etanol a 100% a 4°C, até a etapa de extração do DNA.

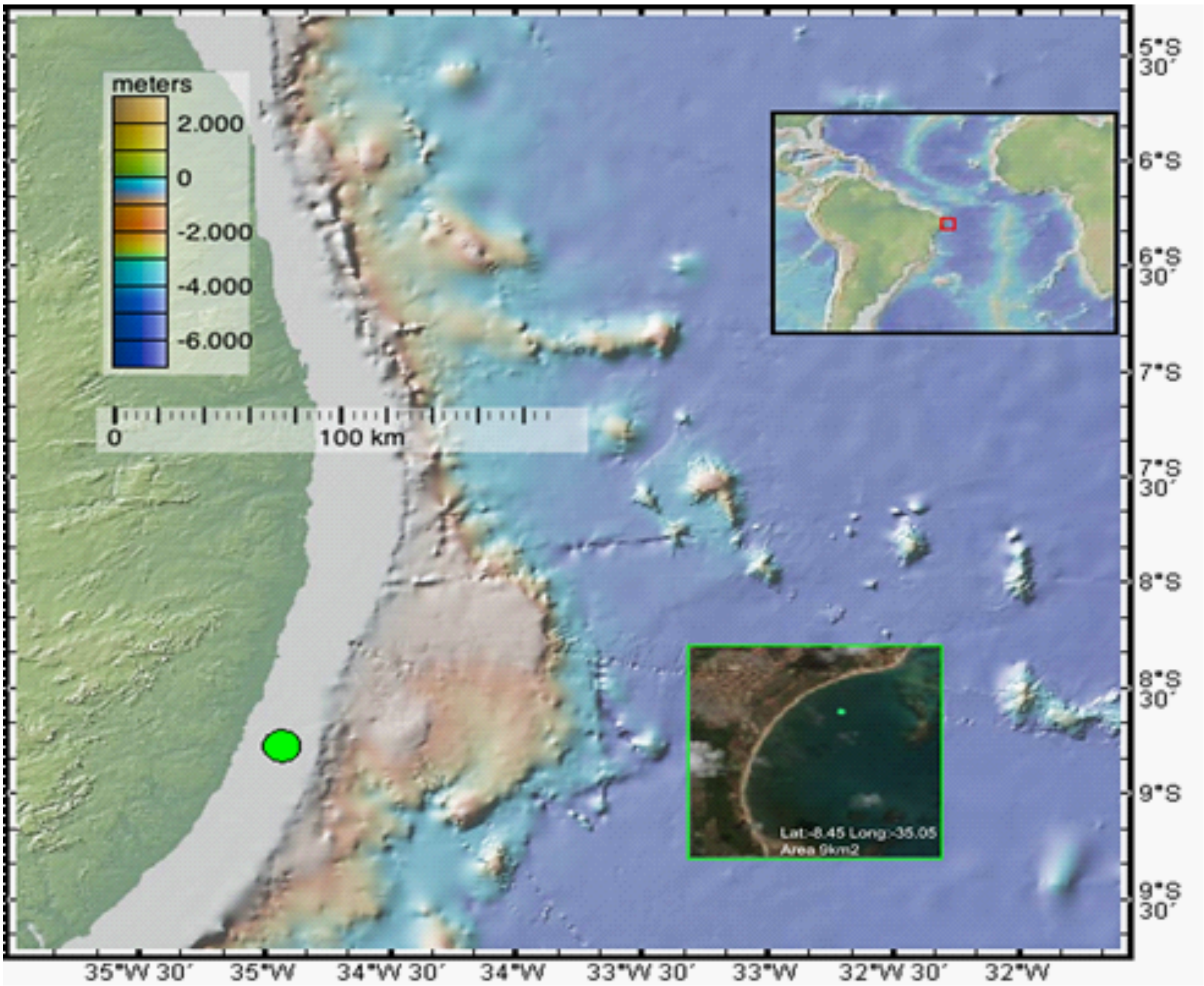


Figura 13 – Mapa da localidade amostrada no Atlântico Sudoeste Tropical. Os insertos à direita mostram a visão macro e aproximada de Tamandaré, Brasil. As coordenadas geográficas do ponto amostrado (círculos preenchido em verde) estão indicadas no inserto com a visão de satélite aproximada. A imagem de satélite foi obtida de Digital Globe (`https://www.digitalglobe.com/`) **Fonte**: Danielle Melo

DNA *BARCODING* E SEQUENCIAMENTO

O DNA total foi obtido usando o kit de extração Blood and Tissue da Qiagen, seguindo o protocolo do fabricante. Para a amplificação dos 710 pb correspondentes a região COI do DNAmt foram utilizados os iniciadores universais apresentados por Folmer (1994): LCO1490 (5'- GGT CAA CAA ATC ATA AAG ATA TTG G - 3') e HCO2198 (5'- TAA ACT TCA GGG TGA CCA AAA AAT CA - 3'). As reações de PCR foram estabelecidas a um volume final de 20 µl, consistindo em 10 µl de Master Mix Go Taq G2

C (Promega), 5 pmol de cada iniciador e 20 a 50 ng do DNA extraído. O protocolo de reação envolveu um passo de desnaturação inicial a 95 ºC durante 1 minuto; seguido por 35 ciclos de desnaturação a 94ºC por 30 segundos, anelamento a 52ºC por 40 segundos e extensão a 72ºC por 1 minuto; com um passo de extensão final a 72ºC durante 5 minutos, realizado no final do último ciclo (modificado de FOLMER et al., 1994).

A purificação dos produtos, sequenciamento e obtenção das sequências consenso foram realizados conforme descrito em Moreira et al. (2013). Resumidamente, os produtos foram purificados por método enzimático e sequenciados com a química BigDye® e a separação dos fragmentos em sequenciador automático. As sequências consenso foram obtidas através da sobreposição das sequências brutas advindas de cada iniciador e edição manual, com o uso da ferramenta Chromas Pro versão 1.5 (Technelysium Pty Ltd). As sequências geradas neste trabalho serão depositadas sob a seção BARCODE do GenBank, incluindo os metadados.

AQUISIÇÃO DOS DADOS

Além das sequências de *P. friderici* geradas para compor o presente estudo, foram utilizadas as sequências obtidas em Melo et al. (2019, *in press*), e 43 sequências relacionadas, obtidas diretamente do Genbank. Informações sobre os dados utilizados como referência são apresentadas na Tabela S5.1..

VARIAÇÃO GENÉTICA INTRA E INTERESPECÍFICA

Para investigar os níveis de variação genética dentro e entre espécies da família Sagittidae, foram usadas as distâncias par-a-par Kimura 2-parâmetro (K2P), a melhor medida de divergência entre sequências de nucleotídeos para estimar pequenas diferenças (HEBERT; RATNASINGHAM; WAARD, 2003; NEI; KUMAR, 2000). As distâncias K2P foram computadas por comparação par-a-par com eliminação dos gaps (KIMURA, 1980), utilizando o Mega versão 6.06 (TAMURA et al., 2013).

RECONSTRUÇÃO FILOGENÉTICA

As sequências consenso geradas foram revertidas para o formato FASTA, comparadas com sequências depositadas no GenBank por meio da ferramenta BLAST (ALTSCHUL et al., 1990) e exportadas para o AliView v. 1.18.1 (LARSSON, 2014), juntamente com as sequências mais similares (capturadas diretamente do Genbank) e aquelas geradas por Melo et al. (2019, *in press*). O conjunto de dados foi traduzido para sequências de aminoácidos usando o código mitocondrial de invertebrados, para a verificação da correta tradução. O conjunto de sequências de aminoácidos foi alinhado com a ferramenta Multiple Sequence Comparison by Log- Expectation (MUSCLE) (EDGAR, 2004) no AliView, e revertidas para o formato de DNA. O alinhamento foi editado manualmente e as sequências dos iniciadores foram removidas. O conjunto final de dados (n=165) conteve 122 sequências de águas neríticas e oceânicas do Brasil, das quais seis corresponderam a *P. friderici* (este estudo), e 116 a *Flaccisagitta enflata* (Melo et al., 2019 *in press*). As 43 restantes, compreenderam as sequências de referência das espécies: *F. enflata* (n=3), *Flaccisagitta hexaptera* (n=3), *Sagitta helenae* (n=3), *Sagitta bipunctata* (n=3), Solidosagitta marri (n=3), *Parasagitta setosa* (n=27) e *Parasagitta* elegans (n=1) (Tabela S5.1).

A história evolutiva de Chaetognatha foi inferida usando o método da Máxima Verossimilhança (MV). O modelo evolutivo Tamura 3-parâmetros (TN93) (TAMURA et al., 2013), com taxa de variação entre os sítios seguindo uma distribuição gamma (+G) e permitindo a existência de alguns sítios invariáveis (+I), foi selecionado com a opção Find best DNA/Protein models (ML) no Mega 6.06 (TAMURA et al., 2013). A árvore inicial para a busca heurística foi obtida automaticamente aplicando os algoritmos neighbor-join e BIONJ a uma matriz de distâncias par-a-par, estimada usando a abordagem Maximum Composite Likelihood (MCL) e selecionado a topologia com maior valor de probabilidade. A porcentagem de árvores nas quais os táxons se associaram foi baseada em 1000 testes. Todas as posições com cobertura inferior a 95% foram eliminadas. O conjunto de dados final conteve 415 posições de nucleotídeos. A árvore ótima calculada foi exportada para a visualização no software FigTree v1.4.4

(`http://tree.bio.ed.ac.uk/software/figtree/`).

RESULTADOS

Foram geradas seis sequências de *P. friderici* que, em adição às 116 sequências a serem publicadas no trabalho de Melo et al. (2019, *in press*), somaram 122 novas sequências COI oriundas do Atlântico Sudoeste e Equatorial. Estas regiões ainda são pouco representadas nos bancos públicos de dados moleculares de Chaetognatha (em janeiro/2019)

DIVERGÊNCIA ENTRE AS SEQUÊNCIAS COI

A comparação hierárquica das distâncias K2P apresentou resultados díspares nos diferentes níveis taxonômicos (Tabela 9). A média das diferenças interespecíficas, de 0,333 (±0,038), foi superior em mais de uma ordem de magnitude à média das diferenças intraespecíficas, de 0,017 (±0.009). A média das distâncias intraespecíficas foi influenciada pelas sequências idênticas de *F. hexaptera*. Dentre as demais espécies, as distâncias variaram de 0,013 (e *P. friderici*) a 0,024 (*F. enflata* e *S. marri*). A menor distância interespecífica foi entre e *P. friderici* (0,155) e a maior foi entre *P. elegans* e *F. hexaptera* (0,421). Com relação a *P. friderici*, a distância interespecífica mais elevada foi relativa a *P. elegans* (0,355). Não houve discrepância dentre as distâncias interespecíficas.

Tabela 9 – Distâncias par-a-par Kimura 2-parâmetro (K2P) intra- e interespecíficas para espécies de Chaetognatha

	N	**Intra-**		***F. hexaptera***	***F. enflata***	***P. friderici***	***P. elegans***	***S. marri***	***S. bipunctata***
	27	0,013							
F. hexaptera	3	0,000	0,355						
F. enflata	119	0,024	0,315	0,382					
P. friderici	6	0,013	0,155	0,331	0,298				
P. elegans	1	-	0,356	0,421	0,412	0,355			
S. marri	3	0,024	0,290	0,337	0,330	0,292	0,373		
S. bipunctata	3	0,023	0,329	0,413	0,353	0,348	0,353	0,371	
S. helenae	3	0,023	0,283	0, 386	0,308	0,268	0,327	0,303	0,307
	M	0,017				0,333			
	DP	0,009				0,038			

Fonte: Danielle Melo

ANÁLISE FILOGENÉTICA

A árvore ótima gerada por MV (Figura 14) apresentou ramos curtos dentro de cada espécie, enquanto ramos mais longos determinaram a separação das espécies. Todos os nós separando as espécies evidenciaram suporte robusto (79-100%). Por sua vez, os nós internos dos grupos apresentaram suporte robusto em poucos casos, e frequentemente foi inferior a 50%. O ramo que agrupou (n=27) apresentou ramos internos curtos, com baixo suporte para os nós, havendo sido colapsado para melhor visualização da topologia geral e das distâncias entre os grupos. Esse ramo partiu do nó cuja bifurcação originou o ramo com as seis sequências de *P. friderici* aqui obtidas. Adicionalmente, o agrupamento das sequências de *F. enflata* apresentou os mesmos ramos gerados no trabalho de Melo et al. (2019, *in press*), isto é, um ramo único e um ramo múltiplo bifurcado, este incluindo um ramo menor com 19 sequências, e outro com todas as demais. Desse modo, na árvore aqui apresentada (Figura 14), o agrupamento *F. enflata* (n=119) foi igualmente colapsado.

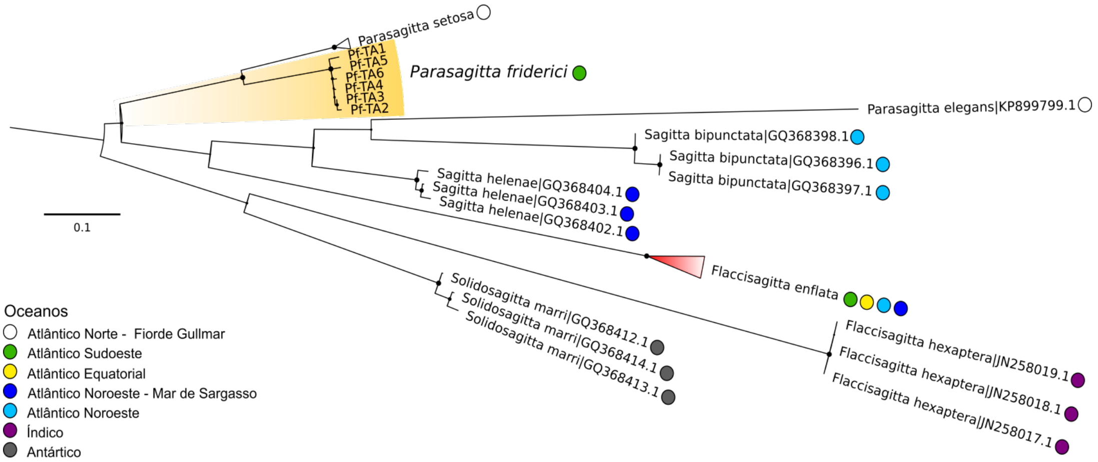


Figura 14 – Topologia da árvore com base no COI. Os nós com suporte > 50% estão indicados por círculos preenchidos em preto. A barra de escala indica a distância entre os ramos estimada pelo número de substituições por posição (0.1). As sequências geradas nesse estudo, de *P. friderici*, estão indicadas pelo plano de fundo em laranja. Os números de acesso para as sequências desse grupo constam na Tabela S5.1. **Fonte**: Ana Paula Moreira

DISCUSSÃO

GERAÇÃO E VALIDAÇÃO DOS DADOS

A busca no GenBank por sequências de nucleotídeos com a palavra-chave COI resultou em 3.107.991 de itens catalogados (maio/2019). No banco de dados do International Barcode of Life Project (`http://www.textitbarcodinglife.org`), uma plataforma específica de consulta a sequências *barcode*, estão disponíveis publicamente 457.364 Barcode Index Numbers de animais (BINs; clusters de sequências relacionadas a espécies) (maio/2019). Deste total, por exemplo, 386.582 correspondem a BINs de Arthropoda, 34.287 de Chordata, 18.299 de Mollusca e 7.290 de Annelida. Chaetognatha, por sua vez, está representado por 81 BINs resultantes de 966 registros oriundos de 13 países, dos quais 966 incluem o nome da espécie, totalizando 95 espécies. Apesar destes números, a maior parte do banco de dados refere-se a amostragens realizadas no Atlântico Norte e Pacífico, enquanto o Atlântico Sul ainda é pobremente representado.

O presente estudo e o de Melo et al. (2019, *in press*) representam um avanço no sentido de preencher esta lacuna. Para a espécie *F. enflata*, apenas três sequências do Atlântico norte estavam disponíveis (JENNINGS; BUCKLIN; PIERROT-BULTS, A., 2010), até que 116 *barcode*s do Atlântico Sudoeste e Equatorial foram sequenciados e depositados no Genbank (MELO, D. C. M. M. et al., 2019, *in press*). As sequências COI aqui fornecidas também são as únicas disponíveis para a espécie *P. friderici*. Além destas, a referida espécie só foi sequenciada quanto a genes ribossomais (18S e 28S), a partir de amostras originárias do mar Mediterrâneo (Atlântico Noroeste) (GASMI et al., 2014). Desta forma, os *barcode*s gerados por este estudo são as únicas sequências gênicas disponíveis de *P. friderici* do Atlântico Sul. Todas as sequências geradas e aqui discutidas incluem mais de 400 sítios homólogos, entre si e com as demais sequências relacionadas e publicamente disponíveis, o mínimo desejável para estudos baseados em DNA *barcoding* (HEBERT; CYWINSKA et al., 2003).

DIVERGÊNCIA DAS SEQUÊNCIAS COI

Não houve sobreposição entre as distâncias K2P inter e intraespecíficas, o que já havia sido relatado para quetognatos em geral (JENNINGS; BUCKLIN; PIERROT-BULTS, A., 2010). A média das distâncias K2P intraespecíficas (0,017), e principalmente os valores observados para *F. enflata*, *S. helenae*, *S. bipunctata* e *S. marri* (0,023 e 0,024), foram superiores quando comparados com os valores relatados para um maior número de espécies de quetognatos (0,0146; 4 gêneros, 14 espécies) (JENNINGS; BUCKLIN; PIERROT-BULTS, A., 2010); assim como para ctenofóros (Coeloplanidae) (0,0036; 11 espécies) (ALAMARU et al., 2017); decápodes (0,00460; 54 espécies); anfípodos gamarídeos (0,00740; 12 espécies) (COSTA, F. O. et al., 2007); e, peixes (0,00390; 207 espécies) (WARD, R. D. et al., 2005). Valores superiores ao limiar sugerido de 0,02 (AVISE; ARNOLD et al., 1987; JOHNS; AVISE, 1998; AVISE, 2000) já foram relatados, embora menos frequentemente. Exemplos deste tipo podem ser citados para duas de um total de 35 espécies de peixes ciprinídeos (0,0381) (SHEN et al., 2016); para dois grupos de anfíbios (variação de 0,070 - 0,180) (VENCES et al., 2005); e ainda para 12% de 1004 espécies de Lepidoptera (distância máxima de 0,0960) (HUEMER et al., 2014). Para metazoários, o nível da variação intraespecífica do COI geralmente não é > 0,03 (COSTA, F. O. et al., 2007; WAUGH, 2007). Esse limiar foi observado para os grupos estudados, apesar dos casos nos quais foram registrados valores ligeiramente superiores ao corte específico sugerido (0,02).

A média das distâncias K2P interespecíficas (0,333) também foi superior aos valores relatados para alguns dos grupos anteriormente citados, exs.: decápodos e anfipodos gamarídeos (COSTA, F. O. et al., 2007); e, peixes - (WARD, R. D. et al., 2005). Em relação à quetognatos, a média de variação interespecífica se aproximou do valor obtido por Jennings, Bucklin e Annelies Pierrot-Bults (2010) para 14 espécies (0,345), das quais, 4 foram inclusas neste trabalho. Por outro lado, a média aqui obtida foi inferior ao valor relatado entre espécies de *Pseudosagitta* (0,454 - KULAGIN; NERETINA, 2017); e superior ao descrito entre espécies de Eukrohnia (KULAGIN; STUPNIKOVA et al., 2013, p. 0, 217 –). Avaliados conjuntamente, os dados apresentados confirmam a elevada diversidade reunida em *Sagitta* e *Flaccisagitta* (incluíndo os grupos reclassificados como *Solidosagitta* e *Parasagitta*) (JENNINGS; BUCKLIN; PIERROT-BULTS, A., 2010; PEIJNENBURG; HAASTRECHT; FAUVELOT, 2005). Este resultado pode decorrer de grandes tamanhos populacionais das espécies (AVISE; BOWEN; LAMB, 1989), como verificado para grupos do zooplâncton em geral (NORRIS, 2000). Os altos valores intra- e interespecíficos obtidos nas comparações realizadas ainda respaldam a hipótese de que os quetognatos divergiram há muito tempo na escala evolutiva, porém desde então, a divergência ocorrida até o presente foi comparativamente inferior (JENNINGS; BUCKLIN; PIERROT-BULTS, A., 2010).

TAXONOMIA E ANÁLISE FILOGENÉTICA

O DNA *barcoding* COI foi bem sucedido em confirmar o gênero de todas as sequências de *P. friderici* identificadas pelo método tradicional da morfologia, o que também foi relatado por Melo et al. (2019, *in press*) para o grupo *F. enflata*. Jennings, Bucklin e Annelies Pierrot-Bults (2010) e Kulagin e Neretina (2017) também já haviam reportado a utilidade desta metodologia para identificar quetognatos. Em uma escala mais ampla, Hebert, Cywinska et al. (2003) realizaram um estudo incluindo 13.000 pares de espécies congêneres, representantes de 11 filos, no qual evidenciaram que é possível o diagnóstico rotineiro ao nível de espécie usando COI.

Na topologia da árvore gerada por MV, *P. friderici* agrupou com ; e *P. elegans* com *S. bipunctata*. Tais agrupamentos foram equivalentes aos observados por Gasmi et al. (2014) para Sagittidae, baseada em sequências ribossomais (gene 28S - LSU rRNA). No geral, *F. enflata*, *S. helenae* e *S. bipunctata* apresentaram a mesma disposição entre si em comparação à árvore gerada por Análise Bayesiana de Jennings, Bucklin e Annelies Pierrot-Bults (2010). Os grupos mais externos foram *F. hexaptera* e *S. marri*, assim como na topologia obtida por MV no trabalho de Melo et al. (2019, *in press*). A disposição dos ramos internos de *F. enflata* reproduziu exatamente aquela encontrada no estudo em questão, onde foram discutidas as relações filogeográficas do grupo no oceano Atlântico Tropical (MELO, D. C. M. M. et al., 2019, *in press*). Assim como neste trabalho, uma das 119 sequências de *F. enflata* (Mar dos Sargaços - GQ368399.1) ficou isolada de todas as demais 118, inclusive da outra sequência retirada do mesmo local de amostragem (Mar dos Sargaços - GQ368400.1). Analogamente, a maioria das espécies anteriormente avaliadas apresentou no mínimo um *barcode* separado dos demais, que se destacou em Análise Bayesiana como ramo independente e mais longo (JENNINGS; BUCKLIN; PIERROT-BULTS, A., 2010). Os dados aqui discutidos demonstram que é desejável ampliar esforços para a melhor compreensão da filogeografia e taxonomia do grupo Chaetognatha.

CONCLUSÕES

Os altos níveis de diversidade observados neste estudo são esperados em espécies holoplanctônicas, que podem estabelecer populações significativamente numerosas no ambiente pelágico. Aqui também foi apresentado o primeiro relato molecular de *P. friderici* no Atlântico Sudoeste, incluindo as únicas sequências de DNA para a espécie nesse oceano, e os únicos *barcode*s (COI) disponíveis para a mesma. Este trabalho, em conjunto ao anteriormente realizado (MELO, D. C. M. M. et al., 2019, *in press*), representam um esforço pioneiro no estudo da diversidade genética por meio de *barcoding*, utilizando quetognatos numericamente abundantes no Atlântico Tropical.

MATERIAL SUPLEMENTAR

Tabela S5.1 - Espécies e informações referentes às sequências *barcode* de Chaetognatha utilizadas como referência no presente estudo.

Espécie	Origem	Data	Coordenadas	Identificação	No de Acesso	Referência
Parasagitta setosa	Fiorde Gullmar - Atlântico Norte	18/nov/11	58.26°N 11.46°L	SE-S3-76 SS-S1-36	KP899799.1 KP899753.1	Marletaz et al., 2015; submissão direta
				SS-S1-50	KP899754.1	
				SS-S1-51	KP899755.1	
				SS-S1-28	KP899756.1	
				SS-S1-24	KP899757.1	
				SS-S1-25	KP899758.1	
				SS-S1-37	KP899759.1	
				SS-S1-49	KP899760.1	
				SS-S1-49	KP899760.1	
				SS-S1-27	KP899761.1	
				SS-S1-39	KP899762.1	
				SS-10	KP857516.1	
				SS-13	KP857519.1	
				SS-17	KP857522.1	
				SS-30	KP857536.1	
				SS-31	KP857537.1	
				SS-40	KP857547.1	
				SS-43	KP857550.1	
				SS-46	KP857553.1	
				SS-47	KP857554.1	
				SS-50	KP857558.1	
				SS-51	KP857559.1	
				SS-55 SS-57	KP857562.1 KP857564.1	

Flaccisagitta enflata	Porto do Recife - Atlântico Sudoeste	21/jun/16	08° 3’ 49.42"S 34°52’11.69"O	PR11	MH244959	Melo et al., 2019 (*in press*)
				PR9	MH244958	
				PR8	MH244957	
				PR7	MH244956	
				PR6	MH244955	
				PR5	MH244954	
				PR4	MH244953	
				PR3	MH244952	
				PR2	MH244951	
				PR1	MH244950	
	Tamandaré - Atlântico Sudoeste	10/mar/16	08° 46’ 22"S 34° 55’ 53"O	TA26	MH244949	
				TA24	MH244948	
				TA22	MH244947	
				TA18	MH244946	
				TA17	MH244945	
				TA15	MH244944	
				TA14	MH244943	
				TA13	MH244942	
				TA12	MH244941	
				TA10	MH244940	
				TA9	MH244939	
				TA8	MH244938	
				TA7	MH244937	
				TA4	MH244936	
				TA3	MH244935	
				TA1	MH244934	
Parasagitta elegans				SE-S3-76	KP899799.1	
				SS-8	KP857567.1	
				SS-7	KP857566.1	
				SS-6	KP857565.1	

				PR12	MH244960	
				PR13	MH244961	
				PR14	MH244962	
				PR15	MH244963	
				PR16	MH244964	
				PR17	MH244965	
				PR18	MH244966	
				PR19	MH244967	
				PR20	MH244968	
				PR21	MH244969	
				PR22	MH244970	
				PR23	MH244971	
				PR24	MH244972	
				PR25	MH244973	
				PR26	MH244974	
				PR27	MH244975	
				PR28	MH244976	
				PR29	MH244977	
				PR30	MH244978	
				PR32	MH244979	
				PR33	MH244980	
				PR34	MH244981	
				PR35	MH244982	
				PR36	MH244983	
				PR38	MH244984	
				PR40	MH244985	
	Arquipélago de São Pedro e São Paulo - Atlântico Equatorial	11/jan/17	00° 55'N 29° 21.17'O	SPSPA4	MH244986	
			00° 54'N 29° 20.55'O	SPSPA5	MH244987	
			00° 55'N 29° 21.17'O	SPSPA6	MH244988	
				SPSPA7	MH244989	

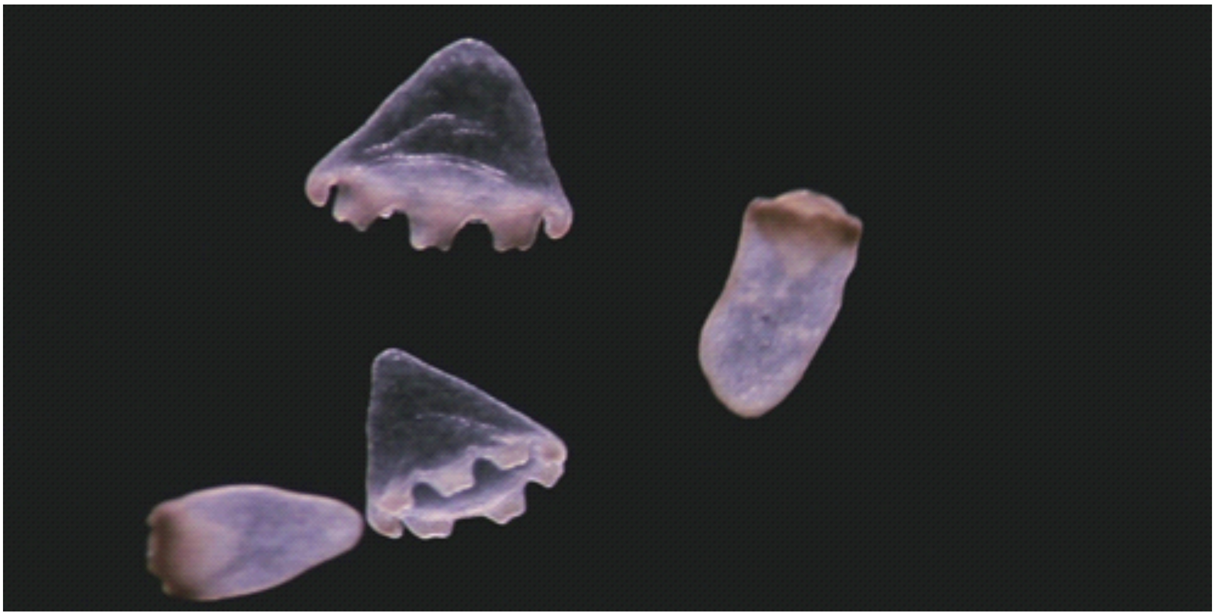
				SPSPA8	MH244990	
				SPSPA9	MH244991	
				SPSPA10	MH244992	
			00° 56.99'N 29° 20.44'O	SPSPA11	MH244993	
			00° 54'N 29° 20.55'O	SPSPA12	MH244994	
				SPSPA15	MH244995	
				SPSPA16	MH244996	
				SPSPA17	MH244997	
				SPSPA18	MH244998	
			00° 55'N 29° 21.17'O	SPSPA20	MH244999	
				SPSPA21	MH245000	
				SPSPA22	MH245001	
				SPSPA23	MH245002	
				SPSPA25	MH245003	
				SPSPA26	MH245004	
				SPSPA27	MH245005	
				SPSPA28	MH245006	
				SPSPA29	MH245007	
				SPSPA30	MH245008	
				SPSPA32	MH245009	
				SPSPA33	MH245010	
				SPSPA37	MH245011	
	Arquipélago de Fernando de Noronha - Atlântico Sudoeste	07/jan/17	03° 49.43'S 32° 24.78'O	FN2	MH245012	
				FN9	MH245013	
				FN12	MH245014	
				FN13	MH245015	
				FN14	MH245016	

				FN15	MH245017	
				FN16	MH245018	
				FN17	MH245019	
				FN18	MH245020	
				FN23	MH245021	
		26/jan/17	03° 48.45'S 32° 24.20'O	FN24	MH245022	
				FN25	MH245023	
			03° 47.29'S 32° 23.9'O	FN28	MH245024	
				FN29	MH245025	
			03° 47.36'S 32° 23.25'O	FN30	MH245026	
			03° 48.45'S 32° 24.20'O	FN32	MH245027	
			03° 47.29'S 32° 23.9'O	FN36	MH245028	
				FN37	MH245029	
				FN38	MH245030	
	Banco submarino Guará - Atlântico Sudoeste	06/mai/17	04° 5' 24.79"S 36° 18' 03.42"O	GS4	MH245031	
				GS8	MH245032	
				GS9	MH245033	
				GS10	MH245034	
				GS11	MH245035	
				GS14	MH245036	
				GS15	MH245037	
				GS19	MH245038	
				GS20	MH245039	
				GS22	MH245040	
				GS23	MH245041	
				GS25	MH245042	
	Atol das Rocas-Atlântico Sudoeste	02/mai/17	03° 45' 30.84"S 34° 00' 5.42"O	RA6	MH245043	
				RA11	MH245044	
				RA12	MH245045	
				RA15	MH245046	

				RA20	MH245047	
				RA21	MH245048	
				RA22	MH245049	
	Oceano Atlântico Noroeste	25/abr/16	14.00°N 55.00°O	UCONN:Ch15.1.1	GQ368399.1	Jennings et al., 2010
				UCONN:Ch15.1.2	GQ368400.1	
			39.14°N 72.97°O	UCONN:Ch15.2.1	GQ368401.1	
Sagitta helenae			14.04°N 54.89°O	UCONN:Ch16.1.1	GQ368402.1	
				UCONN:Ch16.2.1	GQ368403.1	
				UCONN:Ch16.3.1	GQ368404.1	
Sagitta bipunctata				UCONN:Ch22.1.1	GQ368396.1	
				UCONN:Ch22.1.2	GQ368397.1	
				UCONN:Ch22.2.1	GQ368398.1	
Solidosagitta marri	Oceano Antártico	09/mai/12	68.81°S 76.98°O	UCONN:Ch18.1.1	GQ368412.1	
				UCONN:Ch18.1.2	GQ368413.1	
				UCONN:Ch18.1.3	GQ368414.1	
Flaccisagitta hexaptera	Oceano Índico	-	-	NIOBZC17	JN258017.1	Nair et al., 2015
		-	-	NIOBZC18	JN258018.1	
		-	-	NIOBZC19	JN258019.1	

Source: Danielle Melo

6 ARTIGO 4 - PROPOSAL OF A TROPHIC RELATIONSHIP BETWEEN CHAETOGNATHA AND CNIDARIA BASED ON COI MITOCHONDRIAL SEQUENCES



Estágios larvais de Medusozoa. **Fonte**: `http://planktonchronicles.org`

ABSTRACT

This is the first study in Brazil to propose a trophic relationship between Chaetognatha and Cnidaria based on molecular data (COI gene - DNA *barcode*). Cnidaria COI sequences were detected in tissue samples from two specimens of *Flaccisagitta enflata* collected in the surroundings of Fernando de Noronha Archipelago, Tropical Western Atlantic. The methodology used followed all the requirements for a safe molecular manipulation, making the possibility of contamination unlikely. A search carried in BLAST showed that both sequences provided here presented a combination of highest query coverage and match identity with *Nemopilema nomurai* (Cnidaria: Scyphozoa), supporting the hypothesis that they belong to a species of jellyfish. Since gelatinous taxa are known to integrate the broad diet of Chaetognatha, it is possible that *F. enflata* has ingested this type of item, which was not fully digested until the moment of sampling and was not visualized by the transparency method. Thus, the record of Scyphozoa by the COI marker suggests a trophic relationship between the respective taxon and *F. enflata*. Future studies using the association of markers as well as specific methodologies may constitute a new perspective on how to evaluate the trophic ecology of key zooplankton species, including the abundant *F. enflata* in the Atlantic ocean.

Keywords: DNA *barcode*. Food item. Oceanic island. Tropical Atlantic. Zooplankton.

INTRODUCTION

Zooplankton is composed of an extensive diversity of taxa, among which Chaetognatha is one of the most representatives in terms of abundance and frequency (Casanova, 1999). This phylum is known to gather carnivorous species of voracious predatory character, which makes them important builders of the planktonic communities by affecting the distribution, density and occurrence of their prey in environment (CHENEY, 1985). Its ecological relevance also extends to higher trophic levels, since it constitutes an important trophic link between Copepoda and fish of small to large size, including those of commercial interest (REEVE, 1970; ROGER, 1994). Thus, chaetognaths also may act as biological indicators of marine areas with attractive fishing potential.

Among the species widely distributed in the global oceans, *Flaccisagitta enflata* (Grassi, 1881) is a highly frequent planktonic chaetognath in Brazilian waters (Tropical Western Atlantic). In this region, most studies involving this species focus on its spatial distribution, sometimes discussed with other types of data, such as biomass estimates or analysis of maturity stages (LIANG, T. H.; VEGA-PÉREZ, 1994; LIANG, T. H.; VEGA-PÉREZ, 2001; SOUZA, C. S. D.; LUZ; MAFALDA JR., 2014). The trophic ecology, on the other hand, has still been poorly explored for this species (e.g. LIANG, T. H.; VEGA-PÉREZ, 1995; MARAZZO; MACHADO; NOGUEIRA, C. S. R., 1997). In a study developed in the Humboldt Current System (Chile), it was demonstrated that *F. enflata* is an important carnivore in the surface layer of the water column, playing an essential role in the zooplankton community structure and in regional trophodynamics (GIESECKE; GONZALEZ, 2008). Thus, it is interesting to evaluate aspects related to the feeding of this species, to better understand the role of Chaetognatha as active predators in the marine food web.

The present investigation proposes a trophic relationship between *F. enflata* and Cnidaria (Scyphozoa), based on molecular data obtained with the cytochrome c oxidase subunit I gene (COI), part of the mitochondrial DNA (DNA *barcode*). Data of this scope are pioneers in Brazil, and through deeper investigations and refinement of methodologies, may provide a new perspective on how to evaluate the trophic ecology of key zooplankton species.

MATERIALS AND METHODS

SAMPLING

Cnidaria COI sequences were obtained from two specimens of *F. enflata* collected in the surroundings of Fernando de Noronha, Tropical Western Atlantic (TWA) (03°49.43’S and 32° 24.78’W) (Figure 15). Sampling was conducted by a horizontal tow in the surface layer of the water column, using a bongo plankton net of 500 μm mesh size and 0.60 m of mouth diameter. The sampled material was washed rapidly in 3% sterile saline solution, and immediately fixed and preserved in 100% ethanol. In the laboratory, the chaetognaths were sorted from the sample as soon as possible, and the target species was identified according to specialized literature (CASANOVA, 1999). Each organism was subsequently dissected with pre-sterilized disposable blades. The tissue fragments obtained (25 mm^3) were kept in separate Eppendorf tubes, preserved in 100% ethanol and at a temperature of 4°C, until the DNA extraction step.

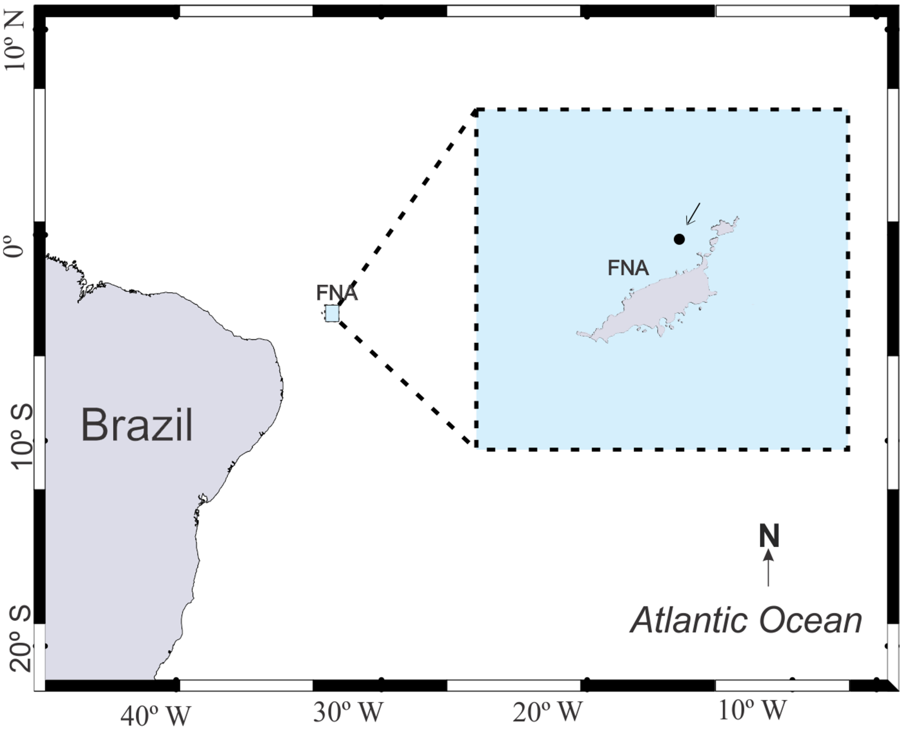


Figure 15 – Sampling station in Fernando de Noronha Archipelago, where the two specimens of *Flaccisagitta enflata* approached in the present study were collected. **Source**: Simone Lira

The plankton sample addressed in this article is part of a broader study, from which phylogeographic aspects of *F. enflata* were evaluated at neritic and oceanic TWA sites (MELO, D. C. M. M. et al., 2019, *in press*). All biological material was obtained under the licenses of Ministério do Meio Ambiente (MMA): Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio - Number 17689) and the Sistema de Autorização e Informação de Biodiversidade (SISBio - Number 47270-5).

DNA *BARCODING* AND SEQUENCING

Total DNA of *F. enflata* was obtained using the Blood and Tissue extraction kit from Qiagen, following the manufacturer's protocol. Posteriorly, a polymerase chain reaction (PCR) was performed using the universal primers proposed by Folmer (1994) for COI gene: LCOI LCO1490 (5'- GGT CAA CAA ATC ATA AAG ATA TTG G - 3') and HCO2198 (5'- TAA ACT TCA GGG TGA CCA AAA AAT CA - 3'). This primer pair amplifies nearly 710 bp. The reactions were established at a final volume of 20 µl, consisting of 10 µl of Master Mix Go Taq G2 C (Promega), 5 pmol of each primer, and 20 to 50 ng of extracted DNA. The reaction protocol involved an initial denaturation step at 95°C for 1 minute; followed by 35 cycles of denaturation at 94ºC for 30 seconds, annealing at 52ºC for 40 seconds and extension at 72ºC for 1 minute; with a final extension step at 72ºC for 5 minutes performed at the end of the last cycle (modified from Folmer, 1994). The ExoSap-IT commercial system (USB Corporation, Cleveland, OH, USA) was used to purify the PCR products. These products were then sequenced and edited to generate the consensus sequences, which were compared with publicly available data in GenBank, using the Nucleotide - Basic Local Alignment Search Tool (BLAST).

The two COI sequences treated in this study were deposited in GenBank with the denomination of Cnidaria sp. (Accession Numbers MK577998 and MK577999).

RESULTS AND DISCUSSION

The present study reports the occurrence of two specimens of *F. enflata* that presented COI sequences incompatible with the genetic identity of this species. This result was obtained through sequencing 118 *F. enflata* organisms, of which 116 were satisfactorily sequenced and evaluated with a phylogeographic approach in the TWA (MELO, D. C. M. M. et al., 2019, *in press*). It is worth mentioning that all organisms were previously selected, so that only the most conserved after fixation and without apparent stomach contents were sent to the genetic analyzes. The specimens were kept apart of any contaminating source as soon as sorted from the samples, and all steps prior to DNA extraction (sample handling, organisms screening and dissection with disposable slides) were performed under stringent cleaning conditions and using sterile or previously autoclaved materials. DNA extraction, amplification and sequencing also followed the requirements for a safe molecular manipulation and were conducted in proper laboratory environment. Thus, the possibility of biological contamination is considered unlikely.

The two COI sequences obtained had final sizes of 691 and 595 bp (MK57799.8 and MK57799.9, respectively). A search carried in BLAST showed that they presented a combination of highest query coverage and match identity with *Nemopilema nomurai* Kishinouye, 1922 (Cnidaria: Scyphozoa), among all available sequences in GenBank. Both sequences provided here exhibited an identity match higher than 82% with this species. Although we could not identify our sequences at the specific level, the query coverage and identity values combined corroborate with the hypothesis that they belong to a species of jellyfish. Among the four sequences detected by BLAST, three were sampled in Japan (LC055090.1, LC055083.1 and LC055030.1) (GOTOH et al., 2017) and one in China (KU360831.1) (DONG et al., 2016). This fact reflects the general distribution of species, cited as a subtropical pelagic jellyfish (60°N - 25°N, 117°E - 152°E), endemic and highly frequent off the East Asian Marginal Seas (UYE, 2008). No records of its distribution in the Atlantic ocean were found. Therefore, is suggested that the data here presented refers to a species of Scyphozoa of the Atlantic, whose COI sequences are currently not available in GenBank.

It is know that the Chaetognatha's diet is significantly diverse, since they are able to consume a wide size spectrum of classes and stages of zooplankton development (PEARRE JR., 1980). The species can be considered since opportunistic carnivores, preying those organisms found in greater abundance in the environment (e.g. Copepoda - SULLIVAN, 1980; MARAZZO; MACHADO; NOGUEIRA, C. S. R., 1997); to selective carnivores, whose diet would be based mainly on the size, shape and/or aggregation behavior of their prey (FEIGENBAUNV, 1991). The food item most consumed and the size of the prey may also be modified according to the stage of maturity of the chaetognaths (PEARRE JR., 1980; VEGA-PÉREZ; LIANG, T. H., 1992; LIANG, T. H.;

VEGA-PÉREZ, 1995; MARAZZO; MACHADO; NOGUEIRA, C. S. R., 1997). Remarkably, copepods are the main component of the stomach contents of the species, evaluated in the light of several studies (GIBBONS, 1992; VEGA-PÉREZ; LIANG, T. H., 1992; LIANG, T. H.; VEGA-PÉREZ, 1995; MARAZZO; MACHADO; NOGUEIRA, C. S. R., 1997). However, alternative items can be consumed in smaller proportions, such as fish larvae, other crustaceans (Euphausiids, Cladocerans) and gelatinous and semi-gelatinous taxa, including other chaetognaths (intra and interspecific cannibalism), Appendicularians and jellyfish (e.g. ALVARIÑO, 1975; LIANG, T. H.; VEGA-PÉREZ, 1995; GIESECKE; GONZALEZ, 2008; VEGA-PÉREZ; SCHINKE, 2011). It has been verified, for example, that *F. enflata* is predator of gelatinous items in general (GIESECKE; GONZALEZ, 2008), being able to consume Hydromedusae in more advanced stages of maturity (MARAZZO; MACHADO; NOGUEIRA, C. S. R., 1997). In this sense, the sequences discussed here may reflect a food item consumed by the species, but which could not be visualized in the intestinal tube from the transparency method. This method may fail to evidence certain structures consumed that were not fully digested until the moment of sampling, as the example of remaining mandibles of Copepoda (LIANG, T.-H.; ARA, et al., 2003) and body structures of Cnidaria (LINDSAY et al., 2015). This is likely to be the case of the present investigation, regarding the record of Scyphozoa with the COI marker, suggesting a trophic relationship with *F. enflata*.

It is important to mention that the gene targeted here is widely applied to the diagnosis of metazoans. This occurs due to its wide distribution in the animal kingdom and to the fact that it is species-specific in many cases, even among phylogenetically close species (HEBERT; RATNASINGHAM; WAARD, 2003). Such advantages have allowed its use in several investigations, including studies concerning trophic relationships based on the analysis of stomach contents, from invertebrates to large marine predators (BUCKLIN; STEINKE; BLANCO-BERCIAL, 2011). Lindsay et al. (2015), for example, suggest that COI will be extremely useful in identifying of Cnidaria, since satisfactory results were obtained with preliminary analyzes using fish and shrimp stomachs, as well as seabird scats. Other authors indicate the use of COI specific primers in studies of this scope, especially if targeted at predators with diversified diets, such as Chaetognatha (BUCKLIN; STEINKE; BLANCO-BERCIAL, 2011). The combined use of distinct markers (as COI and 16S, for instance) also may help to broaden the list of cataloged prey, as well as investigate other issues more deeply, as different patterns of feeding over an observed period. Future studies on Chaetognatha should consider such aspects.

This paper is the first proposal turned to the trophic ecology of Chaetognatha based on genetic data in Brazil. Although still costly, molecular analyzes constitute reliable and effective methods at scientific application, and can to establish relevant advance in assessing the complex relationships that make up the marine food chain.

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7 CONSIDERAÇÕES FINAIS

Os resultados gerados por esta Tese oferecem uma nova visão sobre o filo Chaetognatha, reunindo as publicações dos últimos setenta anos e estabelecendo um ponto inicial para sua investigação molecular em ambientes neríticos e oceânicos do Brasil. De maneira especial, esta Tese incluiu dados inéditos sobre a filogeografia e estrutura genética populacional de *Flaccisagitta enflata*, uma espécie numericamente dominante no oceano Atlântico, e que desempenha um papel fundamental na cadeia trófica marinha. Dados de diversidade intra e interespecífica também foram apresentados, com a inclusão de seis novas sequências da espécie *Parasagitta friderici*, até então não sequenciada quanto a genes mitocondriais. O marcador COI, amplamente difundido entre os metazoários, ainda foi utilizado na proposta de uma relação trófica entre Chaetognatha e um grupo relacionado à sua dieta.

Neste contexto, foi possível chegar às seguintes considerações:

1. O estudo de revisão indicou que menos da metade das espécies de Chaetognatha descritas para o Brasil são citadas com alta frequência. Esta questão evidencia a necessidade de que investigações possam ser direcionadas a ambientes ainda pouco explorados, como sistemas bentônicos e de maiores profundidades (> 200 m). Estes últimos, em especial, podem ainda ampliar a extensão da distribuição vertical conhecida de algumas espécies.

2. O uso do marcador COI constitui um método auxiliar eficaz à identificação tradicional de Chaetognatha, uma vez que dos 118 espécimes de *Flaccisagitta enflata* sequenciados a partir deste gene, 116 apresentaram correspondência espécie-especifica.

3. A diversidade genética de *F. enflata* foi em geral elevada, exibindo valores superiores à diversidade de outros quetognatos amplamente distribuídos, como *Eukrohnia hamata*.

4. A espécie *F. enflata* evidencia uma população panmítica no Atlântico Oeste Tro-

pical, algo esperado para um organismo holoplanctônico com baixas taxas de mutação ao longo de sua história evolutiva (540 M.A.). Contudo, as pequenas estruturações observadas sugerem menores níveis de conectividade, o que pode estar relacionado a alterações locais da circulação oceânica (banco submarino Guará) e à presença de uma barreira física limitante à migração da espécie (Porto do Recife).

5. A diferenciação genética aqui observada também reforça a premissa atual de que espécies holoplanctônicas nem sempre apresentam dispersão desenfreada, e que há uma necessidade cada vez mais crescente de reavaliação daquelas populações designadas como demograficamente abertas.
6. As estimativas demográficas ainda nos permitiram inferir que a hipótese de tamanhos populacionais estáveis não pode ser rejeitada para a maioria das localidades avaliadas (PR, FN, GS, RA and SPSPA). Estudos adicionais podem confirmar este resultado, buscando associá-lo às condições ambientais do Atlântico Tropical em uma escala evolutiva.
7. As variações genéticas intra e interespecífica nas espécies avaliadas reuniram valores superiores de diversidade em relação a muitos outros grupos animais. Isto é indicativo de populações numerosas, e respalda a hipótese de que Chaetognatha mantém baixos níveis de divergência atuais.
8. Técnicas moleculares também podem ser úteis em investigar aspectos ecológicos. Este contexto foi proposto no sexto capítulo, onde o marcador COI indicou duas sequências não equivalentes à identidade de *F. enflata*. Os dados obtidos indicaram maior correspondência com Scyphozoa, grupo que pode compor naturalmente a dieta de Chaetognatha. Uma relação trófica foi, assim, sugerida.

Os estudos compreendidos nesta Tese tiveram como objetivo principal expandir o conhecimento sobre um dos grupos mais abundantes e frequentes nos sistemas marinhos. Devido a sua ampla distribuição e grande importância ecológica, investigações que abordem aspectos ainda pouco explorados são de suma relevância. Como exposto, a aplicação da ferramenta molecular COI atendeu satisfatoriamente os objetivos propostos, o que pode incentivar seu uso em estudos futuros envolvendo Chaetognatha. A utilização combinada de marcadores (por ex., mitocondriais e nucleares) e o aumento do tamanho amostral também podem reforçar as investigações, ajudando a identificar e esclarecer os padrões filogeográficos das espécies. Espera-se que o presente trabalho ainda possa atuar como uma ferramenta de auxílio a estudos gerais sobre o zooplâncton, no tocante a aspectos de dispersão, diversidade, e conectividade genética estabelecidas no domínio pelágico.

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