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**Filogeografia e atividade alimentar do gênero *Ophioblennius* no oceano Atlântico**

Dissertação submetida ao Programa de Pós-Graduação em Ecologia da Universidade Federal de Santa Catarina para a obtenção do Grau de Mestre em Ecologia.

Orientador: Prof. Dr. Sergio Ricardo Floeter  
Co-orientador: Prof. Dr. Alberto Lindner

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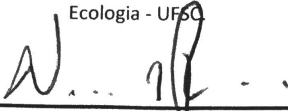
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**"Filogeografia e atividade alimentar do gênero *Ophioblennius* no oceano Atlântico"**

Por

**Naomi Silveira Lastrucci**

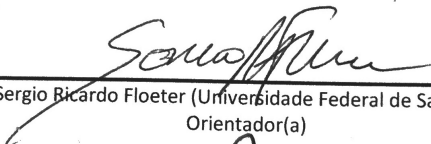
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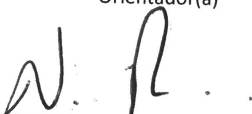
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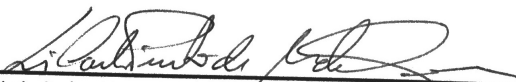
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An enormous thank you to Lucas, without whom most of this thesis would not have been possible. Thank you for all your hard work throughout this project: heading field trips, collecting samples and data, running statistical analyses, drawing maps, revising manuscript drafts, and overall helping me pull everything together. Thank you to the rest of my lab colleagues for all their support, especially to those who aided in making this project happen: to Júlia for helping me with the lab procedures and computer programs I needed to complete the genetic study; to Juan, Otavio, and Hugu for helping us collect fish and bite rate data; to Ana for helping me with phylogeographic analyses and explaining the concepts of connectivity; to Renato for offering useful suggestions to improve the project; and to Fiuza for providing information on the aquarium trade. Thank you to Anchieta for providing the data and fish collected from Bahia, and for accepting our invitation to be a coauthor of the paper. And thank you to Thiony Simon, who helped us immensely in the beginning of my Master's program and who played

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"Imagination is more important than knowledge. Knowledge is limited. Imagination encircles the world."  
Albert Einstein





## RESUMO

Apesar da importância dos estudos filogeográficos e ecológicos para a compreensão de processos biogeográficos, poucos estudos avaliaram esses aspectos simultaneamente para peixes recifais no oceano Atlântico. Este estudo analisou a filogeografia e estrutura populacional do gênero de peixe recifal *Ophioblennius* no Atlântico e Pacífico Leste através da amplificação de DNA mitocondrial citocromo b de indivíduos coletados em três regiões do Brasil e o anexo dos dados aos de estudos anteriores. Além do estudo filogeográfico foram conduzidas análises de taxas de mordida de *Ophioblennius* em sete sites do Atlântico para avaliar a influência de variações ambientais e morfológicas na sua atividade alimentar. Análises de filogeografia e estrutura populacional confirmaram que indivíduos da Bahia e de Fernando de Noronha pertencem à espécie *O. trinitatis*, mas a população de Santa Catarina, no sul do Brasil, foi identificada como uma espécie africana, até agora não descrita, registrada nas ilhas de São Tomé e Príncipe, no Golfo da Guiné. Esse resultado indica uma dispersão a longa distância pelo Atlântico com ocupação subsequente de um nicho desocupado no sul do Brasil. Taxas de mordida apresentaram uma correlação positiva com temperatura e inversa com tamanho corporal total, o que sugere uma influência de condições morfológicas e ambientais no metabolismo. Indivíduos de *Ophioblennius* parecem ser filogeograficamente bem diversificados com alta similaridade entre suas espécies, o que sugere uma adaptabilidade ecológica frente a variações em temperatura e comprimento total, uma vantagem que provavelmente facilitou seu estabelecimento ao longo do oceano Atlântico.

**Palavras-chave:** biogeografia, fluxo gênico, conectividade, taxas de mordida



## ABSTRACT

Despite the importance of phylogeographic and ecological studies in understanding biogeographic processes, few have evaluated both these aspects simultaneously for reef fishes in the Atlantic Ocean. This study analyzed the phylogeography and population structure of the reef fish genus *Ophioblennius* in the Atlantic and East Pacific through the amplification of cyt-b mtDNA from individuals collected in three regions of Brazil and the appending of the new data to that collected in previous studies. Aside from the phylogeographic study, an analysis of *Ophioblennius* bite rates was conducted in seven sites of the Atlantic evaluating the influence of morphological and environmental variations on its feeding activity. Phylogeographic and population structure analyses confirmed that individuals from Bahia and Fernando de Noronha belong to the northeastern Brazil species *O. trinitatis*, but the Santa Catarina population in southern Brazil identified as the yet unnamed African species also found in the São Tomé and Príncipe islands in the Gulf of Guinea, a result that reveals long distance dispersal across the Atlantic with subsequent occupation of an empty niche in southern Brazil. Bite rates were positively related to temperature and inversely related to individuals' total body size, suggesting an influence of morphological and environmental conditions on metabolism. *Ophioblennius* individuals appear to be phylogeographically well diversified with high ecological similarity among its species, reflecting an adaptability to variations in temperature and body length, an advantage which likely facilitated its establishment throughout the Atlantic Ocean.

**Keywords:** fish biogeography; gene flow; fish connectivity; fish bite rates



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# 1. INTRODUÇÃO

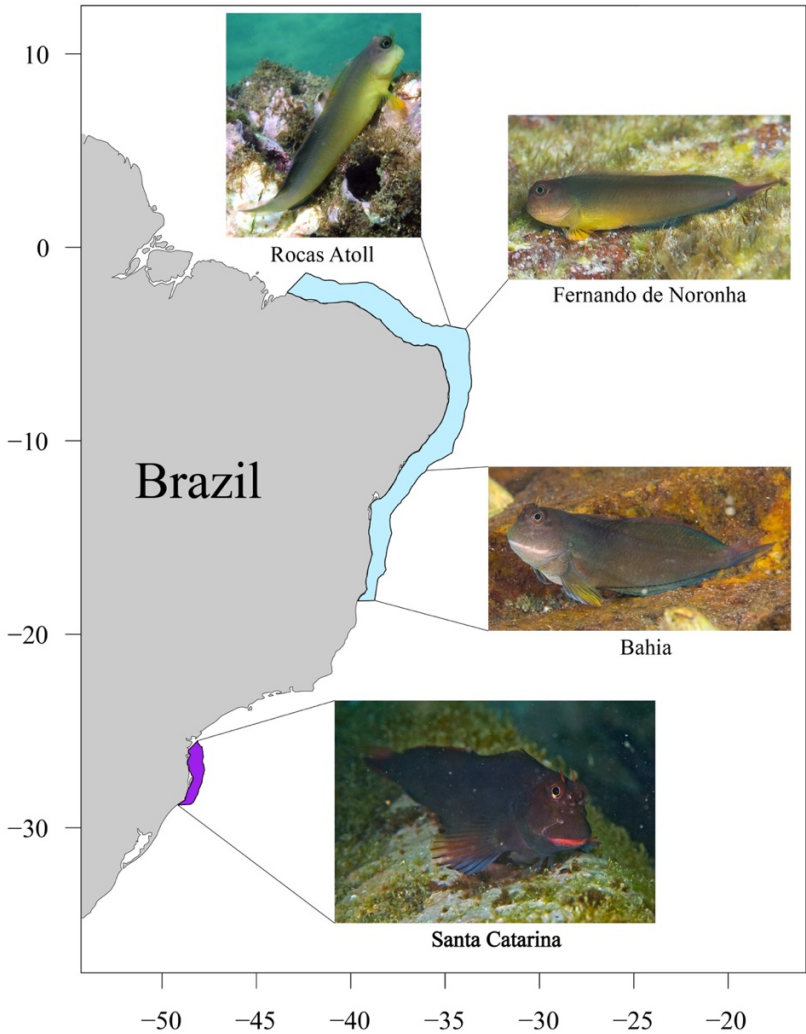
Para compreender os processos complexos que influenciam os padrões de biodiversidade na Terra, é importante levar vários conceitos biológicos em consideração. Em estudos de organismos marinhos, dois desses conceitos importantes são a filogeografia e a ecologia alimentar. Filogeografia se trata do estudo dos processos históricos que influenciam a distribuição geográfica contemporânea de indivíduos, realizado através de análises genéticas, principalmente genética de populações (AVISE, 2000). Um conceito filogeográfico importante é o de conectividade, que se trata da troca de indivíduos ou informação genética entre populações geograficamente separadas (COWEN et al., 2007). Enquanto isso, a ecologia alimentar estuda a relação entre indivíduos e seu alimento (GERKING, 1994), e dentre muitos aspectos da ecologia alimentar de um animal, a plasticidade ecológica é importante por se tratar da capacidade de um organismo de alterar a sua ecologia em resposta a variações ambientais (PRICE et al., 2003).

Estudos de filogeografia e conectividade genética de organismos recifais contribuem para o entendimento sobre os processos que influenciam a especiação e moldam a biogeografia nos oceanos. Com os avanços das análises genéticas nas últimas décadas, houve um aumento no número de estudos que tratam da conectividade populacional das espécies marinhas (JONES et al., 2007; BOWEN et al., 2016), pois esses são importantes para a conservação e manejo de recursos naturais (PALUMBI, 2003, 2004; JONES et al., 2007). Enquanto isso, estudos da plasticidade ecológica de espécies recifais (e.g. LIEDKE et al., 2016) são essenciais para complementar análises de conectividade, já que demonstram o potencial dos organismos para adaptação a uma dada amplitude de fatores ambientais através de suas variações morfológicas e comportamentais, o que conseqüentemente pode contribuir para a diversificação genética. Por exemplo, a hipótese da “taxa de especiação” é um de três mecanismos que explicam o efeito da energia na diversidade de espécies (MORA, 2015). Segundo essa hipótese, o aumento nas taxas de mutação e no metabolismo causado por temperaturas altas pode aumentar o polimorfismo e as taxas reprodutivas de organismos, respectivamente, o que favorecerá sua habilidade adaptativa e especiação (HARMELIN-VIVIEN, 2002). Porém, apesar de sua importância, são poucos os estudos que avaliam conjuntamente estes aspectos para peixes recifais no oceano Atlântico.

No Atlântico, a Província Brasileira se estende da desembocadura do rio Amazonas até a costa do estado de Santa Catarina, mais seus quatro conjuntos de ilhas oceânicas (FLOETER et al., 2008) e é composta por uma diversidade de condições bióticas (habitats recifais) e abióticas (temperatura da água; FLOETER et al., 2001; FERREIRA et al., 2004). A costa nordestina contém recifes biogênicos com temperaturas da água variando entre 24 e 29°C, enquanto as regiões costeiras do sudeste e do sul apresentam recifes rochosos e águas mais frias, entre 17 e 27°C (LONGO et al., 2014). As ilhas oceânicas apresentam recifes predominantemente rochosos (com exceção de Atol das Rocas, que apresenta recifes biogênicos) e suas águas variam entre 23 e 30°C de temperatura. Essa diversidade de fatores ambientais permite uma plasticidade ecológica de espécies recifais presentes ao longo da costa brasileira.

Um candidato exemplar para a avaliação da filogeografia e plasticidade ecológica no Atlântico é o gênero *Ophioblennius*, um peixe recifal presente ao longo do oceano Atlântico e no leste do Pacífico. Originalmente classificado como uma única espécie com duas subespécies, *O. atlanticus atlanticus* e *O. atlanticus macclurei* (SPRINGER, 1962; MUSS et al., 2001), o clado do Atlântico hoje se divide em cinco espécies (RANGEL; MENDES, 2009): *O. atlanticus* na Lusitânia (Açores, Madeira, e Canárias; BRIGGS; BOWEN, 2012) e em Cabo Verde, *O. macclurei* no Caribe, *O. trinitatis* na Província Brasileira, e duas espécies a serem descritas – uma em São Tomé e Príncipe no leste do Atlântico tropical e uma nas ilhas oceânicas de Ascensão e Santa Helena localizadas no meio do Atlântico.

No Brasil, populações de *Ophioblennius* ocorrem do nordeste (incluindo as ilhas oceânicas de Arquipélago de São Pedro e São Paulo, Fernando de Noronha, Atol das Rocas e Arquipélago de Trindade e Martim Vaz) até o sul de Santa Catarina (ANDERSON et al., 2015), com uma lacuna de distribuição entre o sul da Bahia e o norte de Santa Catarina onde poucos indivíduos e nenhuma população residente são conhecidos (obs. pess.; Fig 1).



**Figura 1** – Mapa da Província Brasileira mostrando a distribuição de populações de *Ophioblennius* do Nordeste (azul) e do Sul (roxo), com uma comparação visual de indivíduos.

Apesar da distribuição extensa do gênero e sua definição como consumidor primário, seus padrões alimentares continuam pouco conhecidos. O que se sabe é que indivíduos são diurnos, com adultos apresentando comportamento territorial com defesa agressiva de recursos contra outros peixes (MEDEIROS et al., 2014).

As espécies desse gênero são conhecidas por possuírem desova demersal, sendo que os ovos eclodem após cinco dias (MARRARO; NURSALL, 1983; ROBERTSON et al., 1990; MUSS et al., 2001) e possuem uma fase larval planctônica de aproximadamente 50 dias (LABELLE; NURSALL, 1992; MUSS et al., 2001). Indivíduos de *Ophioblennius* no Brasil parecem ser polimórficos, com dois morfotipos distintos observados (MENDES, 2007): adultos no Nordeste e nas ilhas normalmente atingem um comprimento máximo entre 4 e 10 centímetros (até 15 cm na Bahia) e apresentam coloração clara, enquanto adultos no Sul aparentemente atingem comprimentos entre 10 e 20 centímetros e apresentam uma coloração preta com faixas brancas na cabeça e boca vermelha (Fig 1). Apesar dessas marcantes diferenças morfológicas, ainda não está claro se essas populações são geneticamente e/ou ecologicamente distintas. Devido a essas variações intraespecíficas em *O. trinitatis* ao longo da costa brasileira e ilhas oceânicas, é necessária uma revisão completa do táxon (MEDEIROS et al., 2014). Portanto, uma comparação filogeográfica e ecológica de populações de *Ophioblennius* contribuirá ao entendimento de sua plasticidade ecológica e sua conectividade ao longo da costa brasileira.

## **Objetivos Gerais**

Os objetivos deste estudo são divididos em duas partes: uma filogeográfica e uma ecológica.

- Filogeográfica: realizar uma análise filogeográfica do gênero *Ophioblennius* no oceano Atlântico e no Pacífico Leste.
- Ecológica: avaliar a plasticidade ecológica do gênero *Ophioblennius* através de uma análise de sua atividade alimentar ao longo do Atlântico.

## *Objetivos específicos*

- avaliar a sua especiação e conectividade ao longo do oceano Atlântico;

- avaliar a sua conectividade ao longo da Província Brasileira (costa e ilhas oceânicas);
- comparar taxas de mordida entre populações do Atlântico; e
- avaliar a influência da temperatura e do tamanho na sua taxa alimentar.

### **Perguntas e Hipóteses**

1. Existe divergência genética entre populações de *Ophioblennius* do Nordeste e do Sul do Brasil?
  - Baseado na lacuna de distribuição na costa brasileira e a existência de dois morfotipos que diferem em tamanho e coloração, populações ao longo do Brasil possuem divergência genética entre o Nordeste e o Sul, mas ainda com conectividade alta o suficiente para não serem classificadas como espécies distintas.
2. Condições ambientais e morfológicas influenciam a atividade alimentar de *Ophioblennius*?
  - A atividade alimentar apresenta diferenças significativas entre populações devido a diferenças em condições ambientais (temperatura da água) e morfológicas (tamanho dos peixes).

## **2. CAPÍTULO ÚNICO / SINGLE CHAPTER**

### **FILOGEOGRAFIA E ATIVIDADE ALIMENTAR DO GÊNERO *OPHIOBLENNIUS* NO OCEANO ATLÂNTICO**

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### **PHYLOGEOGRAPHY AND FEEDING ACTIVITY OF THE GENUS *OPHIOBLENNIUS* IN THE ATLANTIC OCEAN**



*Targeted journal: Journal of Fish Biology*

**Phylogeography and feeding activity of the genus *Ophioblennius* in the Atlantic Ocean**

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## Abstract

This study analyzed the phylogeography and population structure of the reef fish genus *Ophioblennius* through the analysis of cyt-b mtDNA collected from individuals in the Atlantic and East Pacific. An analysis of *Ophioblennius* bite rates was also conducted in the Atlantic to evaluate the influence of morphological and environmental variations on the genus' feeding activity. Phylogeographic and population structure analyses confirmed that individuals from Bahia and Fernando de Noronha belong to the northeastern Brazilian species *O. trinitatis*, but the Santa Catarina population in southern Brazil was identified as the yet unnamed African species found in the São Tomé and Príncipe islands in the Gulf of Guinea, a result that indicates long distance dispersal across the Atlantic. Bite rates were positively related to temperature and inversely related to individuals' total body size, suggesting an influence of morphological and environmental conditions on metabolism. The *Ophioblennius* genus appears to be phylogeographically well diversified with high ecological similarity among species, reflecting adaptation to variations in temperature and size, an advantage which likely facilitated its establishment throughout the Atlantic Ocean.

**Keywords:** fish biogeography; gene flow; fish connectivity; fish bite rates

## Introduction

Studies of phylogeography and genetic connectivity of reef organisms contribute to the understanding of the dynamic processes that underlie speciation and shape the biogeography in the oceans. Such studies of marine connectivity have increased in recent decades (Jones et al. 2007, Bowen et al. 2016), as they are important tools for marine conservation and resource management (Palumbi 2003, Palumbi 2004, Jones et al. 2007). Studies of the ecological plasticity of reef species (e.g. Liedke et al. 2016), meanwhile, can serve to complement connectivity analyses by demonstrating the potential of organisms to adapt to a given range of environments through morphological and behavioral variations, which consequently may contribute to diversification. For example, the “speciation rate hypothesis”, one mechanism to explain the effect of energy on the diversity of species (Mora 2015), postulates that the rise in the rates of mutation and metabolism caused by higher temperatures will consequently increase the polymorphism and reproductive rates of organisms, respectively, favoring their adaptive ability and speciation (Harmelin-Vivien 2002). However, despite their importance, there are few examples of studies evaluating both aspects for reef fishes in the Atlantic Ocean.

In the Atlantic, the Brazilian Province extends from the mouth of the Amazon River to the coast of the state of Santa Catarina as well as its four oceanic islands (Floeter et al. 2008) and comprises a diversity of biotic and abiotic factors (Floeter et al. 2001, Ferreira et al. 2004). The northeastern coast consists of biogenic reefs with water temperatures ranging between 24 and 29°C, while the southeastern and southernmost coasts feature rocky reefs and colder waters ranging from 17 to 27°C (Longo et al. 2014). The oceanic islands feature rocky reefs (except Rocas Atoll, which features biogenic reefs) with water temperatures ranging between 23 and 30°C (Tyberghein et al. 2012). This diversity of environmental factors allows an ecological plasticity of reef species present throughout the Brazilian coast.

A good candidate for evaluating phylogeography and ecological plasticity in the Atlantic is the Redlip blenny, genus *Ophioblennius*, a reef fish present throughout the Atlantic as well as the East Pacific. Originally considered a single species divided into two subspecies, *O. atlanticus atlanticus* and *O. atlanticus macclurei* (Springer 1962, Muss et al. 2001), the Atlantic clade has since been divided into five species (Rangel &

Mendes 2009): *O. atlanticus* in Lusitania (Azores, Madeira, and Canaries; Briggs & Bowen 2012) and Cape Verde, *O. macclurei* in the Caribbean, *O. trinitatis* in the Brazilian Province, and two species yet to be described – one in São Tomé and Príncipe in the Tropical East Atlantic (TEA) and one in the Mid-Atlantic islands of Ascension and St Helena. In Brazil, *Ophioblennius* populations occur from the northeast (including oceanic islands) to the south of Santa Catarina (Anderson et al. 2015), with a distribution gap between the south of Bahia and the north of Santa Catarina where few individuals and no distinct populations occur (authors' pers. obs.).

Despite the genus' vast distribution and definition as a primary consumer, its feeding patterns remain overlooked. Individuals are known to be diurnal, with adults exhibiting territorial behavior by occupying permanent restricted home ranges (territories) with hostile defense of resources from intruder fishes (Medeiros et al. 2014). Their life history includes benthic eggs that hatch after five days (Marraro & Nursall 1983, Robertson et al. 1990, Muss et al. 2001) and a planktonic larval phase of approximately 50 days (Labelle & Nursall 1992, Muss et al. 2001).

Individuals of *Ophioblennius* in Brazil appear to be polymorphic, with two distinct morphotypes observed (Mendes 2007). Adults in the Northeast and oceanic islands normally reach a maximum length between 4 and 10 centimeters (up to 15 cm in Bahia) and are lightly colored, while adults in the South appear to reach lengths between 10 and 20 cm and are black in color with white stripes on the head and red mouths. Despite these marked differences, it is still unclear whether these populations are genetically and/or ecologically distinct. Intraspecific variations in *O. trinitatis* along the Brazilian coast and oceanic islands suggest that this taxon needs a thorough revision (Medeiros et al. 2014). Therefore, a phylogeographic and ecological comparison of *Ophioblennius* populations will contribute to the understanding of its ecological plasticity and its connectivity along the Brazilian coast.

This study aimed to conduct a phylogeographic analysis of *Ophioblennius* to infer speciation and connectivity throughout the Atlantic Ocean, with emphasis on its connectivity along the Brazilian coast. It also aimed to complement these findings with a study of the genus' ecological plasticity by comparing bite rates among Atlantic populations to evaluate the influence of environmental and morphological factors on feeding activity. The following hypotheses were tested: 1) that based on the sizable distribution gap on the Brazilian coast and the

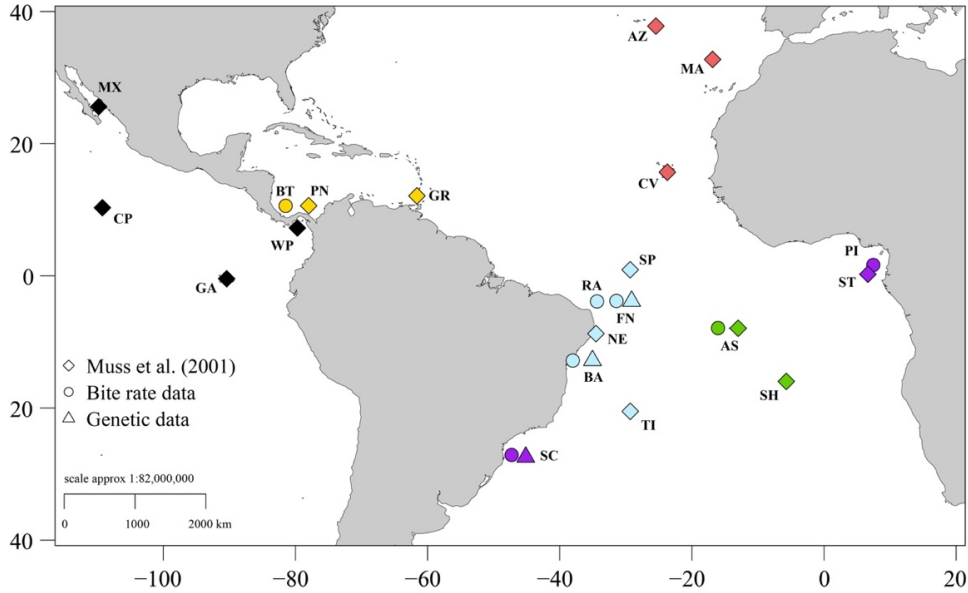
existence of two distinct morphotypes differing in size and coloration, populations in Brazil will exhibit genetic divergence between the Northeast and the South, but still possess a high enough connectivity not to warrant classification as separate species; and 2) that feeding activity will differ significantly among populations due to differences in environmental (water temperature) and morphological (total body length) conditions.

## **Materials and Methods**

### *Phylogeographic analysis*

Muscle tissue samples were collected from the right pectoral fin of *Ophioblennius* individuals in three locations: Santa Catarina, Bahia, and Fernando de Noronha. After collection, the tissue samples were stored in ethanol 96% for further analysis. For each tissue (individual), DNA was extracted using a Qiagen DNeasy Blood & Tissue kit and amplified using polymerase chain reaction (PCR) procedures. An 820-bp segment of mtDNA cytochrome b was amplified with two primers (Muss et al. 2001): a heavy-strand primer (5'-GTGATCTGAAAACCACCGTTG-3'; Song 1994) and a light-strand primer (5'-AATAGGAAGTATCATTGCGGT TTAGTG-3'; Taberlet et al. 1992). PCR amplifications were modified from Muss et al. (2001) and included an initial denaturing step at 94°C for 120 seconds, followed by 35 to 40 amplification cycles (94°C for 42 seconds, 54°C for 30 seconds, 72°C for 55 seconds) and a final extension at 72°C for 300 seconds.

Additional sequences of *Ophioblennius* cyt-b fragments from Muss et al. (2001) (including the Brazilian populations of NE Brazil, St. Paul's Rocks, and Trindade Island) were kindly provided by the authors for comparison with the new sequences in this study (Fig 1). DNA sequences were edited using Sequencher and aligned with ClustalX. A maximum-likelihood phylogeographic tree was attained through PhyML (Guindon et al. 2010) and constructed in PAUP 4.0 using 1000 bootstrap replicates. The most appropriate nucleotide substitution model was estimated using the Akaike Information Criterion (AIC) in jModelTest (Guindon & Gascuel 2003, Darriba et al. 2012). The Pacific species *O. steindachneri* was defined as the outgroup for the Atlantic clade (Muss et al. 2001).



**Figure 1** – Map indicating locations in the Atlantic and East Pacific where genetic and bite rate data were collected, including genetic sequences attained from Muss et al. (2001). Colors correspond to species as suggested by the haplotype analysis (see Results). AS = Ascension Island, AZ = Azores, BA = Bahia, BT = Bocas del Toro, CP = Clipperton, CV = Cape Verde, FN = Fernando de Noronha, GA = Galapagos, GR = Grenada, MA = Madeira, MX = Mexico, NE = Northeastern Brazil, PI = Príncipe Island, PN = Panama, RA = Rocas Atoll, SC = Santa Catarina, SH = St. Helena, SP = St. Paul's Rocks, ST = São Tomé, TI = Trindade Island, WP = West Panama.

Genetic connectivity among populations was evaluated using a haplotype analysis. A median-joining haplotype network was constructed in the software Network 4.6 using a dataset of *cyt-b* sequences. Populations were grouped and color-coded by region, with tones representing different populations within each marine biogeographic province: Brazil, Caribbean, Mid-Atlantic, East Atlantic, and Tropical Eastern Pacific (Floeter et al. 2008). Haplotype and nucleotide diversity were calculated in DnaSP 5.10 (Rozas et al. 2003), and population structure was evaluated through pairwise  $F_{st}$  and AMOVA (Weir & Cockerham 1984, Excoffier et al. 1992, Weir 1996) with Tajima's  $D$  (Tajima 1983) and Fu's  $S$  (Fu 1997) neutrality tests using Arlequin 3.5 (Excoffier & Lischer 2010).

### *Feeding activity*

Feeding activity was recorded in Brazil at four sites in Santa Catarina (Barra da Lagoa beach, Pântano do Sul beach, Xavier Island, and Taquaras beach), one site in Bahia (Porto da Barra), four sites in Fernando de Noronha (Conceição beach, Sancho Bay, Raquel, and Porto), and two sites in Rocas Atoll (Ancoras and Falsa Barreta). Data was collected in 2003 and 2007 from Fernando de Noronha, in 2009 from Bahia, in 2015 from Santa Catarina, and in 2016 from Rocas Atoll. Observations were carried out through free diving (snorkeling), always during the day from 1000 to 1500 hours, according to the feeding peak observed by Medeiros et al. (2014). Additional data for other species in the *Ophioblennius* clade was collected in 2002 from Bocas del Toro (*O. macclurei*), in 2015 from Ascension Island (henceforth referred to as *Ophioblennius* sp.As), and in 2016 from São Tomé and Príncipe islands (henceforth referred to as *Ophioblennius* sp.St) for comparison with the Brazilian populations (Fig 1). Separate sampling periods for summer (23.1–27°C) and winter (18–23°C) were conducted in Santa Catarina due to the variation in the mean water temperature between these seasons.

In each site, the focal-animal sampling method was used (Lehner 1996), which for this study consisted in following and observing a single individual for three minutes. To avoid possible interference in the feeding activity of each individual, the diver waited one minute before each observation for the fish to grow accustomed to their presence and subsequently followed at a minimum distance of two meters. For each individual, total length was visually estimated and the number of bites in

the substratum was counted. A bite was considered when the fish hit the substrate with its jaw open, regardless of further ingestion (Longo et al. 2014). Taking into consideration that *Ophioblennius* feed by taking several bites in quick succession between pauses (the “foray” mode), each bite was counted individually as opposed to considering bursts of quick bites as a single bite each. The number of bites a fish took in three minutes was considered its bite rate. Water temperature was recorded during the observation of each individual using a dive computer.

A generalized linear model (GLM) with Poisson distribution was used to evaluate the influence of temperature and individuals’ body length (TL) on feeding activity. Bite rates as categorized by region were compared using a notched boxplot to highlight the 95% CI of medians (Krzywinski & Altman 2014), with points used to represent the number of bites of each fish in each location. All analyses were performed using the packages “Scales”, “Vegan”, and “Car” from R software version 3.2.4 (R Core Team 2016).

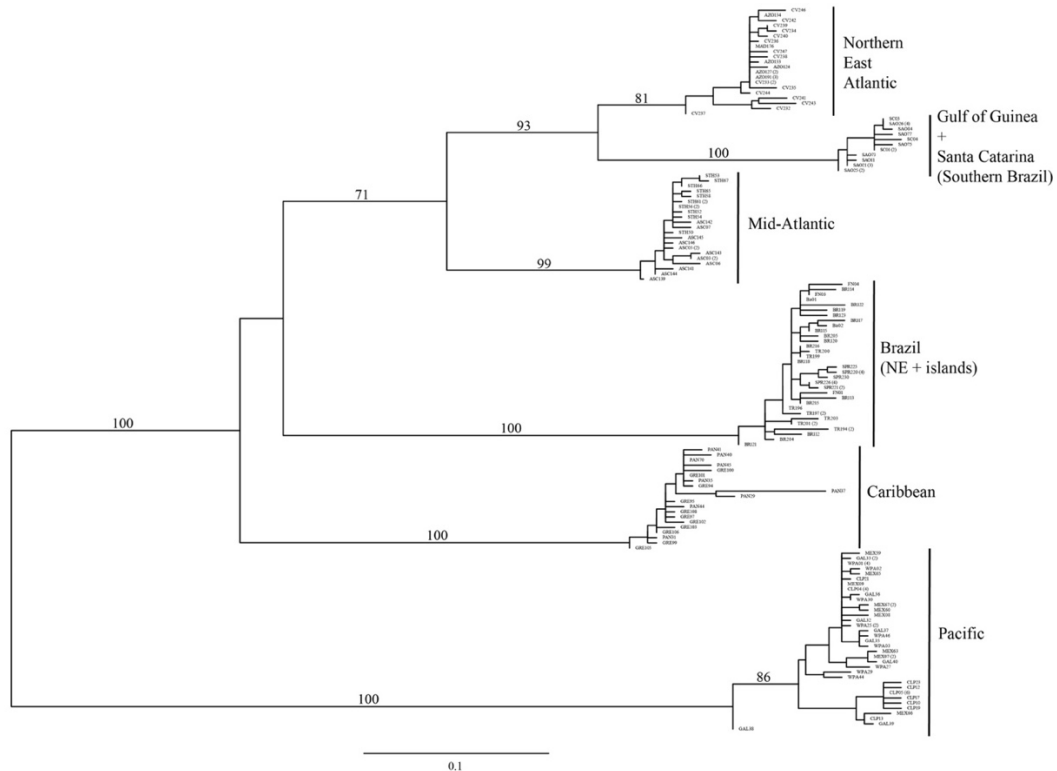
## Results

### *Phylogeography*

A total of 181 *Ophioblennius* sequences were analyzed after the addition of four Santa Catarina, two Bahia, and three Fernando de Noronha sequences obtained in this study. The latter sequences were edited to the same length used by Muss et al. (2001): “630 bp beginning 120 nucleotide sites from the tRNA glutamic acid region”. The most appropriate nucleotide substitution model was determined by jModelTest to be GTR.

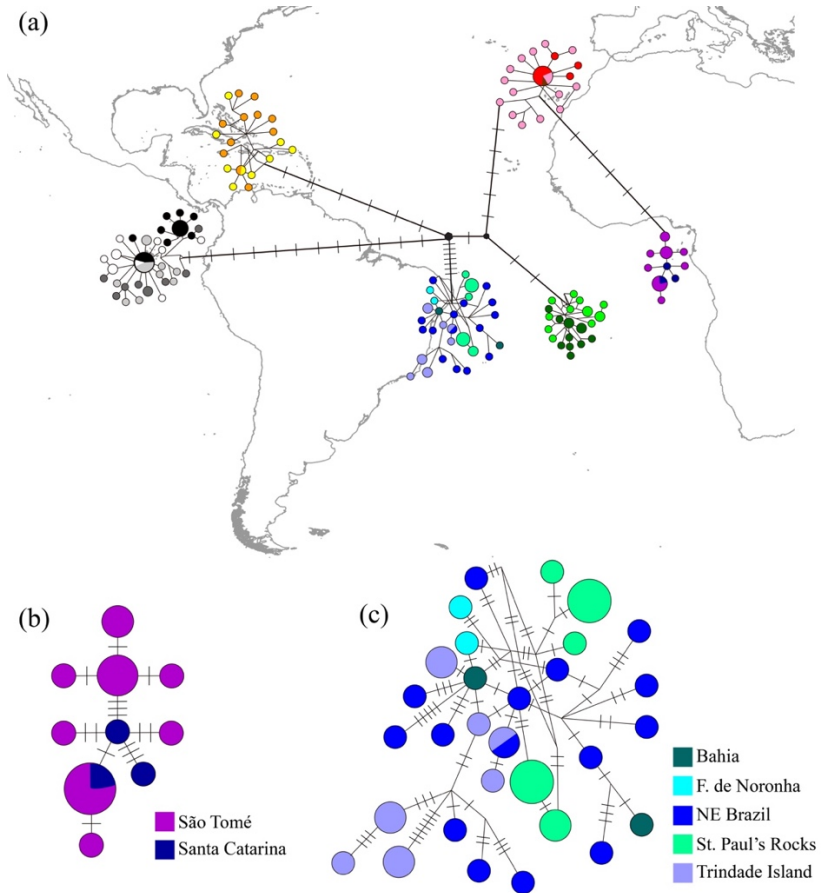
The phylogeographic analysis of *Ophioblennius* in the Brazilian Province revealed that northeastern Brazil (Fernando de Noronha, Bahia, NE Brazil, St. Paul's Rocks, and Trindade) constitutes a monophyletic group while the Santa Catarina population is closely related to the São Tomé and Príncipe species *Ophioblennius* sp.St (Fig 2). An 11% sequence divergence was observed between the Santa Catarina population and the *O. trinitatis* clade, most likely indicating the former is a separate species. Bahia and Fernando de Noronha showed no significant genetic distance from the Brazilian sequences analyzed by Muss et al. (2001). Bootstrap support for branches was considered robust at a minimum of 70% of the 1000 bootstrap replicates used.





**Figure 2** – Neighbor-joining tree of *Ophioblennius* mtDNA cytochrome b lineages. Phylogenetic nodes were evaluated using 1000 bootstrap replicates, and nodes with 70% support are indicated.

Two sequences shorter than 630 bp from the phylogeographic analysis were excluded from the haplotype study to avoid errors: one from Santa Catarina and one from Fernando de Noronha. The haplotype network of 179 individuals revealed 131 haplotypes across all regions (Fig 3), with high haplotype diversity and low nucleotide diversity observed in almost all regions (Table 1). The network shows a connection between Santa Catarina and São Tomé and Príncipe, with one haplotype shared between these regions. Bahia and Fernando de Noronha grouped into the northeastern Brazil region, with no haplotypes shared between these populations and those from the study conducted by Muss et al. (2001). Tajima's D and Fu's F averaged negative and statistically insignificant ( $p \geq 0.05$ ) for all populations (Table 1).



**Figure 3** – Median-joining haplotype networks based on *Ophioblennius* mtDNA cytochrome b sequences: a) all *Ophioblennius* haplotypes in the Atlantic and East Pacific, color-coded by region with different tones representing separate populations – East Pacific = black/gray/white, Caribbean = orange/yellow, Brazil = blue/blue-green, Mid-Atlantic = green, northern East Atlantic = red/pink/brown, Tropical East Atlantic = purple – and mutations between regions (one tick = approx. five mutations); b) São Tomé/Santa Catarina network with mutations between nodes (one tick = one mutation); c) Brazil network with mutations between nodes (one tick = one mutation).

**Table 1** – Summary statistics of *Ophioblennius* with the cytochrome b dataset: number of individuals (n), number of haplotypes (hd), nucleotide diversity ( $\pi$ ), haplotype diversity (h), Tajima's D, and Fu's F.

|                       | n  | hd | $\pi$  | h     | Tajima's D | Fu's F  |
|-----------------------|----|----|--------|-------|------------|---------|
| <b>Brazil</b>         |    |    |        |       |            |         |
| Bahia                 | 2  | 2  | 0.0048 | 1.000 | 0.000      | 1.099   |
| F. de Noronha         | 2  | 2  | 0.0064 | 1.000 | 0.000      | 1.386   |
| NE Brazil             | 15 | 15 | 0.0104 | 1.000 | -1.586     | -10.067 |
| Santa Catarina        | 3  | 3  | 0.0042 | 1.000 | 0.000      | -0.341  |
| St. Paul's Rocks      | 12 | 5  | 0.0052 | 0.803 | 0.963      | 1.004   |
| Trindade              | 10 | 7  | 0.0106 | 0.933 | 0.846      | -0.054  |
| <b>Caribbean</b>      |    |    |        |       |            |         |
| Grenada               | 11 | 11 | 0.0065 | 1.000 | -1.119     | -8.031  |
| Panama                | 9  | 9  | 0.0128 | 1.000 | -1.227     | -3.380  |
| <b>Mid-Atlantic</b>   |    |    |        |       |            |         |
| Ascension Island      | 13 | 11 | 0.0070 | 0.974 | -1.036     | -5.163  |
| St. Helena            | 12 | 10 | 0.0044 | 0.970 | -1.254     | -6.207  |
| <b>East Atlantic</b>  |    |    |        |       |            |         |
| Azores                | 9  | 4  | 0.0014 | 0.583 | -1.610     | -1.283  |
| Cape Verde            | 16 | 15 | 0.0116 | 0.992 | -1.444     | -7.594  |
| São Tomé and Príncipe | 14 | 8  | 0.0054 | 0.890 | -0.422     | -1.570  |
| <b>Pacific</b>        |    |    |        |       |            |         |
| Clipperton            | 17 | 9  | 0.0121 | 0.846 | 0.488      | 0.679   |
| Galapagos             | 9  | 8  | 0.0131 | 0.972 | -1.149     | -1.469  |
| Mexico                | 11 | 9  | 0.0119 | 0.964 | -1.126     | -1.605  |
| West Panama           | 13 | 9  | 0.0077 | 0.910 | -1.347     | -1.848  |
| <b>Mean</b>           |    |    |        |       | -0.6124    | -2.4690 |
| <b>SD</b>             |    |    |        |       | 0.8508     | 3.4925  |

Based on the results of the haplotype network, populations were grouped according to probable species division for the population structure study: *O. atlanticus* (Azores, Cape Verde, and Madeira), *O. macclurei* (Grenada and Panama), *O. trinitatis* (Bahia, Fernando de Noronha, NE Brazil, St. Paul's Rocks, and Trindade), *Ophioblennius* sp.As (Ascension Island and St. Helena), *Ophioblennius* sp.St (São Tomé and Príncipe and Santa Catarina), and *O. steindachneri* (Clipperton, Galapagos, Mexico, and West Panama). The AMOVA results indicate that most of the genetic variability in *Ophioblennius* mtDNA corresponds to differences among species, which account for 89.88% of the variation in this genus (Table 2). Estimated genetic differentiation was 0.899 among groups (Fct), 0.233 among populations within groups (Fsc) and 0.922 within populations (Fst), with all values being statistically significant ( $p < 0.001$ ; Table 2).

**Table 2** – Analysis of molecular variance (AMOVA) used to estimate genetic differentiation among groups (Fct), among populations within groups (Fsc) and within populations (Fst). Populations were evaluated by species, with Santa Catarina grouped with São Tomé and Príncipe based on the haplotype network results.

|                                 | AMOVA |
|---------------------------------|-------|
| Among groups                    | 89.88 |
| Among populations within groups | 2.36  |
| Within populations              | 7.76  |
| $\Phi_{sc}$                     | 0.233 |
| $\Phi_{st}$                     | 0.922 |
| $\Phi_{ct}$                     | 0.899 |

Pairwise Fst comparisons of the six Brazilian populations reveal that the five northeastern populations have relatively low Fst values in relation to each other but high Fst values in relation to Santa Catarina (Table 3). When compared to São Tomé and Príncipe, Santa Catarina returned a low Fst value (Fst = 0.127). Bahia and Fernando de Noronha both showed negative Fst values in relation to each other (Fst = -0.167) and NE Brazil (BA = -0.123, FN = -0.037), low Fst values in relation to Trindade (BA = 0.216, FN = 0.196), and intermediate Fst values in relation to St. Paul's Rocks (BA = 0.468, FN = 0.437). Fst values in Brazil were statistically insignificant ( $p \geq 0.05$ ) for all Fernando de Noronha and Bahia

comparisons except with St. Paul’s Rocks. Santa Catarina Fst values were statistically significant ( $p < 0.05$ ) for comparisons with NE Brazil, St. Paul’s Rocks, and Trindade, but statistically insignificant for the comparison with São Tomé and Príncipe.

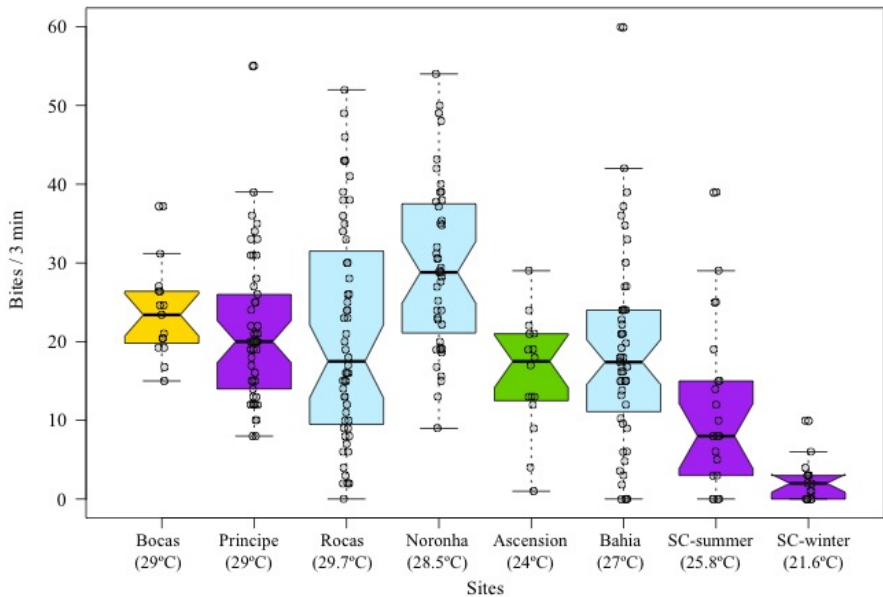
**Table 3** – Pairwise Fst values for all populations of Brazil and the Gulf of Guinea: Fernando de Noronha (FN), Bahia (BA), NE Brazil, St. Paul’s Rocks (SPR), Trindade Island (Trin), Santa Catarina (SC), and São Tomé and Príncipe (ST&P).

|           | FN     | BA     | NE Brazil | SPR   | Trin  | SC    |
|-----------|--------|--------|-----------|-------|-------|-------|
| BA        | -0.167 | –      |           |       |       |       |
| NE Brazil | -0.037 | -0.123 | –         |       |       |       |
| SPR       | 0.437  | 0.468  | 0.302     | –     |       |       |
| Trin      | 0.196  | 0.216  | 0.134     | 0.393 | –     |       |
| SC        | 0.952  | 0.958  | 0.909     | 0.951 | 0.910 | –     |
| ST&P      | 0.948  | 0.951  | 0.925     | 0.949 | 0.929 | 0.127 |

*Feeding activity*

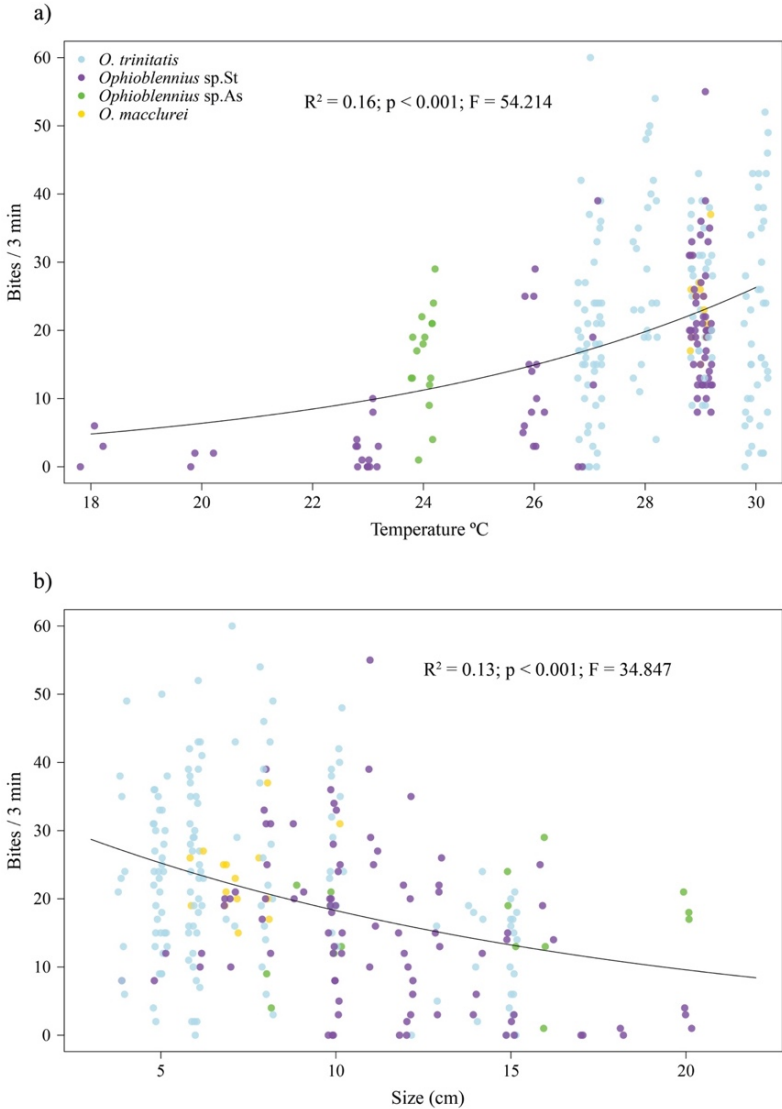
The bites of 269 individuals across seven regions were counted. An average ( $\pm$ SE) of 18.4 ( $\pm$ 1.9) bites/3 min were counted in Bahia, 11.6 ( $\pm$ 2.3) in Santa Catarina in summer and 2.2 ( $\pm$ 0.6) in winter, 29.6 ( $\pm$ 1.6) in Fernando de Noronha, 20.9 ( $\pm$ 1.9) in Rocas Atoll, 15.9 ( $\pm$ 1.8) in Ascension Island, 23.5 ( $\pm$ 1.5) in Bocas del Toro, and 21.2 ( $\pm$ 1.3) in São Tomé and Príncipe.

Bite rates did not differ among regions, although there was a noticeable influence from water temperature and individuals’ total body length (Fig 4). The only apparent difference in feeding activity was a lower average feeding rate observed in Santa Catarina in winter in relation to all other populations.



**Figure 4** – Bite rates of *Ophioblennius* populations in the Atlantic. Colors correspond to species: purple = *Ophioblennius* sp.St; blue = *O. trinitatis*; green = *Ophioblennius* sp.As ; yellow = *O. macclurei*. Each point corresponds to the number of bites of an individual observed in that region.

The GLM analysis revealed a tendency towards a positive correlation between water temperature and bite rates (Fig 5a; adj  $R^2 = 0.16$ ,  $p < 0.001$ ), and towards a negative correlation between size and bite rates (Fig 5b; adj  $R^2 = 0.13$ ,  $p < 0.001$ ).



**Figure 5** – Scatterplot with generalized linear model (GLM) analyses of bites in relation to a) mean water temperature (in °C) and b) total body length (in cm). Each point represents an individual.



## Discussion

This study is the first to show that Brazilian populations of *Ophioblennius*, previously believed to be a single species (i.e. *O. trinitatis*) widely distributed from northeastern to southern Brazil and the oceanic islands, in fact belong to two distinct species. The species *O. trinitatis* occurs in northeastern Brazil and the four oceanic islands, while populations from Santa Catarina, southern Brazil, belong to the species that occurs in São Tomé and Príncipe in the Gulf of Guinea, Africa.

The presence of the same *Ophioblennius* species in Africa and in southern Brazil may be due to natural larval dispersal across the Atlantic Ocean, although other processes cannot be ruled out. After a phylogeographic gap between northeastern and southern Brazil was established, it was then determined whether their ecological patterns were distinct as well by comparing feeding activity among *Ophioblennius* populations along the Brazilian Province.

Santa Catarina individuals are red-lipped and notably larger than their northeastern neighbors, suggesting they might also exhibit different feeding patterns. Differences in bite rates (Fig 4) may be related to differences in average water temperature, which may also influence total body length (Choat & Robertson 2002). Temperature tends towards being directly proportionate and body length towards being inversely proportionate to bite rates (Fig 5). Phylogeographic differences have no apparent influence on the feeding activity of *Ophioblennius* species. Instead, bite rates appear to be influenced primarily by the environmental condition of temperature.

### *Phylogeography*

The presence of an African species in southern Brazil may be attributed to at least four factors: 1) transportation of fish or larvae across the Atlantic via ship ballast water or attachment to oil platforms, 2) rafting on floating objects (e.g. Hoeksema et al. 2012), 3) release of *Ophioblennius* individuals through the aquarium trade, and 4) natural dispersal of larvae across the Atlantic.

Gobies and blennies may be particularly apt to dispersal and invasion via ballast-water transport due to their nature as crevice-dwelling fishes (Wonham et al. 2000). However, cases of blenny invasions via this means are not well represented in the literature. Introduction via oil platforms

(Falcón et al. 2015) is unlikely as there is no direct transportation from São Tomé and Príncipe to Santa Catarina. However, there has been at least one documented blenny invasion via oil platforms in the case of *Parablennius pilicornis*, which invaded the Tristan da Cunha archipelago by occupying encrustations of dead barnacle shells (Wanless et al. 2010), so this means of invasion cannot be completely ruled out for *Ophioblennius*. Invasion via the aquarium trade is also an unlikely explanation, as this fish is not considered “appealing” and has no documented sales in Brazil (pers. comm. with Fiuza, T. M. J.).

This study proposes that the best explanation for the presence of an African *Ophioblennius* species in southern Brazil is either natural larval dispersal or rafting across the Atlantic. *Ophioblennius* larvae have a planktonic phase of approximately 50 days (Labelle & Nursall 1992, Muss et al. 2001), which would allow them sufficient time to traverse the Atlantic and settle in Brazil. Long distance dispersal events from east to west have been suggested for other Atlantic reef fishes, such as *Chromis limbata*, with a probable pelagic larval duration (PLD) of 18–19 days (Anderson et al. in prep); *Acanthurus monroviae* (Moura 2000, Luiz et al. 2004), with a possible PLD of 45–70 days (Horta e Costa & Gonçalves 2013); *Aulostomus strigosus* (Bowen et al. 2001), with a PLD of approximately 93 days (Bowen et al. 2006); *Epinephelus marginatus* (Heemstra 1991), with a PLD of 20–40 days (Andrello et al. 2013); and *Parablennius pilicornis* (Bath 1977), with a PLD of approximately 33 days (Beldade et al. 2007).

Muss et al. (2001) suggested that the *Ophioblennius* clade originated in the East Pacific/West Atlantic region, and that dispersal from the West to the East Atlantic may have occurred through three possible routes: (1) the North Atlantic Gyre; (2) the Equatorial Undercurrent; or (3) the South Atlantic Gyre. The authors hypothesize that *Ophioblennius* larvae are likely endowed with enough thermal tolerance to survive in the cold current (20°C) between Brazil and Africa, a distance which could be traversed in 35–105 days (Scheltema 1971) or even 43–70 days (Chesher 1966), theoretically within the larval duration of the genus. Therefore, the Gulf of Guinea may have been colonized by *Ophioblennius* larvae from the Caribbean, forming a new species *Ophioblennius* sp. St that subsequently traversed the Atlantic again on the South Equatorial Current and successfully occupied an empty niche in the south of Brazil. However, due to limited sampling in Santa Catarina, it is not yet possible

to infer this route of migration; thus far, the less likely migration route from Santa Catarina to the Gulf of Guinea cannot be ruled out.

Anderson et al. (in prep) also proposed the above three hypotheses in their study to explain the presence of the Eastern Atlantic damselfish *Chromis limbata* in southern Brazil, and concluded that “natural colonization seems to be the most likely explanation”. Though this study proposes the same explanation for the *Ophioblennius* observations, further understanding of potential blenny invasions via ship ballast water transportation of adults is required before this explanation can be dismissed.

The new Bahia and Fernando de Noronha sequences generated herein are, as expected, included in the northeastern Brazil clade previously determined by Muss et al. (2001), confirming that these populations are part of the species *O. trinitatis*. This finding is consistent with the morphological similarities observed among individuals in Bahia, Fernando de Noronha, and northeastern Brazil, particularly light brown coloration and smaller average body size compared to individuals in southern Brazil. The difference in species observed between northeastern and southern Brazil is corroborated by the gap observed between Bahia and Santa Catarina where no populations of *Ophioblennius* occur.

The Caribbean-to-Brazil pattern found in this study’s maximum-likelihood tree contrasts with the Brazil-to-Caribbean pattern found by Muss et al. (2001) in their parsimony tree. However, despite a lack of bootstrap support for either tree, an ancestral Caribbean scenario is believed to make more sense (pers. comm. with Bowen, B. W.).

Although population structure could not be thoroughly determined for Santa Catarina, Bahia, and Fernando de Noronha due to a small sampling size (i.e.  $n = 2$  for BA,  $n = 2$  for FN,  $n = 3$  for SC), the analysis in this study shows that the haplotype and nucleotide diversities observed among these populations follow the same tendencies as the analysis carried out by Muss et al. (2001): high haplotype diversity with low nucleotide diversity. The expectation of a broader study of these populations would be a similar pattern of high haplotype diversity and low nucleotide diversity, indicating a recent population expansion after a period of relatively low effective population size in both Brazilian species, as the rapid population growth would favor the retention of new mutations (Grant & Bowen 1998). This hypothesis may be corroborated by the negative, albeit statistically insignificant, values of Tajima’s  $D$  and Fu’s  $F$ , which indicate a potential recent population expansion. It may

also be explained by the haplotype network (Fig 3), in which several haplotypes are exclusive to one individual and few haplotypes are shared among populations within regions. The shared haplotype between the Santa Catarina and São Tomé and Príncipe populations suggests a recent colonization.

The AMOVA results point to higher genetic variation of *Ophioblennius* mtDNA among regions than among or within populations. The pairwise  $F_{st}$  analysis supports the evidence of a recent migration of *Ophioblennius* between the São Tomé and Príncipe region and Santa Catarina. The negative  $F_{st}$  values observed among Bahia, Fernando de Noronha, and NE Brazil indicate no population structure in this region, while the higher  $F_{st}$  values of these populations in relation to St. Paul's Rocks and Trindade Island indicate low to intermediate population structure in Brazil's oceanic islands.

### *Feeding activity*

The noticeable influence of water temperature on the feeding rates of *O. trinitatis* supports the hypothesis that feeding activity could be influenced by environmental factors and morphological traits (Barneche et al. 2009). The higher bite rates observed in warmer waters suggests that a rise in temperature is directly proportionate to an increase in metabolism (Clarke & Johnston 1999), which could stimulate a greater feeding frequency in individuals. Similar patterns have been observed in other reef fish species, such as the blenny *Parablennius pilicornis* (Mendes et al. 2009), the ocean surgeonfish *Acanthurus bahianus* (Floeter et al. 2005), and damselfishes of the genus *Stegastes* (Barneche et al. 2009), particularly the Brazilian damselfish *Stegastes fuscus* (Aued 2012). In all these studies, feeding rates are significantly greater in areas of higher mean water temperature, corroborating the direct influence of temperature on the metabolism of thermo-dependent organisms (Clarke & Johnston 1999; Schmidt-Nielsen 2002).

Differences in bite rates of the Santa Catarina population between summer and winter further supports the hypothesis of water temperature's influence on feeding activity. Though only adults ( $\geq 10\text{cm}$ ) were observed for both seasonal periods in this region, the summer data (23.1–27°C) yielded higher feeding frequencies than the winter data (18–23°C). The warmer waters in summer likely accelerate the metabolism of the fish and stimulate them to feed on substrate more often (Barneche et al. 2009),

while in colder winter waters their limited energy seems to be conserved for the defense of their territorial resources. This agonistic behavior was observed in the field during this study: within the three-minute observation period, many adults observed in winter directed more bites towards intruding fish than towards the substrate within their territories.

These results are also consistent with the hypothesis of body length influence on feeding activity. Smaller juvenile fish exhibit high metabolism and are inclined to feed more frequently to continue growing before they settle into permanent territories (Barneche et al. 2009). Larger adults, on the other hand, exhibit a lower metabolism and appear to concentrate more of their energy on agonistic behavior (i.e. territorial defense). A negative correlation between body size and bite rates was also found in the genera *Stegastes* and *Pomacentrus* (Barneche et al. 2009), which corroborates the expectation that a lower specific metabolism ( $O_2$  consumption/mass/time) in larger individuals will cause them to exhibit lower feeding activity than smaller individuals, regardless of temperature (Yager & Summerfelt 1993).

All *Ophioblennius* species in the Atlantic are geographically separate; no two species coexist in sympatry, indicating that they originated via geographic isolation and remained isolated, with no migration (except possibly between Africa and Santa Catarina). However, although their feeding rates may vary within species (see *Ophioblennius* sp.St in Fig 4), they remain similar across geographical regions with similar water temperature (Fig. 4). It can be speculated that the ecological behavior of *Ophioblennius* changed little following speciation, perhaps due to the lack of sympatry between congeners, a different scenario compared to other reef fish genera in which multiple congeners or closely related species coexist in reefs and develop distinct feeding habits, e.g. *Stegastes* (Robertson 1995) and *Haemulon* (Rocha et al. 2008, Pereira et al. 2014).

This study confirms that the genus *Ophioblennius* is highly diversified in the Atlantic, and shows that there is no connectivity between the northeastern and southern regions of Brazil. A thorough description of the São Tomé and Príncipe species *Ophioblennius* sp.St, as well as the redefinition of the Santa Catarina *Ophioblennius* from *O. trinitatis* to the newly described species in the Gulf of Guinea, is recommended. The new population structure data in this phylogeographic study, when compared to the analysis conducted by Muss et al. (2001), follows the same pattern of low genetic differentiation within regions (or,

more accurately, clades, when the Santa Catarina population is grouped with the African *Ophioblennius* sp.St as opposed to the Brazilian *O. trinitatis*). The bite rates in the genus *Ophioblennius* indicate, at the same time, high similarity among its species at similar temperatures, but high variation within a single species at different temperature regimes, which may reflect adaptation to a broad range of variations in temperature and body size, an advantage which may have facilitated its distribution and establishment throughout the Atlantic Ocean.

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### 3. CONSIDERAÇÕES FINAIS

Populações de *Ophioblennius* ocorrem em todo o oceano Atlântico e na região leste do Pacífico, sendo que o clado do Atlântico se divide em cinco espécies de acordo com as províncias biogeográficas, segundo a literatura (MUSS et al., 2001). Porém, este estudo confirma que existe uma exceção a esse padrão: a presença de uma espécie africana no sul da Província Brasileira. O clado de *O. trinitatis* no nordeste do Brasil consiste de um grupo monofilético, que inclui Bahia e Fernando de Noronha, enquanto a população de Santa Catarina é geneticamente mais próxima à população de São Tomé e Príncipe. A análise de estruturação populacional corrobora os resultados filogeográficos, indicando que existe conectividade populacional entre as populações do nordeste do Brasil e entre Santa Catarina e São Tomé e Príncipe. Santa Catarina também compartilha um haplótipo com São Tomé e Príncipe, o que indica que essa migração é um evento recente.

O estabelecimento dessa população em Santa Catarina pode ter ocorrido através de três meios: 1) transporte de peixes ou larvas pelo Atlântico via água de lastro ou plataformas de petróleo, 2) *rafting* por objetos flutuantes, 3) invasão pelo comércio de aquário, e 3) dispersão larval natural pelo Atlântico. A invasão da espécie pelo comércio de aquário teoricamente pode ser descartada como explicação devido à atual falta de registros de vendas desse peixe no Brasil. Peixes blenídeos podem ser mais adaptados para dispersão e invasão associados aos cascos e incrustações de navios devido ao seu hábito de ocupar fendas nas rochas (WONHAM et al., 2000), porém casos de invasão de blenídeos por esse meio ainda não estão bem documentados. Além disso, larvas de *Ophioblennius* provavelmente teriam dificuldade em sobreviver nas condições de água de lastro por tempo suficiente para atravessar o Atlântico. Porém, existe pelo menos um caso documentado de invasão do blenídeo *Parablennius pilicornis* via plataforma de petróleo (WANLESS et al., 2010); portanto, não podemos descartar completamente esse meio de invasão como hipótese para *Ophioblennius*. A explicação mais provável para o estabelecimento dessa população em Santa Catarina é a dispersão larval natural ou *rafting* do golfo da Guiné até o sul do Brasil pela Corrente Equatorial Sul, seguido do estabelecimento em um nicho desocupado em Santa Catarina. As larvas de *Ophioblennius* sobrevivem por até 50 dias, o que permitiria que atravessassem o Atlântico dentro dos

períodos de viagem estimados de 35 a 105 dias (SCHELTEMA, 1971) ou 43 a 70 dias (CHESHER, 1966).

O estudo ecológico de *Ophioblennius* indica que as diferenças observadas na atividade alimentar entre populações são influenciadas pela temperatura média da água e pelo comprimento total dos indivíduos, o que apoia a nossa hipótese. A taxa elevada de mordidas no verão comparado com inverno em Santa Catarina também apoia a hipótese sobre a influência da temperatura da água na atividade alimentar de *Ophioblennius*. Indivíduos de *Ophioblennius* se alimentam através de várias mordidas rápidas no substrato entre pausas, um método chamado “foray”, e esses hábitos alimentares são consistentes por todo o gênero, o que indica que o modo de alimentação não é um fator que influencia as diferenças na atividade alimentar observadas neste estudo.

A influência da temperatura na atividade alimentar de *Ophioblennius* apoia a hipótese de que o aumento de temperatura é diretamente proporcional ao aumento na taxa metabólica (CLARKE; JOHNSTON, 1999), o que estimula um aumento na taxa de mordidas dos peixes. Os resultados ecológicos também apoiam a hipótese da influência de comprimento total na atividade alimentar; peixes juvenis apresentam um metabolismo mais elevado em relação a adultos, portanto juvenis tendem a se alimentar com maior frequência, enquanto adultos, além de apresentarem uma taxa alimentar menor devido ao seu metabolismo reduzido, também concentram parte de sua energia em atividade agonística para defesa territorial.

Todas as espécies de *Ophioblennius* no Atlântico são geograficamente separadas; não existe caso em que duas espécies coexistam em simpatria, indicando que se originaram via isolamento geográfico. Porém, apesar do seu comportamento ecológico variar de acordo com temperatura da água e tamanho corporal, ele permanece semelhante ao longo de regiões geográficas. Podemos supor que o comportamento ecológico de *Ophioblennius* permanece constante devido à falta de simpatria entre espécies, um cenário diferente ao de outros gêneros de peixe recifal, em quais várias espécies coexistem em recifes e desenvolvem hábitos alimentares distintos (e.g. *Stegastes*, *Haemulon*, *Sparisoma*, etc.).

A partir desse estudo, concluímos que o gênero *Ophioblennius* é bastante diversificado no Atlântico, sem conectividade filogeográfica entre as regiões nordeste e sul do Brasil, o que contraria as nossas expectativas. Recomendamos uma descrição completa da espécie de São

Tomé e Príncipe *Ophioblennius* sp.St, como também a redefinição da espécie de Santa Catarina de *O. trinitatis* para essa nova espécie descrita no golfo da Guiné. Os dados de estruturação populacional observados neste estudo parecem seguir o mesmo padrão da análise de Muss et al. (2001) de baixa diferenciação genética entre clados, porém outros estudos com amostragem maior seriam necessários para confirmar este resultado. O clado apresenta uma amplitude elevada na sua atividade alimentar diante de grandes variações de temperatura e comprimento, o que indica uma vantagem de alta adaptabilidade que pode contribuir à sua especiação no oceano Atlântico.

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