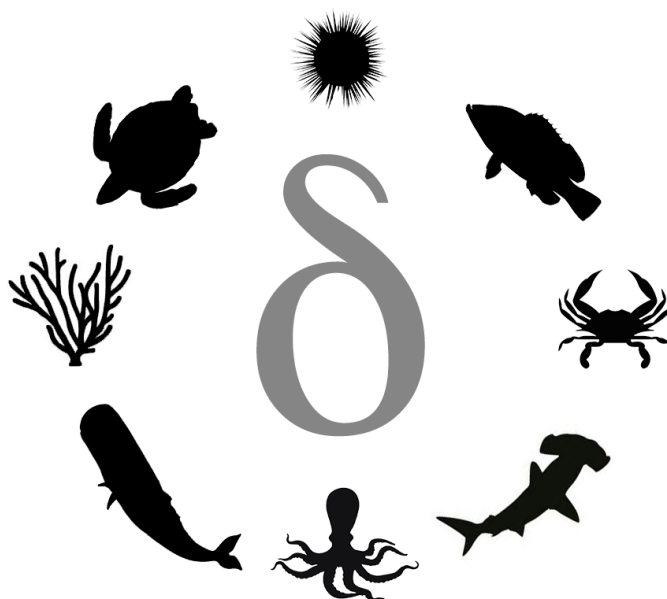


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CENTRO DE CIÊNCIAS HUMANAS E NATURAIS
PROGRAMA DE PÓS GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS



**Nicho e endemismo em ambientes entremarés
recifais: uma abordagem utilizando isótopos
estáveis**

Ryan Carlos de Andrades

Vitória
2018

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Ryan Carlos de Andrades

Orientador: Dr. Jean-Christophe Joyeux
Co-orientador: Dr. Tommaso Giarrizzo

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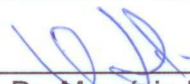
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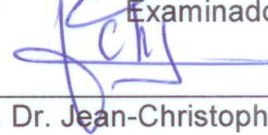
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"The fate of remote islands is rather melancholy, even after one has made allowances for all the human excellence that has remained or developed again in some of them after our invading civilizations settled down. The reconstitution of their vegetation and fauna into a balanced network of species will take a great many years. So far, no one has even tried to visualize what the end will be."

Charles S. Elton há 60 anos atrás.

"Se quiser buscar realmente a verdade, é preciso que pelo menos um vez em sua vida você duvide, ao máximo que puder, de todas as coisas."

René Descartes

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RESUMO

Embora o conceito de nicho ecológico possa variar de acordo com o campo da ecologia estudado, sua essência constitui em entender a forma que organismos vivem sob distintas condições bióticas e abióticas. Nesta tese eu procuro, por meio do estudo da estrutura das comunidades e uso da técnica de isótopos estáveis, compreender a forma que organismos marinhos coexistem em recifes entremarés. Os estudos foram conduzidos em seis ambientes entremarés insulares e costeiros da Província Brasileira: Atol das Rocas, Fernando de Noronha e Trindade representando ilhas oceânicas, e Salinópolis (Pará), Jericoacoara (Ceará) e Anchieta (Espírito Santo) representando ambientes costeiros. Os capítulos da tese revelam progressivamente a importância e organização ecológica destes ambientes. Assim, o primeiro capítulo faz uma breve introdução do tema da tese, seguido pelo segundo que destaca a elevada taxa de endemismo de peixes nos recifes entremarés de ilhas, ressaltando a fragilidade deste ambiente e de suas espécies endêmicas frente a impactos pontuais e crônicos. O terceiro capítulo consiste em um estudo da estrutura das comunidades de peixes dos seis sítios, revelando que todas as comunidades foram dominadas em composição e número por espécies de pequeno porte e adaptadas à vida no entremarés. Em ilhas, espécies endêmicas foram as mais representativas, sendo responsáveis pela estruturação das comunidades e sua distribuição esteve correlata a diferentes variáveis estruturais. O quarto capítulo faz uso de análises isotópicas de $\delta^{13}\text{C}$ e $\delta^{15}\text{N}$ para evidenciar, através de modelagens, que as teias tróficas nas ilhas são mais longas e complexas, e que as espécies criptobênticas do entremarés, incluindo espécies endêmicas, são as mais vulneráveis à pressões de competição intra e interespecíficas. O quinto capítulo é voltado ao estudo dos impactos esperados em ilhas após invasão por uma espécie exótica. Para tal, usou-se dados de densidade e assinaturas isotópicas na zona costeira para simular a presença do invasor nas ilhas. Embora grande parte das espécies demonstraram ser fracas competidoras frente a uma potencial invasão, a vulnerabilidade das espécies endêmicas à presença da espécie invasora chama a atenção devido às baixas capacidades de competição e pelo restritos territórios de vida. O sexto capítulo reporta a morte por dessecação de espécies residentes e não-residentes do entremarés, ressaltando as rigorosas pressões abióticas deste ambiente sobre sua fauna. Por fim, o sétimo capítulo é uma nota técnica apresentando relações peso-comprimento e comprimento-comprimento de peixes das ilhas estudadas, inclusive de espécies endêmicas da Província Brasileira, publicado afim de contribuir com futuros trabalhos na elaboração de estimativas precisas de biomassa. Em suma, o nicho em ambientes entremarés recifais das ilhas oceânicas brasileiras revela, pela primeira vez, comunidades com elevados níveis de diversidade trófica e de seus recursos basais, mas ao mesmo tempo frágeis no que diz respeito ao seu elevado endemismo, à vulnerabilidade competitiva de suas espécies endêmicas, à presença de espécies invasoras e ao risco de desaparecimento frente à subida do nível do mar.

Palavras-chave: Nicho isotópico, poças de marés, SIBER, *Omobranchus punctatus*

ABSTRACT

Although the concept of ecological niche can vary according, its essence lies in understanding the fit of organisms living under specific abiotic and biotic conditions. This thesis examined the coexistence of marine organisms using stable isotopes from an Eltonian niche view, though many aspects also cover Grinnellian and Hutchinsonian perspectives. The surveys were conducted in six oceanic and coastal intertidal environments of the Brazilian Province: Rocas Atoll, Fernando de Noronha and Trindade Island and Salinópolis (Pará state), Jericoacoara (Ceará state) and Anchieta (Espírito Santo state) representing three oceanic and three coastal sites, respectively. The chapters hereafter reveal the importance and ecological functioning of intertidal habitats from a niche and endemism perspective. The first chapter is an introductory chapter, whereas the second highlights the high fish endemism rates found worldwide in oceanic islands intertidal environments, drawing attention to the fragility of this ecosystem. Chapter three is a fish community structure study, which reveals the dominance of intertidal communities by small-sized and resident species. Also, endemic species were abundant in the islands and key to structuring communities. The fourth chapter evidenced through modeling spatial data and stable isotopes analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) that food chains in islands are longer and more complex than in coastal sites and that cryptobenthic species are the most vulnerable species to intra and interspecific competition pressures. Chapter five focused on the potential impacts of an invasive species on island intertidal reef communities. Invader density data and stable isotopes signatures in coastal sites were used to simulate the impact on the islands. We verified that mostly intertidal species are vulnerable to a hypothetical invasion, however endemic species vulnerability is especially worrisome due to low competition resistance and small life territory. The sixth chapter reports on the unexpected death by desiccation of resident and non-resident intertidal fishes, highlighting the harsh conditions that these species experience. Chapter seven presents a set of length-weight and length-length relationships for Brazilian island fishes, including endemics. Summarizing, the niche performed by intertidal species revealed, for the first time, island communities to have high trophic diversity and rich resources at the base of the food chain and endemic species fragility in face of imminent biological invasions and sea-level rise.

Key words: Isotopic niche, tidepool, SIBER, *Omobranchus punctatus*

CAPÍTULO 1

INTRODUÇÃO GERAL

Nicho ecológico compreende um termo bastante utilizado no campo da biologia, no entanto suas definições e abordagens podem variar de acordo com o conceito assinalado por diferentes autores na literatura clássica (Soberón 2007, Peterson et al. 2011). Em termos gerais, o nicho Grinnelliano (Grinnell 1917) diz respeito a distribuição das espécies e os requerimentos ambientais necessários para tal, enquanto o nicho Eltoniano enfatiza as interações bióticas, ou seja, as competições intra e interespecífica, e a predação, como as principais forças determinantes do nicho ecológico de uma espécie (Elton 1927). Na segunda metade do século 20 diversos autores inspirados nos trabalhos de Joseph Grinnell e Charles Elton propuseram novas definições, inserções e adequações ao conceito de nicho ecológico (Udvardy 1959, Van Valen 1965, Alley 1982). O trabalho de George E. Hutchinson se destaca pela unificação das abordagens de nicho e em sua proposta de hipervolumes de n-dimensões, levando em conta os requerimentos ambientais e interações biológicas das espécies (Hutchinson 1957, 1978).

Por ser um conceito amplo com definições muitas vezes ambíguas, sua aplicação se mostrou difícil e seu uso foi, durante um tempo, ignorado em diversos trabalhos no campo da ecologia (Chase & Leibold 2003). No entanto, recentes revisões e abordagens acerca do tema colocaram novamente o nicho ecológico em perspectiva, e como um dos principais temas a ser abordado no que diz respeito a distribuição de espécies e interações biológicas (Chase & Leibold 2003, Soberón 2007, Peterson et al. 2011). Neste sentido, a presente tese engloba o nicho ecológico em suas diferentes abordagens, utilizando isótopos estáveis como ferramenta para elucidar padrões tróficos de ocupação de nichos e competição entre espécies. Adicionalmente, o papel de espécies endêmicas, principalmente em ambientes insulares, é inserido no contexto de nicho a fim de ressaltar o papel ecológico e a vulnerabilidade de tais espécies que compreendem um grupo único no que diz respeito a matriz de biodiversidade de ambientes naturais (Lamoreux et al. 2006).

Os capítulos dessa tese estão organizados de forma a informar a razão do presente trabalho ter sido desenvolvido no ecossistema entremarés e sua vulnerabilidade face a perturbações naturais e não-naturais (Capítulo 2), a distribuição das espécies de peixes, seus requerimentos ambientais e o papel das espécies endêmicas das ilhas em entremarés recifais da Província Brasileira (Capítulo 3), o nicho isotópico e a competição intra e interespecífica em ambientes entremarés (Capítulo 4), o impacto em ambientes entremarés oceânicos e a vulnerabilidade de

suas espécies endêmicas frente a uma potencial presença de uma espécie invasora (Capítulo 5), a inesperada fragilidade de espécies do entremarés frente as severas flutuações naturais deste ambiente (Capítulo 6) e o fornecimento de novas métricas de relações morfológicas essenciais para estimativas robustas de biomassa e tamanho de espécies endêmicas e residentes do entremarés da Província Brasileira (Capítulo 7).

Mais especificamente, o Capítulo 2 trata-se de uma *Letter* publicada no periódico *Science* onde a escolha pelo ecossistema entremarés é justificada a partir da constatação de sua elevada vulnerabilidade a impactos (e.g. mudanças climáticas e aumento do nível do mar) e, em contrapartida, por abrigar uma elevada taxa de endemismo de peixes em ambientes entremarés insulares, quando comparado ao endemismo destes locais considerando todos seus ambientes (entremarés e infralitoral). O Capítulo 3 (em formato de submissão para a revista *Scientific Reports*) estuda a estrutura da comunidade de peixes de seis ambientes entremarés, sendo três costeiros e três oceânicos, revelando o papel fundamental de espécies endêmicas como estruturadoras de comunidades de poças de marés e as variáveis ambientais determinantes para a distribuição das espécies sob uma abordagem de nicho Grinnelliana.

O Capítulo 4 (em formato de submissão para a revista *Ecology Letters*) utiliza de análises de isótopos estáveis ($\delta^{13}\text{C}$ e $\delta^{15}\text{N}$) para investigar aspectos do nicho Hutchinsoniano e Eltoniano. O capítulo fornece uma determinação da teia trófica e o nicho da comunidade de ambientes entremarés recifais costeiros e oceânicos considerando desde produtores primários a consumidores de topo. Adicionalmente, dados de densidade e assinaturas isotópicas foram utilizados para construir modelos preditivos de competição intra e interespecífica entre peixes do entremarés. O Capítulo 5 (em formato de submissão para a revista *Marine Ecology Progress Series*) aborda uma das questões centrais no que tange a extinção de espécies endêmicas e impactos a comunidades nativas insulares, a invasão de espécies. Neste capítulo foi simulada a presença de *Omobranchus punctatus*, uma espécie de pequeno porte invasora de águas costeiras do Atlântico oriunda do Indo-Pacífico, e investigado seu potencial nicho em uma hipotética invasão aos ambientes oceânicos da Província Brasileira e seu impacto sobre as espécies endêmicas das ilhas. As métricas utilizadas neste capítulo foram similares as utilizadas para mensurar a competição no Capítulo 4.

O Capítulo 6 trata-se de uma publicação no periódico *Journal of Applied Ichthyology*, onde é relatado diferentes eventos de mortandade de peixes do entremarés devido a dessecação, os quais são inesperados dado a natureza resistente às flutuações ambientais das espécies do entremarés. Ao total são cinco espécies registradas, sendo que duas dessas (nove indivíduos) pertencentes as famílias Gobiidae e Blenniidae, as quais possuem adaptações morfológicas e fisiológicas para suportarem o estresse ambiental presente no ambiente em que vivem. O Capítulo 7 consiste em uma nota técnica publicada também no periódico *Journal of Applied Ichthyology* e encerra a tese fornecendo dados de relações peso-comprimento e comprimento-comprimento de nove espécies (seis endêmicas) das ilhas da Província Brasileira. Todas as relações apresentadas são inéditas para a ciência.

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CAPÍTULO 2

FRINGE ON THE BRINK: INTERTIDAL REEFS AT RISK

Letter publicada no periódico Science

National Council for Science and Technology (CONACYT) and other prominent figures in the S&T establishment, as well as leaders of major industry organizations, had provided the government with a detailed plan for implementing these long-overdue S&T policy changes (4). However, as Peña Nieto's term draws to a close, funding of Mexican S&T development has been disappointingly low.

The first 3 years of Peña Nieto's term were promising. The president called annual meetings of the rarely convened General Council for Scientific Research, Technological Development, and Innovation (5), and S&T federal expenditure increased to about 0.6% (6)—an improvement, even if still far short of the promised 1%. However, over the next 2 years, the overall budget for S&T was reduced (to 0.5% of the gross domestic product) and the budget allocated to CONACYT decreased more than 25% (7). The scarce funds earmarked for S&T were invested in industrial innovation, leaving little support for S&T projects at universities and research centers. As a result, current basic research projects are at risk of shutting down, and the number of fellowships for graduate students stopped growing for the first time in 25 years (8). Students who had hoped for a career in science have started to look elsewhere.

President Peña Nieto still has an opportunity to place the nation back on the path toward a knowledge-based economy. Innovative technologies developed by industry and basic research conducted in academia play complementary roles in strengthening the intellectual wealth of a country, and equivalent resources should be allotted accordingly. If the 2018 federal budget for S&T receives a substantial increase, and particularly, if CONACYT's budget was recovered from the drastic cut suffered this year, it could both mitigate the current S&T emergency and set a precedent for future administrations.

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Fringe on the brink: Intertidal reefs at risk

The rocky areas between low and high tide, known as intertidal reef habitats, are one of the most at-risk marine ecosystems (1, 2) as a result of coastal urbanization, sewage, and fisheries (2). Although they provide essential ecological services to society, such as shoreline protection, carbon uptake, tourism, and recreation (2), intertidal reefs are usually omitted from discussions of anthropogenic impacts and conservation planning, even those focused on the current crisis of reef environments. Anthropogenic climate change and sea-level rise could soon lead to the disappearance of endemic species in these fringe habitats (3).

Intertidal reefs on oceanic islands often host more endemic species than the surrounding waters. In Brazil's oceanic islands of Rocas Atoll, Fernando de Noronha, and Trindade, endemism levels for intertidal tidepool fishes (38.5 to 44.4%) are substantially higher than for the whole ichthyofauna each of these oceanic islands

harbors (4.5 to 9.6%) (4, 5). Similar patterns are found elsewhere, from Hawaii, where endemism in intertidal fishes is 32% (compared with 25% overall) (6), to Australia and New Zealand, where it reaches 64% and 61.7%, respectively (7–9).

In tropical regions, many endemic intertidal or shallow-water fishes have only been described in the past 10 years, and many more species are likely yet to be found. From parasites to fishes to migratory birds, a broader species set becomes increasingly vulnerable as water levels rise and intertidal zones are submerged. As we invest time and money in surveys of the deep ocean, we must not forget that the centimeters-deep water on the coast also needs protection.

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The intertidal reef of Brazil's island of Fernando de Noronha is home to a wealth of endemic species.

PHOTO: GLOBAL_PICS/ISTOCKPHOTO

CAPÍTULO 3

ENDEMIC FISH SPECIES STRUCTURING OCEANIC INTERTIDAL REEF ENVIRONMENTS

Artigo submetido ao periódico *Scientific Reports*

Title**Title Page**

Endemic fish species structuring oceanic intertidal reef environments

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Abstract

Intertidal reef environments are facing a global crisis as climate changes are causing sea-level rise. Synergistically, other human-induced impacts (e.g., sewage, habitat loss) caused by concentration of human population proximity to shore enhance the natural vulnerability of intertidal ecosystem. However, the effect these threats coupled with a limited knowledge of some aspects of intertidal fish ecology have long been neglected. Here, we tested whether oceanic intertidal fish communities differ from coastal ones using standardized sampling methods applied in tidepools of three oceanic and three coastal sites in the tropical southwestern Atlantic (Brazilian Province). Oceanic intertidal fish communities were distinctly structured at the trophic and composition levels. The noteworthy endemism species rate (38%, 39% and 44%) and high densities in oceanic intertidal habitats were supported by resident species restricted to mid and high-shore tidepools in which herbivores were the major trophic group while carnivores dominated mainland sites. Physical (substrate type, pool height, subtidal distance and rock coverage), biological (sessile animal coverage) and chemical (salinity) parameters act as the driving forces influencing fish spatial occupancy. Here, clear evidences of high fish endemism and importance of endemics structuring oceanic communities may act as the last straw in favor to oceanic intertidal reef conservation.

Introduction

An extraordinary characteristic of the marine life is its high diversity estimated above one million species¹. However, likewise to terrestrial ones, indiscriminate use of marine ecosystems and resources has been promoting changes in biota²⁻⁵, massively impacting communities structure and ecosystem services⁵⁻⁷. In this context, reef environments (e.g., coral and rocky reefs) are pointed out as one of priority habitats for conservation (MPAs - marine protected areas as example of effort) planning to ensure support to biodiversity and reef services such as fish stocks maintenance, carbon uptake, tourism and shoreline protection^{8,9}.

Intertidal reef habitats are located at the land-ocean interface and provide the same essential ecological services than other reef types¹⁰. Surprisingly, they have been neglected or minimized in discussions involving management and conservation planning to solve, or at least mitigate, the reef environmental crisis^{5,11-13}, even when recognizing that the intertidal ecosystem is probably one of most impacted ecosystem in the marine realm^{5,13}. Their vulnerability arises from easy access, proximity of urban areas, intensive use in tourism, harvesting activities and sea level rise. Compounding factors include characteristically short displacements by small-sized species with strong site fidelity and specialized habitat requirements^{14,15} and use as nursery grounds for ecologically and commercially important species¹⁶⁻¹⁹, replenishing adult fish populations in subtidal habitats^{18,20}.

Intertidal fishes present diverse life strategies, living all (i.e., permanent residents) or part of their life cycle (i.e., secondary residents and transient species) in tidepools^{21,22}. The structural complexity, partial isolation and species richness of tidepools can be used as proxy to assessment of a wealth ecological and anthropic impacts scenarios to gain more understanding of marine systems over time^{10,23,24}. Intertidal environments are good templates to study marine systems because it is possible to measure community metrics (i.e., density or biomass) in an actual tridimensional data (volume). Among other benefits is the efficient record of all fish taxa, including small-sized and cryptic species - important links between lower and high trophic levels²⁵ - which are underestimated during subtidal fish samplings (e.g., visual censuses,²⁶).

During its isolation from the sea, tidepool water greatly varies, in temperature, salinity, pH and dissolved oxygen, and this variation is closely related to pool characteristics such as height in relation to sea level, substrate nature, benthic cover,

superficial area and volume ¹⁰. The combination between water parameters and pool characteristics strongly influences the distribution of fish species in the intertidal space and the fish community structure in each tidepool ^{19,27,28}. In tropical habitats, a most-important role in structuring fish communities is expected to be played by biotic interactions while in temperate habitats the wider fluctuations in abiotic conditions would structure community seasonally ²⁹. However, the distribution patterns of tropical tidepool fishes may be dependent of substrate characteristics ³⁰ and sub-tropical and temperate tidepool fishes may present diel variations and variability in habitat use to avoid intra and inter-specific competition and predation ^{27,31–33}. These contrasting findings point out the necessity of more tidepool studies to understand how the interactions between biotic and abiotic factors structure fish communities.

In comparison to continental shelves, oceanic environments have received little attention due to isolation and logistic challenges. However, the number of island studies has been growing substantially during the last decades, with endemism emerging as a key feature shaping island community ecology ^{34–37}. Although progress has been made, many aspects of oceanic intertidal fishes (*e.g.*, evolution, systematics and ecology) remain poorly known ^{16,18,19,38}. Thus, we address intertidal fishes in oceanic and coastal tidepools to test whether fish communities (*i.e.*, taxonomic and trophic structure) differ between regions and determine the importance of a wide habitat features and taxonomic factors acting as structuring drivers these communities. Additionally, we evidence the structuring role of endemic species in oceanic communities and discuss the evolutionary aspects of successful colonization of this group. Concomitantly, we provide new data for tidepool fish communities in two non-studied MPAs in the South Atlantic, the only atoll in the South Atlantic (Rocas Atoll) and Fernando de Noronha Archipelago.

Results

Community structure

Fifty-nine taxa belonging to 21 families were sampled, 28 in the coastal region (Salinópolis, Jericoacoara and Anchieta) and 35 in the oceanic region (Rocas, Noronha and Trindade) (Supplementary Table S1). Endemism levels were noteworthy in oceanic sites, 39% (7 of 18 species) for Rocas, 44% (8 of 18 species)

for Noronha and 38% (5 of 13 species) for Trindade and remarkably higher than the total reef fish endemism (subtidal and intertidal) (Figure 1).

Communities differed significantly between coastal and oceanic regions (ANOSIM Global $R = 0.5$; $p < 0.01$) and among sites (ANOSIM Global $R = 0.7$; $p < 0.01$; all pairwise ANOSIM with $p < 0.05$). In addition, SIMPER analysis evidenced that endemic species strongly structured intertidal communities in oceanic sites (Figure 2). As expected from ANOSIM results, nMDS ordination segregated pools between regions (Figure 3A) and, not as distinctively, among sites within regions (Figure 3B).

Trophic groups predominance were dissimilar between oceanic and coastal regions (ANOSIM Global $R = 0.2$; $p < 0.01$) indicating prevalence of herbivores in oceanic habitats and carnivores in coastal ones. In fact, trophic groups differed in density and biomass in both regions (Kruskall-Wallis; $p < 0.05$; Figure 4). Except for biomass in the coastal region, the two main trophic groups (carnivores and herbivores) within each region differed significantly (Mann-Whitney; $p < 0.05$). When trophic groups were segregated into subcategories (feeding habits), territorial herbivores (THER) and mobile invertebrate feeders (MINV) were predominant among herbivores and carnivores, respectively.

Patterns of tidepool species use

Multivariate regression tree (MRT) indicated seven explanatory variables structuring intertidal fish fauna: Region, Sessile animal coverage, Subtidal distance, Substrate, Rock coverage, Pool height and Salinity (Figure 5). Variance explained by the tree was 56%, individual splits explained 18% (Region), 10% (Animal coverage), 6% (Subtidal distance), 6% (Substrate), 6% (Rock coverage), 5% (Pool height) and 5% (Salinity). MRT Error was low (0.443), CV Error was 0.726 and SE 0.075. The first two axes of Principal Component Analysis accounted for 47.74 and 21.7 of between-groups sums of squares. Axes intersplit correlations were high (0.93 and 0.86), which confirmed the strong species-environment variables relationship, including for endemic taxa.

Discussion

Endemism and herbivory are key factors that guide composition and trophic structure of oceanic intertidal fish communities in SW Atlantic islands. This

contrasts with previous findings on reef fishes in general, mainly based on studies at Rocas, such that community structure in oceanic and coastal sites differ due to high density of planktivorous fishes at islands ^{39,40}. The rarity or absence of effective planktivores in tidepools at islands and elsewhere ^{41,42} may let one of the other trophic groups to take the lead. To matching their distribution to prevailing conditions, the prevalent trophic groups can also require tracking the changes and adaptive solutions to occur in determined environment. Changes in environment conditions exist and may impose exceeding steep adaptive gradients to biota. For example, the higher feeding pressure of herbivores in oceanic islands, compared to coastal sites, was related to high density and biomass of territorial herbivores *Entomacrodus* species and *Ophioblennius trinitatis*. The colonization success of these combtooth blennies in intertidal oceanic ecotones may be explained by an adaptive set of physiological, morphological and behavioral traits to life under intertidal harsh conditions (e.g., high temperature and salinity changes, wave impact and desiccation risk) ^{19,38,43,44}. In addition, this family comprises many amphibious species ⁴⁵. According to recent findings ⁴⁵, repeated evolution of amphibious behavior in fish is directly related to the successful colonization of novel environments. The intertidal zone offers optimal conditions to expose fishes to a dual, aquatic and terrestrial, life through the oscillation of tides. The rockskippers *Entomacrodus* along many Blenniidae and a number of Gobiidae can emerge from water under abiotic (e.g., water temperature, dissolved oxygen and pH) or biotic pressure (e.g., competition or predation) surviving on dry ground during a significant period of time if necessary ^{46,47}. Under these conditions, fishes may avoid dehydration using crevices or under algae ^{15,48,49}, although desiccation cannot always be avoided ⁴⁴.

However, colonization and permanency in oceanic islands is more complex than in contiguous habitats, requiring successful larval dispersion and recruitment that are partly dependent upon island features such as isolation, area, age and sea-level fluctuations ⁵⁰. In our study, intertidal gobiids are absent from the most isolated island, Trindade ¹⁸, including the intertidal/shallow-water, widespread and iconic frillfin gobies *Bathygobius*. Several species of the family, none intertidal, are present in subtidal reefs ⁵¹. A recent study concerning isolation and evolution on Trindade Island tidepool fishes¹⁸ hypothesized that *Bathygobius* reproductive traits such as parental care, adhesive demersal eggs and short pelagic larval duration (PLD) may

limit long-distance dispersal from the continental shelf 1,200 km away (but probably much less during the Pleistocene). On the other hand, in blenniids, long PLDs (49 days and over 1,000 km in *Ophioblennius atlanticus*,⁵²) may partly explain the presence of *Entomacrodus* sp. and *Ophioblennius trinitatis* in all Brazilian islands. However, *Tomicodon* sp. is abundant in Trindade even with Gobiidae having shorter PLDs than Gobiidae⁵³, suggesting other factor(s) than PLDs or Pleistocene stepping-stones are associated to *Bathygobius* absence in Trindade. Further studies involving ecological traits and genetic structure of Gobiidae may help elucidate this issue.

Our data support the prediction that intertidal environments in oceanic islands of the southwestern Atlantic are mainly structured by endemic reef fish species. Direct comparisons of most abundant species in subtidal and intertidal habitats also clearly evidenced the importance of endemics in the intertidal. For instance, in Trindade the most abundant species in subtidal habitats are non-endemics *Cephalopholis fulva*, *Melichthys niger* and *Thalassoma noronhanum*⁵⁴, whereas in tidepools the endemics *Entomacrodus* sp. and *Malacoctenus brunoi* are two of the three most abundant species. Also, endemic taxa were related to several environmental variables showing a wealth of adaptations to live in intertidal waters. In Rocas and Noronha, endemics *Bathygobius brasiliensis* and *Scartella itajobi* were associated to water salinities regimes in tidepools, while in Trindade niche habitat requirements to endemics seems related to pool height to *Entomacrodus* sp. and *Malacoctenus brunoi*.

Unlike the noticeable oceanic intertidal importance, while tidepools are one of the easiest marine ecosystems to access and study in oceanic islands, they have remained, neglected. For instance, there is only one published work on tidepool fish communities in any south Atlantic oceanic islands¹⁸, compared to a number of works on subtidal reef fish communities^{53,52,54,55}. Additionally, resident small-sized species in general inhabit a small territory or are restricted to sparse rocky shores. Such species are highly vulnerable to local impacts such as oil spill, commercial exploitation and recreational activities. Endemic populations in oceanic islands are especially at risk since their extent of occurrence is restricted to a shallow fringe around the islands. Logistics involved in monitoring, if not creating, marine protected areas of -or starting at- intertidal habitats are straightforward and probably relatively cheap in comparison to other marine habitats. Here, high fish endemism in

intertidal reef environments present as a ubiquitous pattern worldwide ^{13,27} reaching over to 60% in Australia and New Zealand ^{22,57,58}. Sea-level rise associated to climate changes and local anthropogenic impacts (e.g., sewage, reef trampling and organisms removal) induce profound changes in natural intertidal dynamic and may lead to depletion and extinction of endemic populations. Future reef conservation planning must consider intertidal reef areas as one of most vulnerable reef habitats ¹³. We hope this study puts into perspective the urgency in considering intertidal habitats as a priority in conservation planning and management before their fish populations are suppressed by local and global threats.

Methods

Study areas

Tropical intertidal habitats of six southwestern Atlantic sites belonging to Brazilian Province were sampled for fish communities, three in oceanic environments, Rocas Atoll (03°51'S; 33°49'W), Fernando de Noronha Archipelago (03°50' S; 32°25' W) and Trindade Island (20°30'S; 29°20'W), and three in coastal environments, Salinópolis (00°36'S; 47°21'W), Jericoacoara (02°47'S; 40°30'W) and Anchieta (20°49'S; 40°36'W) (Figure 1). Briefly, tidepools are mostly situated in moderately flat areas built primarily by phonolite rocks or biogenic carbonate substrate in oceanic sites and biogenic carbonate or beach rocks in coastal sites (Supplementary Figure S1). Further environmental data are provided in Supplementary Information.

Field sampling

Fifteen tidepools were sampled in each site and all field expeditions were performed during the dry season periods of 2014 (Rocas Atoll) and 2015 (other sites). Tidepools were chosen at random during the ebb tide where there is not connectivity to the sea or to other pools. A set of environmental variables was recorded for each sampled pool. Pool water temperature, salinity and pH were measured right before sampling with a digital thermometer (0.1 degree precision), refractometer (1 psu) and pH meter (0.1 unit), respectively. Measurements (bathymetry and topography) were made immediately after water variables sampling using a 10 x 10 cm grid with depth measured at each intersection point. Pool surface area (water surface), planar area (bottom area with relief taken into account) and volume were calculated through the kriging method. Also, at each grid point, substrate type and benthic

organisms were identified. Benthic cover was expressed in percentage. Substrate types were categorized as follows: mud (silty substratum), sand (grain size < 1 mm), gravel (grains ≤ 50 mm) and rock (consolidated substrate > 50 mm) and also expressed in percentage. The rugosity index was generated by the ratio between surface area and planar area. The height of each tidepool was defined as the vertical distance between pool water surface and sea level at low tide. Subtidal and supralittoral distances were measured using a 30m metric-tape.

Fish were sampled using hand nets after application of the anesthetic clove oil ($40 \text{ mg}\cdot\text{l}^{-1}$), an efficient and selective method not-inducing mortality in non-target fauna⁵⁹. After collection, individuals were frozen at -20°C and key specimens were sorted and fixed in 10% formaldehyde and later preserved in 70% ethanol. Measurements for total length and wet weight were taken with calipers (0.1 mm) and digital balance (0.01 g). Species were classified in relation to their degree of residency in pools following published works on studied areas^{18,60,61} as well as underwater observations by the authors. Fishes grouped as Permanent residents can spend their entire life in pools and are frequently highly adapted for intertidal life. Secondary residents or opportunists spend only part of their life-history in tidepools, usually as juveniles or remain trapped in pools after high tide feeding incursions. Transients, which are species that only occasionally or accidentally enter in tidepools, generally have no specialized adaptations for intertidal life, and normally occur in large tidepools for a short period of time (from a tidal cycle to several weeks)^{19,22,62}. Species also were assigned to main trophic groups (i.e., carnivores, herbivores, omnivores and detritivores) and their subcategories (macro-carnivores, mobile invertebrate feeders, omnivores, territorial herbivores and roving herbivores) based on classical and current literature for Atlantic fishes trophic ecology^{63–65,39}, complemented by *in situ* observations by the authors.

Data analysis

Similarity analysis (ANOSIM) was used to investigate whether tidepool community composition and trophic structure differed between oceanic and coastal sites and among sites. Both tests used a Bray-Curtis similarity matrix built on log-transformed species density ($\text{ind}\cdot\text{m}^{-3}$). Non-metric multidimensional scaling (nMDS) was used to visualize data dispersion. In the same routine, similarity percentages analysis (SIMPER) was applied to verify what species were the most representative at a level

of cumulative contribution of 80% for each site. All analyses above were performed in PRIMER v6 ⁶⁶. To better evaluate the representativeness of trophic groups in tidepool communities, trophic structure was evaluated within sites through Kruskal-Wallis and Mann-Whitney paired tests using fish densities ($\text{ind}\cdot\text{m}^{-3}$) of main trophic groups (i.e., carnivores, herbivores, omnivores and detritivores) ⁶⁷.

We used multivariate regression trees (MRTs) combined to a Principal Component Analysis (PCA) of the dependent (fish density) and independent (environmental) variables to predict how explanatory variables influence the density of intertidal fish species that represented 90% of the total density. MRT was performed in R software ⁶⁸ through mvpart package ⁶⁹ using eighteen environmental explanatory variables, two categorical and sixteen numerical: Region (oceanic and coastal), Substrate type (carbonate and non-carbonate), three variables describing inorganic substrate structure (Sand, Gravel, and Rock coverage), three variables depicting the biological cover (Algae, Sessile animal, and Turf algae cover), three physicochemical water parameters (Water temperature, salinity, and pH) and seven tidepool morphometrical or positional parameters (Depth, Rugosity, Volume, Surface area, Pool height, Distance to subtidal and to supralittoral). Prior to analysis, environmental data were standardized to the same mean (with standard deviation of 1) and fish densities were log-transformed. Thus, we built a hierarchical tree to graphically represent the combination of best explanatory variables and indicator species in order to allow deductions about species realized niche ^{70,71}.

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Author Contributions

Conceived, design and performed the experiments: R.A., J.A.R-F, R.M.M, T.G. and J.-C.J. Wrote the first draft: R.A. All authors reviewed, discussed and commented on the manuscript.

Competing financial interests statement

There are NO competing financial interests.

Figures

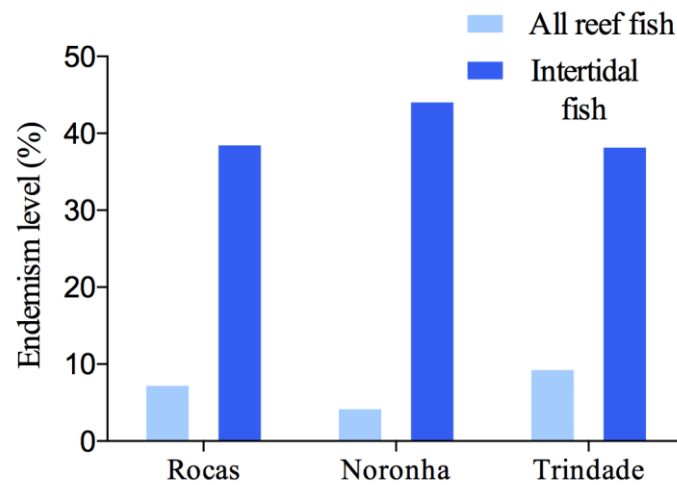


Fig. 1. Fish endemism levels in all reef fish fauna and intertidal fish at oceanic sites. Source of endemism data for all species^{40,54,72}.

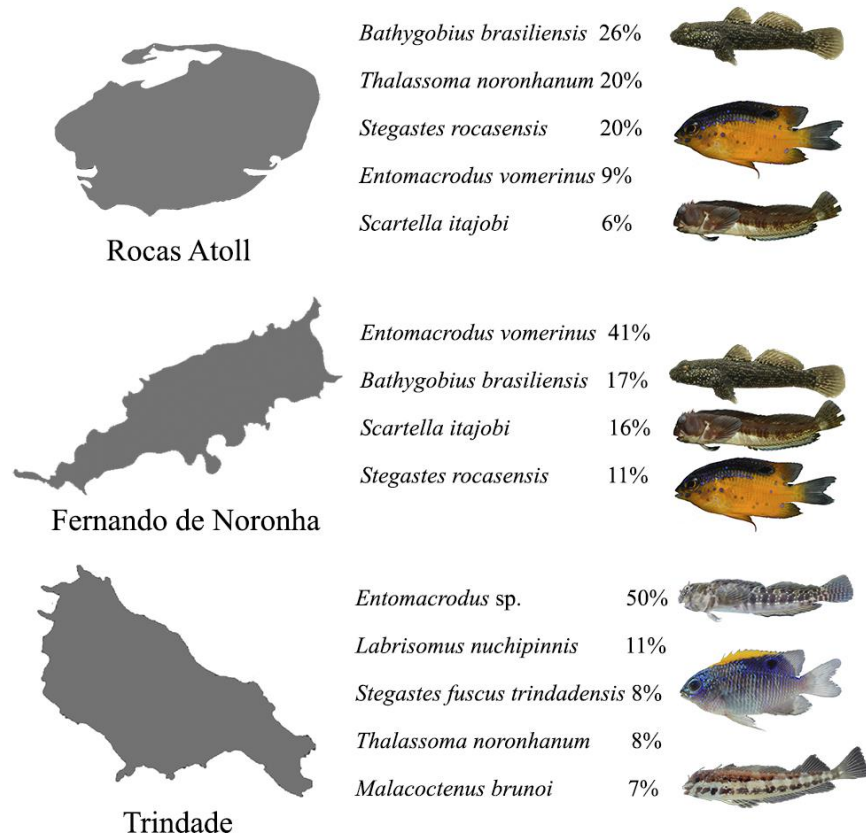


Fig. 2. Contribution of species density (80%) in each community of studied islands. Endemic species (also represented in photos) are *Bathygobius brasiliensis*, *Stegastes rocasensis* and *Scartella itajobi* in Rocas Atoll, *Bathygobius brasiliensis*, *Scartella itajobi* and *Stegastes rocasensis* in Noronha and *Entomacrodus* sp., *Stegastes fuscus trinidadensis* and *Malacoctenus brunoi* in Trindade. Map data ©2017 Google, edited and assembled in CorelDraw X5. Fish photos: R. Andrades, R. Macieira and J.-C. Joyeux.

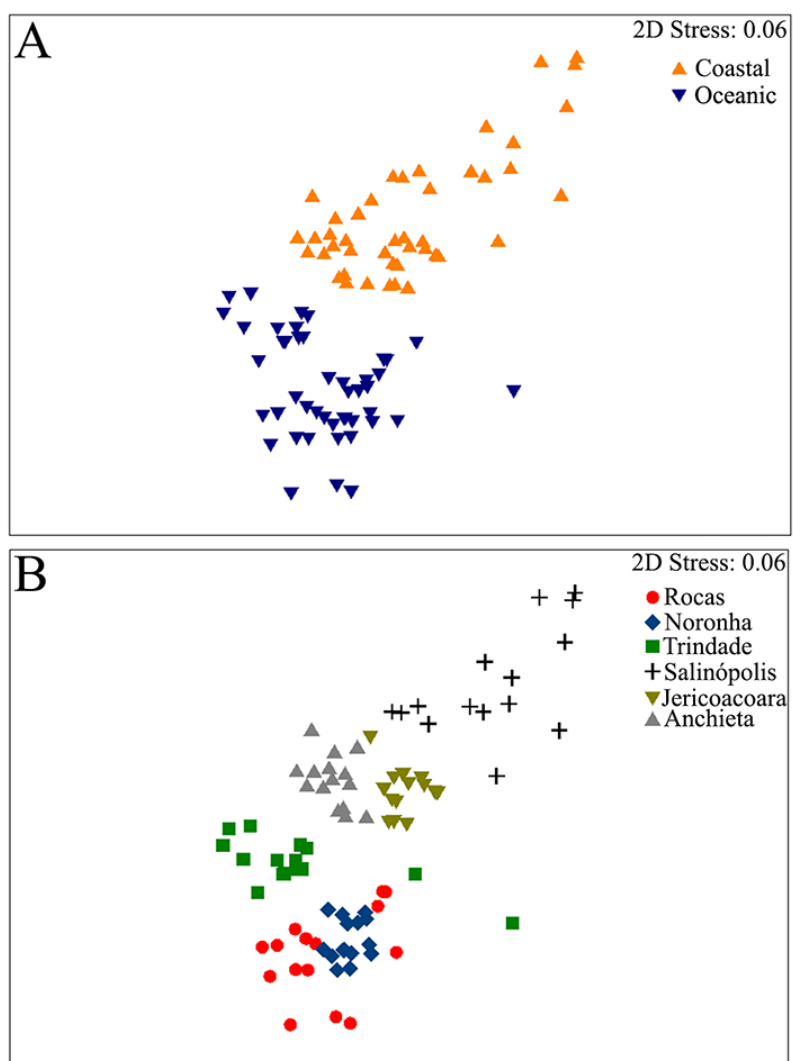


Fig. 3. Multidimensional scaling using fish density data in tidepools ($N = 90$) in regions (A) and sites (B).

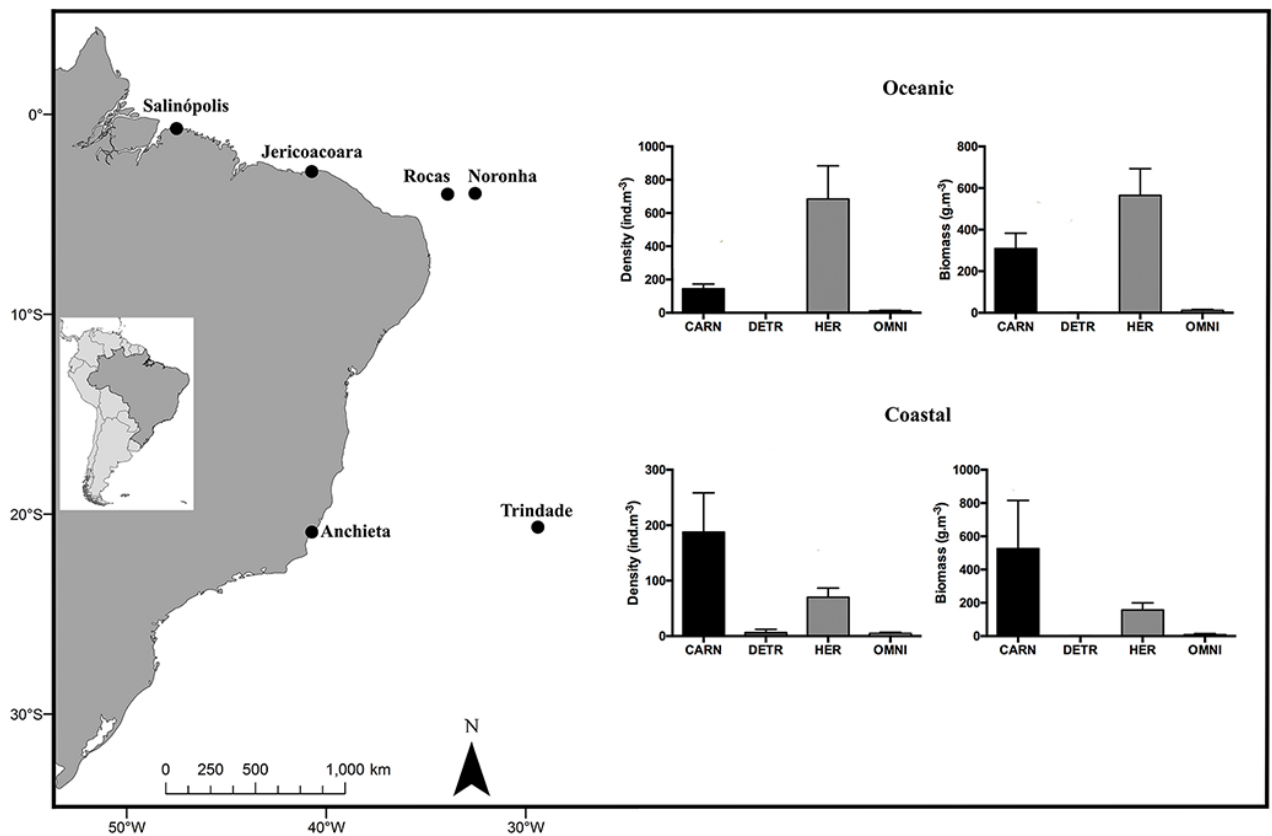


Fig. 4. Study sites in the southwestern Atlantic (left) and mean (+SE) fish density and biomass of the main trophic groups (CARN = carnivores, DETR = detritivores, HER = herbivores and OMNI = omnivores) in oceanic and coastal regions. Map data ©2017 Google, edited and assembled in CorelDraw X5.

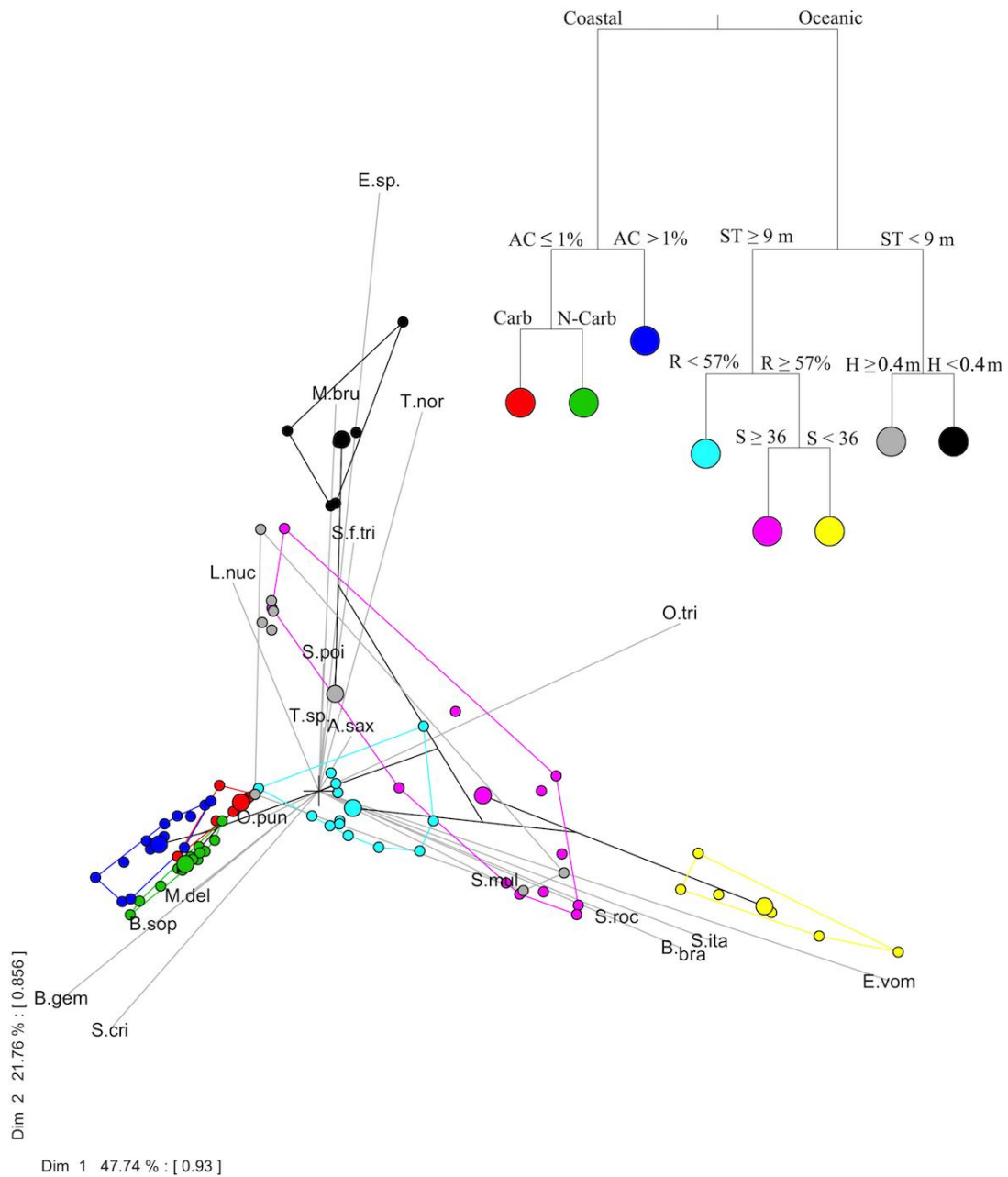


Fig. 5. Multivariate regression tree (MRT) analysis with the tree (top-right) and combined Principal Component Analysis (PCA) diagram for the tidepool fish species and environmental explanatory variables. Coloured dots represent each tree leaf. MRT explanatory variables are Region (Oceanic and Coastal), Sessile animal coverage (AC), Subtidal distance (ST), Substrate (Carbonate = Carb and Non-carbonate = N-Carb), Rocky coverage (R), Pool height (H) and Salinity (S). Fish species shown in PCA are *Abudefduf saxatilis* (A.sax), *Bathygobius brasiliensis* (B.bra.), *Bathygobius soporator* (B.sop), *Bathygobius geminatus* (B.gem), *Entomacrodus* sp. (E.sp.), *Entomacrodus vomerinus* (E.vom), *Labrisomus nuchipinnis* (L.nuc), *Malacoctenus delalandii* (M.del), *Malacoctenus bruno* (M.bru), *Omobranchus punctatus* (O.pun), *Ophioblennius trinitatis* (O.tri), *Scartella cristata* (S.cri), *Scartella itajobi* (S.ita), *Scartella poiti* (S.poi), *Starksia multilepis* (S.mul), *Stegastes fuscus trinidadensis* (S.f.tri), *Stegastes rocasensis* (S.roc), *Thalassoma noronhanum* (T.nor), *Tomicodon* sp. (T.sp.).

Endemic fish species structuring oceanic intertidal reef environments

Andrades et al.

Supplementary Material

SM1- Brief description of studied areas in the southwestern Atlantic Ocean.

SM2 – Supplementary Table 1: Intertidal reef fish species sampled in the present study.

Methods

Studied sites in the southwestern Atlantic

Oceanic sites

Rocas Atoll (03°51' S; 33°49' W) is the only atoll in the South Atlantic, distant 266 km of the mainland (state of Rio Grande do Norte). It has an elliptical shape and is primarily built by coralline algae, vermetid gastropods and hermatypic corals. Tidal regime is semidiurnal with mesotides reaching 3.8 m. At high tide, water almost covers the entire atoll, including all tidepools¹. Climate is tropical with water temperature and salinities values in tidepools ranging 28-34°C and 35-39, respectively (present study). Rocas Atoll probably is one of the most near-pristine areas of the Southwestern Atlantic being the first Marine Reserve established in Brazil (1978). However, effective monitoring and enforcement only began in 1991². No public visitation is allowed.

Fernando de Noronha Archipelago (03°50' S; 32°25' W) is located 345 km from the continent (state of Rio Grande do Norte) and belongs to the same volcanic ridge than Rocas Atoll. The study was conducted on the main island, Fernando de Noronha, where phonolite intertidal reefs often occur associated with biogenic carbonate substrate composed by encrusting coralline algae. Tidal regime is semidiurnal with mesotides (3.2 m maximum). Climate is similar to that of Rocas with temperature around 25°C and 27°C in air and water, respectively³. In tidepools, temperature varied 27-35°C and salinity 35-40 (present study). Most of Fernando de Noronha and surrounding waters are included in a National Marine Park created in 1988, ensuring some protection from fishing activities and control over tourism. In 2001, Noronha and Rocas were declared a World Heritage Site by UNESCO (United Nations Educational, Scientific and Cultural Organization) due to their role as oases to marine wildlife and the presence of endemic and endangered seabirds, turtles and reef fish species, among others⁴.

Trindade Island (20°30' S; 29°20' W) is tropical and located 1,160 km off the coast of the state of Espírito Santo; it is the most isolated insular environment of the Brazilian Province⁵. Trindade and, about 40km farther east, Martin Vaz Archipelago are the only emerged sites and the eastern end of the Vitória-Trindade submarine chain (VTC). The VTC comprises a set of 17

volcanic seamounts, sheltering rich fish fauna and benthic reef habitats, that have functioned as stepping-stones and allowed some connectivity between reef populations along the VTC ^{6,7}. Among Brazilian oceanic islands, Trindade has the highest reef fish endemism rate (9.6%; Pinheiro et al. 2015), while being the youngest island (3.7 My; the Noronha-Rocas complex is about 12.3 My-old and Saint Peter and Saint Paul's Archipelago about 9 My-old; Ferrari & Riccomini 1999, Hekinian et al. 2000, Castro 2009). Intertidal habitats of Trindade are made of biogenic carbonate (mostly encrusting coralline algae) and phonolite rocks substrates under semidiurnal microtides reaching 1.7 m ¹⁰. In our study, temperature in tidepools varied 27-34°C and salinities 35-41. Since 1957, the Brazilian Navy occupies the island and it maintains an oceanographic station (POIT – Posto Oceanográfico da Ilha da Trindade). Public visitation of the islands is restricted to research and military purposes, but commercial and recreational fishing is allowed.

Coastal sites

Salinópolis (00°36' S; 47°21' W) is located in the Amazonian region of Brazil (state of Pará), but the influence of the Amazon and other large rivers is moderate in contrast to the direct influence of medium and small estuaries distributed along the Pará coastline. In Salinópolis, the intertidal is mostly inserted into a carbonate reef derived from the Pirabas formation (early Miocene) and composed mainly of fossil coralline algae, corals, sponges and bryozoans ¹¹. The reef is isolated in a large sandy area, tidepools show a relatively low coverage of macroalgae and temperature and salinity ranged 31-35°C and 36-41, respectively (present study). Tidal regime is of semidiurnal macrotides reaching over 5 m. Salinópolis is the main touristic beach-spot on the Pará coastline, and human-related impacts on the beach such as organism removal and reef trampling are expected to be high, especially during summer vacations ¹².

Jericoacoara beach (02°47' S; 40°30' W) is situated in northeastern Brazil, receives little riverine influence and is governed by semidiurnal mesotides (4 m). Quartzite beach rocks with low complexity tidepools covered by dense fleshy macroalgae dominated the intertidal. Seasonally, harsh erosional events driven by sand-dune sediment occur, changing the intertidal-scape covering and uncovering tidepools. Temperature and salinity in tidepools varied 29-32°C and 39-41, respectively (present study). The beach is inserted into Jericoacoara National Park. Created in 2002, the area of *ca.* 9,000 hectares comprises sand dunes, mangrove areas, subtidal and intertidal shores open to public visitation.

Anchieta is a city in the state of Espírito Santo, southeastern Brazil, which shelters Castelhanos beach (20°49' S; 40°36' W), a tropical carbonatic flat reef composed mainly by encrusting coralline algae and stony coral skeletons ¹³. Fleshy macroalgae and sessile animals (sea

urchins and zoanthids) are abundant in tidepools. Water temperature and salinity varied 24-35°C and 36-41, respectively. Tidal regime is semidiurnal microtides reaching 1.8 m¹³. Similar to aforementioned coastal beaches, Castelhanos is touristic and suffers human-related impacts such as reef trampling, organism removal and fishing.

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Supplementary Material

SM2- Table

Supplementary Table S1. Family and species list, fish density (individuals per m³), total length (TL mm) and range (maximum and minimum), main trophic category, feeding habits (MCAR = macro-carnivore, MINV = mobile invertebrate feeder, OMNI = omnivore, DETR = detritivore, THER = territorial herbivore and RHER = roving herbivore) and residency status. Details about literature used to categorize trophic groups, feeding habits and residency status are provided in Material and Methods section.

Family / Species	Density (±SE)		TL range	Trophic category	Feeding habit	Residency status
	Oceanic	Coastal				
Ginglymostomatidae						
<i>Ginglymostoma cirratum</i> (Bonnaterre 1788)	0.1	—	28	Carnivore	MCAR	Secondary resident
Muraenidade						
<i>Gymnothorax funebris</i> Ranzani 1840	—	1 (0.6)	45 – 649	Carnivore	MCAR	Permanent resident
<i>Echidna catenata</i> (Bloch 1795)	0.7 (0.5)	—	296 – 365	Carnivore	MCAR	Permanent resident
<i>Enchelycore nigricans</i> (Bonnaterre 1788)	0.7 (0.7)	—	243 – 762	Carnivore	MCAR	Permanent resident
Ophichthidae						
<i>Myrichthys breviceps</i> (Richardson 1848)	0.047	—	752	Carnivore	MCAR	Secondary resident
Holocentridae						
<i>Holocentrus adscencionis</i> (Osbeck 1765)	1.4 (0.9)	—	116 – 131	Carnivore	MINV	Secondary resident
Batrachoididae						
<i>Thalassophryne nattereri</i> Steindachner 1876	—	0.2 (0.1)	100 – 123	Carnivore	MCAR	Secondary resident
Gobiidae						
Undescribed <i>Barbulifer</i> sp.	—	4.7 (2.5)	11 – 30	Carnivore	MINV	Permanent resident

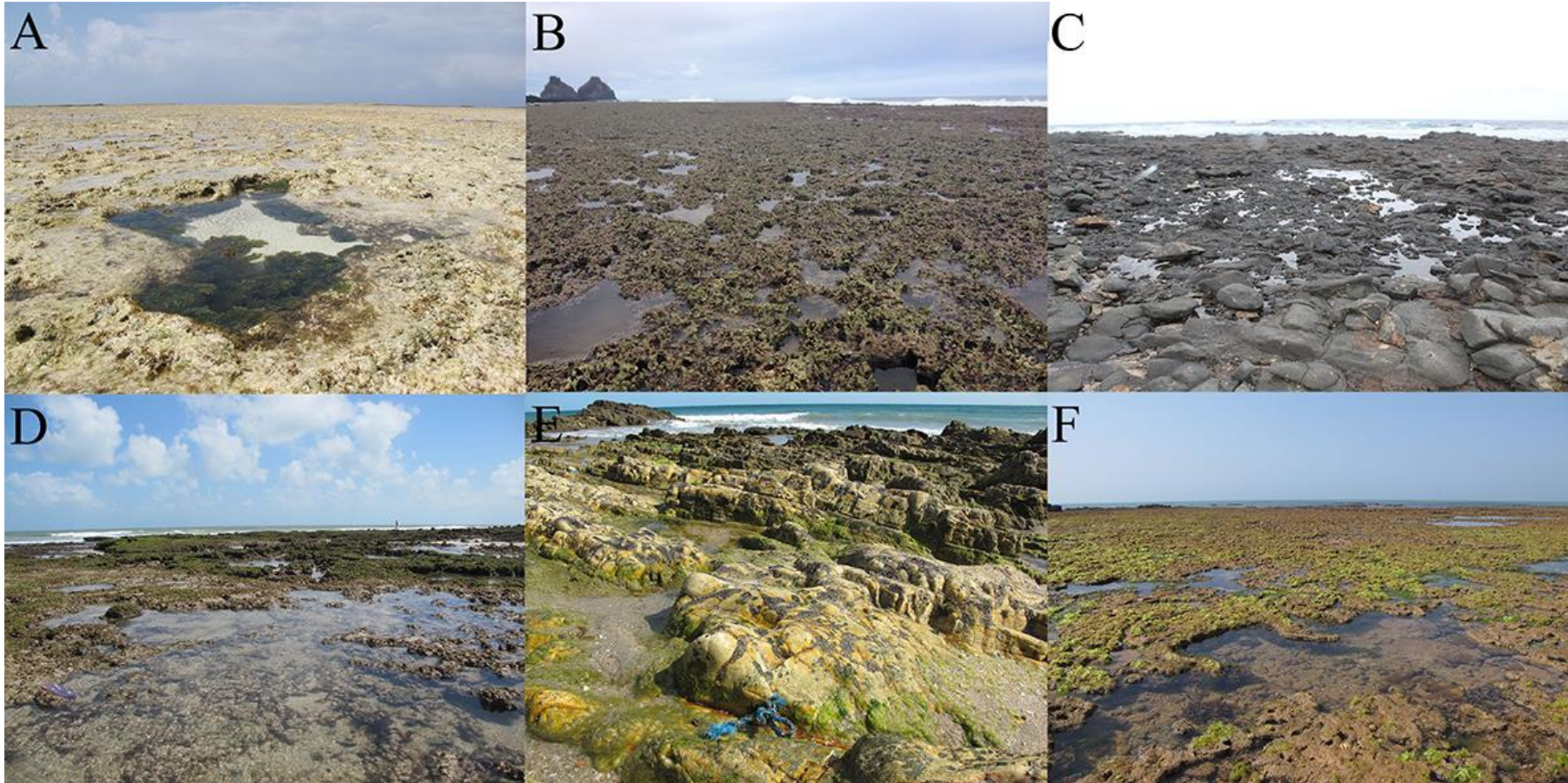
<i>Bathygobius brasiliensis</i> Carvalho-Filho & De Araújo, 2017 ††	69.5 (26.3)	— 133.2 (65.3)	8 – 97	Carnivore	MINV	Permanent resident
<i>Bathygobius geminatus</i> Tornabene, Baldwin and Pezold 2010	—	133.2 (65.3)	13 – 64	Carnivore	MINV	Permanent resident
<i>Bathygobius soporator</i> (Valenciennes 1837)	—	18.6 (7.5)	20 – 106	Carnivore	MINV	Permanent resident
Undescribed <i>Coryphopterus</i> sp. ††	0.3 (0.3)	—	26 – 43	Carnivore	MINV	Secondary resident
<i>Coryphopterus glaucofrenum</i> Gill 1863	—	0.2 (0.2)	27 – 39	Carnivore	MINV	Permanent resident
<i>Ctenogobius boleosoma</i> (Jordan & Gilbert 1882)	—	0.2	13	Carnivore	MINV	Permanent resident
<i>Gnatholepis thompsoni</i> Jordan 1904	1.1 (0.7)	—	22 – 35	Omnivore	OMNI	Secondary resident
<i>Gobiosoma alfiei</i> Joyeux & Macieira 2015	—	0.5 (0.4)	18 – 20	Carnivore	MINV	Permanent resident
Undescribed <i>Gobiosoma</i> sp.	—	4.4 (2.3)	15 – 36	Carnivore	MINV	Permanent resident
Undescribed <i>Lythrypnus</i> sp. ††	2.7 (1.6)	—	11 – 21	Carnivore	MINV	Secondary resident
<i>Priolepis dawsoni</i> Greenfield 1989	1.9 (1.7)	—	13 – 19	Carnivore	MINV	Secondary resident
Pomacentridae						
<i>Abudefduf saxatilis</i> (Linnaeus 1758)	10 (1.7)	4.8 (2.1)	16 – 96	Omnivore	OMNI	Secondary resident
<i>Stegastes fuscus</i> (Cuvier 1830)	—	0.8 (0.4)	21 – 90	Herbivore	THER	Permanent resident
<i>Stegastes fuscus trinidadensis</i> (Cuvier 1830) †	12.7 (7.2)	—	14 – 95	Herbivore	THER	Permanent resident
<i>Stegastes pictus</i> (Castelnau 1855)	0.5	—	35	Herbivore	THER	Transient Permanent
<i>Stegastes rocasensis</i> (Emery 1972) ††	36.2 (12.9)	—	15 – 98	Herbivore	THER	resident Secondary
<i>Stegastes variabilis</i> (Castelnau 1855)	—	0.1	41	Herbivore	THER	resident
Mugilidae						

<i>Mugil curema</i> Valenciennes 1836	—	6.4 (5.8)	26 – 42	Detritivore	DETR	Transient
<i>Mugil curvidens</i> Valenciennes 1836	1.1 (1)	—	44 – 80	Detritivore	DETR	Transient
Dactyloscopidae						
<i>Storrsia olsoni</i> Dawson 1982 ††	0.8 (0.6)	—	22 – 29	Carnivore	MINV	Permanent resident
Blenniidae						
<i>Entomacrodus vomerinus</i> (Valenciennes 1836)	327.2 (150)	—	12 – 106	Herbivore	THER	Permanent resident
Undescribed <i>Entomacrodus</i> sp. †	194.3 (87.6)	—	20 – 69	Herbivore	THER	Permanent resident
<i>Hypleurochilus fissicornis</i> (Quoy & Gaimard 1824)	—	2.7 (2.3)	19 – 51	Carnivore	MINV	Permanent resident
<i>Omobranchus punctatus</i> (Valenciennes 1836)	—	12.2 (7)	32 – 72	Herbivore	THER	Permanent resident
<i>Ophioblennius trinitatis</i> Miranda Ribeiro 1919	45.2 (14.3)	—	46 – 103	Herbivore	THER	Permanent resident
<i>Scartella cristata</i> (Linnaeus 1758)	—	53.6 (16.1)	12 – 93	Herbivore	THER	Permanent resident
<i>Scartella itajobi</i> Rangel & Mendes 2009 ††	60 (19.6)	—	13 – 67	Herbivore	THER	Permanent resident
<i>Scartella poiti</i> Rangel, Gasparini & Guimarães 2004 †	6.6 (5.9)	—	40 – 72	Herbivore	THER	Permanent resident
Labrisomidae						
<i>Labrisomus conditus</i> Sazima, Carvalho-Filho, Gasparini & Sazima 2009 ††	0.5 (0.4)	—	69 – 144	Carnivore	MCAR	Secondary resident
<i>Gobioclinus kalisherae</i> (Jordan 1904)	0.2 (0.2)	—	38 – 72	Carnivore	MCAR	Secondary resident
<i>Labrisomus nuchipinnis</i> (Quoy & Gaimard 1824)	5.3 (2.2)	4.7 (1.5)	35 – 158	Carnivore	MCAR	Permanent resident
Undescribed <i>Malacoctenus</i> sp. ††	4.9 (3.2)	—	23 – 53	Carnivore	MINV	Permanent resident
<i>Malacoctenus bruno</i> i Guimarães, Nunan & Gasparini 2010 †	9.3 (4.4)	—	31 – 52	Carnivore	MINV	Permanent resident
<i>Malacoctenus delalandii</i> (Valenciennes 1836)	—	12.2 (3.9)	18 – 59	Carnivore	MINV	Permanent

						tesresident
<i>Paraclinus arcanus</i> Guimarães & Barcellar 2002	—	0.1	23	Carnivore	MINV	Permanent resident
<i>Starksia multilepis</i> Williams & Mounts 2003 ††	7.7 (3.1)	—	12 – 32	Carnivore	MINV	Permanent resident
Gobiesocidae						
<i>Gobiesox barbatulus</i> Starks 1913	—	0.5 (0.3)	21 – 36	Carnivore	MINV	Secondary resident
Undescribed <i>Tomicodon</i> sp. ††	1 (0.7)	—	20 – 23	Carnivore	MINV	Permanent resident
Undescribed <i>Tomicodon</i> sp. †	11.7 (9.3)	—	10 – 21	Carnivore	MINV	Permanent resident
Labridae						
<i>Halichoeres penrosei</i> Starks 1913	6.7 (3.9)	—	18 – 90	Carnivore	MINV	Secondary resident
<i>Halichoeres poeyi</i> (Steindachner 1867)	—	0.9 (0.8)	64 – 84	Carnivore	MINV	Secondary resident
<i>Sparisoma axillare</i> (Steindachner 1878)	—	0.4 (0.2)	39 – 78	Herbivore	RHER	Secondary resident
<i>Sparisoma frondosum</i> (Agassiz 1831)	0.2	—	35	Herbivore	RHER	Secondary resident
<i>Thalassoma noronhanum</i> (Boulenger 1890)	18.4 (5.6)	—	16 – 72	Carnivore	MINV	Secondary resident
Epinephelidae						
<i>Cephalopholis fulva</i> (Linnaeus 1758)	0.1 (0.1)	—	58	Carnivore	MCAR	Transient
Haemulidae						
<i>Genyatremus luteus</i> (Bloch 1790)	—	2.4 (1.4)	17 – 99	Carnivore	MINV	Transient
Lutjanidae						
<i>Lutjanus jocu</i> (Bloch & Schneider 1801)	—	0.6 (0.3)	21 – 32	Carnivore	MCAR	Secondary resident
Scorpaenidae						
<i>Scorpaena plumieri</i> Bloch 1789	—	0.4 (0.2)	49 – 71	Carnivore	MCAR	Secondary resident

Acanthuridae						
<i>Acanthurus bahianus</i> Castelnau 1855	—	2.6 (1.3)	35 – 43	Herbivore	RHER	Secondary resident
<i>Acanthurus chirurgus</i> (Bloch 1787)	1.6 (1.2)	0.4 (0.3)	33 – 68	Herbivore	RHER	Secondary resident
Tetraodontidae						
<i>Sphoeroides greeleyi</i> (Gilbert 1900)	—	0.3	102	Carnivore	MINV	Transient
† Species endemics to Trindade-Martin Vaz insular complex, †† Species endemics to Rocas-Noronha insular complex.						

Figure S1



Supplementary Figure S1. Intertidal reefs of oceanic islands Rocas Atoll (A), Fernando de Noronha (B) and Trindade Island (C), and coastal sites Salinópolis (D), Jericoacoara (E) and Anchieta (F).

CAPÍTULO 4

NICHE AND COMPETITIVE INTERACTIONS IN INTERTIDAL REEFS: A STABLE ISOTOPES APPROACH

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Niche and competitive interactions in intertidal reefs: a stable isotopes approach

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Summary

Sixty years ago, Hutchinson proposed the unification of the Grinnellian and Eltonian niches in the n-dimensional approach. In 21th century, stable isotopes were incorporated into the ecological niche (isotopic niche) has been applied in a community- and individual-scale over the years. Here, we studied more than one thousand specimens of primary producers and consumers ranging from algal turfs to juvenile sharks to evidence marked differences in consumers, food chain length and community isotopic niches between oceanic and coastal intertidal reefs. In addition, proxies of intra- and inter-specific competition modelled from fish densities, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures showed that cryptobenthic species were the most vulnerable taxa in both oceanic and coastal intertidal environments. Our study sheds light into the vulnerability of intertidal cryptobenthic species and the relevance of the diverse trophic roles displayed by endemic oceanic fishes, which appears to have been conserved over the evolutionary time.

1. Introduction

Ever since the concept of the ecological niche was first defined by Grinnell (1917) and then Elton (1927), the exact meaning, application, and interpretation of this concept in the field of ecology have varied considerably, depending on the context in which it has been applied (Soberón 2007; Peterson *et al.* 2011). The Grinnellian and Eltonian approaches are distinct, with the former focusing on the habitat requirements of species, and the latter mainly on biotic interactions (Grinnell 1917; Elton 1927; Chase & Leibold 2003; Soberón 2007). Thirty years later, Hutchinson (1957, 1978) redefined the ecological niche as an n-dimensional hypervolume of variables that limit the occurrence of a species based on scenopoetic and bionomic components, which represent the niche space it occupies. However, the complexity and ambiguity of quantifying a niche in this manner led to the approach being partially ignored (Chase & Leibold 2003). Since the beginning of the 21st century, many ecologists have adopted models that address the Grinnellian and Eltonian viewpoints separately (Hirzel & Le Lay 2008; Rosado *et al.* 2016). The large databases now available of species presence/absence have permitted the quantification of Grinnellian niches using analytical approaches such as Habitat Suitability Models (Hirzel & Le Lay 2008). However, while species interactions have been recognized as a key feature determining species distribution and niches, the determination of species interactions in the Eltonian niche still represents a major challenge for ecologists (Chase & Leibold 2003; Hirzel & Le Lay 2008; Peterson *et al.* 2011; Araújo *et al.* 2014).

Stable Isotope Analysis (SIA) provides a means of capturing components of both the Grinnellian and Eltonian niches, given that a consumer's stable isotopes provide information on both where and what it ingested (Layman *et al.* 2007a; Newsome *et al.* 2007; Jackson *et al.* 2011). This analytical approach is based on the reduction of the multiple dimensions space of an organism's niche to, typically, two (e.g., $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) axes of elemental isotopes, although additional axes may be used. The portion of this space occupied by individuals or populations, known as the isotopic niche, may provide evidence on migration, anthropogenic pollution, the use of habitats and resources, and trophic relationships, based on the signatures of different isotopes, in particular those of carbon, nitrogen, and oxygen (Fry 2006; Michener & Lajtha 2007; Boecklen *et al.* 2011). Over the past decade, the isotopic niche approach has helped ecologists to quantify food webs and realized niches in the analysis of large-scale avian migrations, deep-sea hydrothermal vents, and the potential impacts of invasive species in natural ecosystems (O'Farrell *et al.* 2014; Catry *et al.* 2016; Reid *et al.* 2016), which would have been extremely difficult based on

traditional field techniques, such as observation and gut content analyses, in particular because these methods provide only a snapshot of the behavior and diet of the target species. In this context, SIA provides a reliable tool for the compilation of food web scenarios, in addition to the investigation of niches, at the species or ecosystem level.

Worldwide, intertidal reefs are one of the marine systems most impacted by human activities (Halpern *et al.* 2008; Andrades *et al.* 2017). These systems face a range of anthropogenic impacts, ranging from trampling and fishing to pollution from sewage, which may affect its biota, ecosystem functioning, and ecological services, such as erosion control and carbon uptake (Thompson *et al.* 2002; Halpern *et al.* 2008). While largely neglected in reef conservation planning, intertidal reefs provide nursery habitats for a number of economically or ecologically important reef fish species, in both coastal and oceanic environments (Krück *et al.* 2009; Macieira *et al.* 2015; Dias *et al.* 2016). In the case of oceanic islands, the vulnerability of these systems is accentuated by the high rates of endemism found in the intertidal waters, where many cryptobenthic species spend their whole life cycle in water only a few centimeters deep, which are threatened by the ongoing rise in sea level (Andrades *et al.* 2017). Intertidal reef landscapes have also been considered to be a useful habitat model for the analysis of the competitive interactions of species for space and resources, focusing on the sessile fauna in particular (Connell 1961; Giller 1984; Louthan *et al.* 2015). While the mobile fauna is logistically difficult to survey and its ecological role in food webs is poorly known (but see Norton & Cook 1999), recent studies have provided essential insights for intertidal ecology (Vinagre *et al.* 2015; Catry *et al.* 2016; Paijmans & Wong 2017). Despite the vulnerability of oceanic intertidal environments, however, virtually nothing is known of the functioning of their ecosystems, mainly in tropical regions.

We studied six tropical intertidal reef sites of the southwestern Atlantic, three on oceanic islands and three on coastal habitats, in order to test whether the oceanic communities differ from the coastal ones in their food webs, consumers, organization, structure, and competitive interactions, using SIA ecological models. To evaluate these potential differences, the following questions and predictions were tested.

1. Are the food chains and consumers of coastal intertidal communities different from those of oceanic environments?

As the oceanic sites presented larger areas of continuous intertidal reefs either within (Rocas Atoll) or bordering (Noronha and Trindade) the study sites, in comparison

with the relatively small and sparse coastal reefs, we expected to find longer food chain lengths in the oceanic communities, given that ecosystem size is a strong predictor of the length of the food chain (Post *et al.* 2000; Post 2002). We also expected to find distinct consumer taxa, based on the data available for the principal consumers, i.e., fish (Capítulo 3). Despite these expectations, it is important to note that this is the first trophic study to include the largest oceanic islands of the southwestern Atlantic.

2. Are the isotopic niches of the oceanic intertidal communities broader than those of the coastal communities?

Based on the assumptions of the Theory of Island Biogeography (MacArthur & Wilson 1967) and related studies (Diamond 1970; Losos & Ricklefs 2009; Borregaard *et al.* 2016; Pinheiro *et al.* 2017), we predicted that the oceanic intertidal environments provide consumers with a greater abundance of resources ($\delta^{13}\text{C}$ range) and empty niches became possible the enlargement of oceanic niche communities (high SEAc values) in relation to coastal sites.

3. Which fish taxa are the most vulnerable in potential intraspecific and interspecific competitive interactions?

As the intertidal communities are structured primarily by small-sized fish species (Gibson & Yoshiyama 1999; Capítulo 3), we predicted that these small resident species, which are restricted to intertidal environments (i.e., have a life territory restricted to depths of less than 3 m), are the weakest competitors (i.e. the most vulnerable taxa).

4. Do endemic island species present evidence of niche conservatism and density compensation in comparison with their mainland sister species?

Here, niche conservatism refers to the classic scenario of niche evolution (Wiens & Graham 2005; Warren *et al.* 2008; Peterson *et al.* 2011), and our principal hypothesis is that the niches of two sister species (endemic and mainland species) will be more similar to one another than either is to the niche of a sympatric, but non-sister species, of the same family. We expected that our selected endemic island species would present niche conservatism, as well as higher densities (i.e., density compensation) than their mainland sister species. This is the first time, to our knowledge, that stable isotopes and isotopic niche models have been used to test for niche conservatism in a evolutionary perspective,

which we hope will open new avenues for the development of future ecological and evolutionary approaches in this field.

2. Material and Methods

2.1 Study areas

Primary producers and consumers were sampled from six tropical intertidal reefs. Three of these sites were oceanic: Rocas Atoll (03°51' S, 33°49' W), the Fernando de Noronha Archipelago (03°50' S, 32°25' W), and Trindade Island (20°30' S, 29°20' W). The three coastal reefs were located at Salinópolis (00°36' S, 47°21' W), Jericoacoara (02°47' S, 40°30' W), and Anchieta (20°49' S, 40°36' W). The intertidal area at Rocas Atoll is composed of biogenic carbonate reefs, while those at Fernando de Noronha Archipelago and Trindade Island (hereafter Noronha and Trindade, respectively) encompass mixed phonolite rocky and biogenic carbonate reefs. At the coastal sites, the reefs at Salinópolis are composed of carbonate/rocky substrates, while that at Anchieta is a carbonate reef, and the Jericoacoara reef is composed of beach rocks. Further details on the study areas are provided in the Supplementary Material.

2.2 Data sampling and stable isotopes preparation

Samples were collected during the dry seasons in 2014 (Rocas Atoll) and 2015 (all other sites) in order to avoid potential environmental bias derived from seasonal effects. The sampling of primary producers focused on the most common green, red and brown macroalgae, the epilithic algal matrix and phytoplankton (the principal sources of Particulate Organic Matter - POM). Hereafter, we refer to the epilithic algal matrix (*sensu* Wilson *et al.* 2003) as algal turf (Connell *et al.* 2014). We also collected fresh and senescent leaves of the red (*Rhizophora mangle*), white (*Laguncularia racemosa*), and black (*Avicennia shaueriana*) mangrove trees from the surrounding coastal mangrove zones to verify their potential contribution to the intertidal food web. Intertidal consumers comprised benthic and nekton marine consumers of different trophic guilds, that is, polychaetes, amphipods, shrimp, sea snails, crabs, sea urchins, octopuses, and fish. A detailed list of the consumer taxa is provided in Table S1.

The macroalgal and algal turf samples were collected using a scraper. The water samples taken for the analysis of POM were sieved through a 60 µm mesh to remove the largest particles and zooplankton, and then filtered through pre-combusted Whatmann GF/F glass-fiber filters. Each filter was then stored in a clean glass vial prior to analysis.

Invertebrates and fish were collected using hand nets. Fish were sampled following the application of clove oil ($40 \text{ mg}\cdot\text{l}^{-1}$) as suggested by Griffiths (2000). This procedure is recommended for sampling intertidal fish due to its efficiency and selectivity in comparison with alternative methods, given that it does not induce mortality in the non-target fauna (Griffiths 2000; Robertson & Smith-Vaniz 2010). Once collected, all consumer specimens were washed in seawater to remove attached detritus and frozen at -20°C . Subsamples of the key and doubtful species were sorted and fixed in a 10% formaldehyde solution, before being preserved in 70% ethanol for the confirmation of the taxonomic identification. To avoid bias in the isotopic signatures induced by ontogenetic (body size) shifts, the invertebrate and fish specimens of each identified taxa were grouped in similar length classes, based on the natural distribution of body sizes observed at each site (Capítulo 3). The accuracy of these size classes was ensured by measurements of carapace length, in the crustaceans, and total length, in the fish, taken using calipers (0.1 mm).

In the laboratory, the gut contents were removed from the amphipod and polychaetes specimens, and the whole body was used as the sample for analysis. In the case of the sea snails, the shell was removed, and the remaining soft tissue constituted the sample for analysis. Samples of muscle tissue were extracted from the abdominal segments of the shrimp and the chelipeds of the crabs, while gonadal tissue was extracted from the sea urchins. In the case of the fish, muscle tissue was removed from the anterior portion of the dorsal fin, except in the shark, *Ginglymostoma cirratum*, from which a sample was obtained after sectioning *c.* 2 cm^2 of the dorsal fin tissue. Small-size fish, that is, individuals with a total length of under 30 mm (e.g., *Tomicodon* sp.), were used whole, following the extraction of the gut contents, scales, fins, and head. For the $\delta^{13}\text{C}$ signatures, we acidified subsamples of the POM, algal turf, calcareous macroalgae, and amphipods with HCl to remove the carbonate content. All samples were dried in a standard laboratory oven at 60°C during 48 hours, and then homogenized.

The samples were analyzed for stable carbon and nitrogen isotopes using continuous-flow isotope ratio mass spectrometry in a Costech elemental analyzer coupled to a Micromass Isoprime isotope ratio mass spectrometer (EA/IRMS). The laboratory data were calibrated using NIST (National Institute of Standards and Technology) reference materials. Stable isotope values are expressed using δ (delta) notation and parts per thousand (‰) as follows:

$$\delta X = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 10^3,$$

Where X is ^{13}C or ^{15}N and $R = ^{13}\text{C}/^{12}\text{C}$ for carbon and $^{15}\text{N}/^{14}\text{N}$ for nitrogen.

The standard reference materials were PDB (Pee Dee Belemnite) for carbon and airborne N_2 for nitrogen.

In order to avoid any bias resulting from chemical interference in the isotopic signatures, we did not extract lipids using chemical solvents, such as methanol-chloroform (Post *et al.* 2007; Boecklen *et al.* 2011). Given this, the $\delta^{13}\text{C}$ signatures of the consumer samples were corrected for lipid-rich tissue samples ($\text{C:N} > 3.5$), following Post *et al.* (2007).

2.3 Data analysis

2.3.1 *Are the food chains and consumers of intertidal coastal communities different from those of oceanic environments?*

We compiled a hierarchical intertidal trophic structure based on the trophic level of each consumer to compare the composition of the upper, mid and lower consumers among the different intertidal systems. For this, posterior modes of the trophic positions of the consumers were calculated using the tRophicPosition package (Quezada-Romegialli *et al.* 2017), which incorporates a Bayesian model for multiple baseline (pelagic and benthic) estimates. Food chain lengths were determined for each community from the range of the $\delta^{15}\text{N}$ signatures (NR), as suggested by Layman *et al.* (2007) and Jackson *et al.* (2011).

2.3.2 *Are the isotopic niches of the oceanic intertidal communities broader than those of the coastal communities?*

The isotopic community niche was evaluated using the SIBER (Stable Isotope Bayesian Ellipses in R; Jackson *et al.* 2011) multivariate ellipse-based model available in the R statistical computing package (R Core Team 2017). Additional isotopic niche metrics were also analyzed to reinforce the observed patterns. These metrics referred to the diversity of resources (CR), species spacing (CD), isotopic clustering, and the evenness and spatial packaging of the data (MNND and SDNND). Further details of these niche/community metrics are provided by Layman *et al.* (2007) and Jackson *et al.* (2011).

For this analysis, we included all the intertidal consumers for which at least three samples were obtained.

2.3.3 Which fish taxa are the most vulnerable in potential intraspecific and interspecific competitive interactions?

Here, we used two proxies of intraspecific and interspecific competitive interactions to better evaluate niche overlap and the partitioning of the isotopic δ -space among intertidal fish species through the stable isotope and abundance data. We first divided the density of each fish species (see Capítulo 3) by its isotopic niche area to obtain an estimate of the intensity of intraspecific competition (intraspecific competition proxy – ICP), as follows:

$$ICP_i = \frac{FD_i}{\text{Ellipses95}_i},$$

Where FD_i is the mean fish density ($\text{ind} \cdot \text{m}^{-3}$) of species i and Ellipses95_i is the small sample size core (i.e. core isotopic niche ellipses) of species i , containing the 95% prediction ellipse interval. This simple approach represents the density of a population in relation to the size of its isotopic niche, with higher ICP values representing a greater degree of intraspecific competition in the species. This is the first time, as far as we are aware, that fish density has been considered together with ellipse-based metrics to determine the intensity of competition within populations.

Interspecific competitive interactions (species competition proxy – SCP) were quantified by considering the amount of overlap in the isotopic niche between two species in relation to the density of the focal species. Specifically, we calculated:

$$SCP_i = \frac{\text{Ellipses95}_i}{FD_i \times (\text{Ellipses95}_i - \text{Ov}_{ij})},$$

Where Ov_{ij} is the overlap of the area of the corrected standard ellipse between species i and j that corresponds to the overlap of the maximum likelihood standard ellipse area within the 95% prediction ellipse interval. We were thus able to measure the effect of species i on species j and *vice versa* through the matrix:

$$\begin{bmatrix} a_{11} & a_{12} & \cdots & a_{1n} \\ a_{21} & a_{22} & \cdots & a_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ a_{m1} & a_{m2} & \cdots & a_{mn} \end{bmatrix},$$

Where a_{ij} is the effect of species j on i . We only evaluated potential competition effects for pairs of species that presented some degree of overlap of their small sample size cored 95% prediction ellipses, otherwise, SCP_i would be equal to FD_i , which is meaningless. Based on the competitive interactions between species and the number of potential competitors, we identified the most successful competitors in each studied community, that is, the species that had the greatest net potential effect in the pairwise comparisons, and, in turn, the species most vulnerable to potential competitive interactions (i.e. weak competitors).

2.3.4 Do endemic island species present evidence of niche conservatism and density compensation in comparison with their mainland sister species?

To test for niche conservatism, we calculated the overlap of the maximum likelihood standard ellipse area within the 95% prediction ellipse interval values between endemic species and their mainland sister species using the SIBER package (Jackson *et al.* 2011). Other confamiliar species present on the islands were also included in the analyses. We rescaled the $\delta^{15}\text{N}$ signatures to trophic position values (calculated as in Post *et al.* 2002) to avoid bias due to local enrichment systems, which permitted direct comparisons between species from different sites.

The species included in this analysis were the endemic Trindade combtooth blenny, *Scartella poiti*, which was compared with molly miller *Scartella cristata* from the mainland (Jericoacoara and Anchieta). The sympatric non-sister species *Ophioblennius trinitatis* was chosen randomly from the same taxonomic family (Peterson *et al.* 1999; Warren *et al.* 2008). We chose an endemic species from Trindade Island for this approach because Trindade species history of speciation is the best understood of any of the oceanic island faunas in the southwestern Atlantic (Pineiro *et al.* 2017).

We also compiled the density ($\text{ind}\cdot\text{m}^{-3}$) of the species at their respective study sites (see Capítulo 3) in search of evidence of density compensation, that is, whether endemic species on oceanic islands occur at higher densities than their mainland sister species, and the probable associated factors.

3. Results

We analyzed a total of 1,115 samples of intertidal components (965 consumers and 150 primary sources). The primary potential sources were similar in all study areas, with algae predominating in the intertidal landscape (Table S2). While we collected samples of the fresh and senescent leaves of mangrove trees (*R. mangle*, *L. racemosa*, and *A. shaueriana* and *A. germinans*) from coastal mangrove forests (48 samples, 18 per coastal site; except for Salinópolis $n = 12$), the strongly depleted $\delta^{13}\text{C}$ signature (mean -28.3‰) indicated clearly that these trees did not play a role in the intertidal food web, so these samples were excluded from the analyses. At the oceanic sites, the $\delta^{13}\text{C}$ signatures of the intertidal primary producers ranged from -22.0‰ (Noronha; POM) to -11.3‰ (Noronha; red algae), while their $\delta^{15}\text{N}$ signatures ranged from 1.8‰ (Trindade; green algae) to 5.2‰ (Rocas; brown algae). At the coastal sites, the $\delta^{13}\text{C}$ signatures ranged from -25.1‰ (Salinópolis; POM) to -11.3‰ (Anchieta; algal turf), while the $\delta^{15}\text{N}$ values varied from 2.2‰ (Salinópolis; green algae) to 7.6‰ (Anchieta; brown algae). While the mean $\delta^{13}\text{C}$ value recorded for the primary producers at the coastal sites (-17.3‰) was lower than that recorded at oceanic sites (-16.2‰), the mean $\delta^{15}\text{N}$ signature was higher at the coastal sites (5.2‰) in comparison with the oceanic sites (3.5‰).

3.1 Do the intertidal communities differ in their food chain length and consumers?

Food chains were slightly longer at the oceanic sites (Rocas, Noronha and Trindade), except in comparison with Anchieta, where the food chain was the longest of any community. The $\delta^{15}\text{N}$ range were 6.34 at Rocas, 6.45 at Noronha, and 6.01 at Trindade, whereas at the coastal sites, values of 5.03 were recorded at Salinópolis, 5.57 at Jericoacoara, and 9.18 at Anchieta. The trophic positions of consumers in the food web varied among communities, with the predators of sea turtle hatchlings (*Johngarthia lagostoma*, *Echidna catenata* and *Cephalopholis fulva*) being the top consumers at the oceanic sites, followed by small-sized carnivores and omnivores (Fig. 1). Endemic insular fish species were distributed throughout the oceanic intertidal food chains, ranging from basal consumers (e.g., *Tomicodon* sp. and *Entomacrodus* sp.) to mid-top consumers (e.g., *Stegastes rocasensis* and *Scartella poiti*), confirming the importance of endemic taxa in the oceanic environments. Invertebrates, i.e., polychaetes, amphipods and sea urchins, comprised the basal consumers at both coastal and oceanic sites, although large invertebrates, such as octopuses and crabs, occupied high trophic positions. Juvenile morays and snappers (*Lutjanus* spp.), and resident intertidal species (*Scartella* and *Bathygobius*) were the top consumers at the coastal sites (Fig. 2). At all sites, the fish were

represented mainly by juvenile reef-dwelling species and small-sized intertidal residents, which is typical of the intertidal reef fauna (Capítulo 3).

3.2 *Are the isotopic niches of the oceanic intertidal communities broader than those of the coastal communities?*

Isotopic niche widths estimated by the standard ellipse area (SEAc) indicated large niches in the oceanic intertidal communities (Fig. 3 and 4A). This was corroborated by the higher Mean distances to centroid (CD), Mean nearest neighbour distances (MNND), and the Standard deviations of the nearest neighbour distances, SDNND (Fig 4 B-D), which all indicate the greater packing of individuals within the isotope δ -space. While the CD values reinforced the existence of larger niches in the oceanic communities, the MNNDs and SDNNDs reflected a higher degree of trophic redundancy at coastal sites in comparison with oceanic ones. The larger niches recorded at the oceanic sites were supported by a greater diversity of basal resources, as confirmed by the broader $\delta^{13}\text{C}$ ranges recorded (Fig. 4E). Niche metrics were similar among the oceanic sites, but varied more among the coastal sites. All niche metrics modeled at Salinópolis indicated a very narrow isotopic niche, whereas Anchieta presented a rich trophic diversity and broad niche. The numerical data on the community metrics are presented in Table 1.

3.3 *Which fish taxa are the most vulnerable in potential intraspecific and interspecific competitive interactions?*

Based on our proxies, we found that fish taxa belonging to different trophic positions incur high potential intra- and interspecific interactions. However, while we predicted that the most vulnerable taxa would be the small-sized resident fish restricted to shallow waters, cryptobenthic resident fish appeared to suffer higher competitive pressure than other species. Although most fish taxa in intertidal reefs may present cryptobenthic characteristics (Capítulo 3), it is important to note that none of the non-cryptobenthic species presented high levels of intraspecific competition or any apparent disadvantage in interspecific interactions, even at Salinópolis, where cryptobenthic fish are rare (Fig. 5; S1 and S2).

The levels of intraspecific competition were high at oceanic sites for *Starksia multilepis* (Rocas), *Entomacrodus vomerinus* (Noronha), and *Tomicodon* sp. (Trindade), and at coastal sites for *Barbulifer* sp. (Salinópolis), *Scartella cristata*, and *Malaccoctenus* sp. (Fig. 5), due to the high population densities of these taxa in relation to their proportionally

narrow niches, which is expected for cryptobenthic reef fishes (Goatley & Brandl 2017). In addition, five of six most vulnerable fish taxa in respect to intraspecific competition are oceanic endemics (*S. multilepis* and *Tomicodon* sp.) and Brazilian Province coastal endemics (*Barbulifer* sp., *Scartella cristata* and *Malacoctenus* sp.). All taxa are represented by small-sized resident species.

The evaluation of the potential interspecific interactions among intertidal species indicated that the species with the weakest competitors were *Coryphopterus* sp., *S. multilepis* and *Storrsia olsoni* at Rocas, *Abudefduf saxatilis*, *Gobioclinus kalisherae* and *E. vomerinus* at Noronha, *Malacoctenus brunoi*, *Tomicodon* sp. and *Mugil curvidens* at Trindade, *Gobiesox barbatulus*, *Sphoeroides testudineus* and *Thalassophryne nattereri* at Salinópolis, *Omobranchus punctatus*, *Acanthurus chirurgus* and *Sparisoma axillare* at Jericoacoara, and *S. axillare*, *Stegastes variabilis* and *Coryphopterus glaucofraenum* at Anchieta. Only five (*A. saxatilis*, *M. curvidens*, *S. testudineus*, *A. chirurgus* and *S. variabilis*) of these 18 species, that is, less than 30%, are non-cryptobenthic (Fig. S1 and S2).

3.4 Do endemic island species present evidence of niche conservatism and density compensation in comparison with their mainland sister species?

The Trindade endemic *Scartella poiti* have retained their ancestral ecological niches from their sister mainland species. The isotopic niche was generally similar to that of the mainland sister species (Fig. 6), and did not overlap with the isotopic niche of the another species of the same taxonomic family *Ophioblennius trinitatis*, as predicted by the niche conservatism hypothesis (Peterson *et al.* 1999, 2011; Wiens & Graham 2005; Warren *et al.* 2008). However, the endemic populations presented no clear evidence of density compensation in intertidal environments. The density of *S. poiti* was 19.5 ind·m⁻³ at Trindade, while density of *S. cristata* was 157.5 ind·m⁻³ at Jericoacoara and 2.0 ind·m⁻³ at Anchieta.

4. Discussion

We tested a set of explicit hypotheses using a substantial dataset, which allowed us to provide a comprehensive overview of the composition and ecological function of tropical intertidal reefs. As expected, the $\delta^{15}\text{N}$ values were higher in the coastal organisms than the oceanic ones, which can be accounted for by the relatively high primary

productivity in coastal waters, in comparison with the islands (Mancini *et al.* 2014). While a linear increase in $\delta^{13}\text{C}$ values between coastal and offshore waters was also expected, the close link between the reef environments and estuarine habitats, which are absent on the study islands, appeared to contribute to the $\delta^{13}\text{C}$ -depleted components recorded at the coastal study sites. This is reinforced by the low $\delta^{13}\text{C}$ values of primary producers and consumers (mostly lower than -20‰) recorded by Giarrizzo *et al.* (2011) in estuarine waters on the Brazilian coast, even though estuarine and terrestrial sources did not play a clear role in the intertidal food webs. In fact, this coastal pattern, and the tendency for higher $\delta^{13}\text{C}$ values in the oceanic environments for both primary producers and consumers, require further investigation, as this was not a primary goal of the present study.

4.1 Do the intertidal communities differ in their food chain length and consumers?

Food chain length (FCL) is crucial to the understanding of community structure and ecosystem processes (Post 2002), and the longer FCLs found in the oceanic intertidal environments are likely the result of the availability of intertidal habitat at these sites, which may also influence their greater availability of trophic resources. As mentioned above, ecosystem size has a strong influence on the FCL (Post *et al.* 2000), so the interconnected intertidal reefs surrounding the study islands may have been more favorable to this parameter in comparison with the relatively limited and impacted coastal environments. In fact, habitat loss associated with coastal urban development may shorten the FCLs of adjacent reef ecosystems (Hempson *et al.* 2017), although it is important to note that some studies have found no evidence of any impact on FCLs (Warfe *et al.* 2013; Young *et al.* 2013).

The organization of the food chain was also distinct between oceanic and coastal sites, with opportunistic predators dominating the top levels of the oceanic intertidal sites. The reef fishes *Cephalopholis fulva* and *Echidna catenata*, and the yellow crab *Johngarthia lagostoma* are recognized as predators of sea turtle hatchlings in the waters around Brazilian islands (Coelho *et al.* 2012; Santos *et al.* 2016), where they take advantage of the abundance of nests of the turtle *Chelonia mydas*. These trophic interactions have resulted in synchronous emergence behaviour in the hatchlings in search of highest survival rate during their passage through the intertidal ecotone towards the open ocean (Santos *et al.* 2016). The endemic species found across the whole food chain reinforces their important ecological role in oceanic systems as key species structuring oceanic intertidal communities (Capítulo 3). In contrast with terrestrial habitats, endemic species are abundant in marine

systems (Hobbs *et al.* 2011). However, this may imply a greater vulnerability of the marine species (Dulvy *et al.* 2003; Hobbs *et al.* 2011). Habitat loss in coastal and oceanic waters is especially harmful to the intertidal fauna because their food chains contain mainly small-sized species with restricted life territories, as observed here. These threats are especially evident in coastal intertidal habitats, where small-sized resident basal and predator consumers may disappear due to acute habitat loss and changes in the coastal zone (Raffaelli & Hawkins 1996; Boström *et al.* 2011).

A further advance of the present study was the identification of the diversity of organisms occupying similar levels in intertidal food chain. Intertidal bottom-grazing trophic roles have been attributed primarily to sea urchins and gastropods in subtropical and temperate studies (Raffaelli & Hawkins 1996; Nielsen 2001; Vinagre *et al.* 2015; Bordeyne *et al.* 2017). In the present study, however, polychaetes, amphipods, small crabs, and even juvenile fish occupied the bottom layers of the intertidal food chain in both coastal and oceanic environments. The analysis of stable isotopes thus revealed new, more complex models for the ecology of tropical reef systems. In previous macroecological studies, for example, the endemic clingfishes, *Tomicodon* spp., were identified as small predators based solely on field observations (Halpern & Floeter 2008), whereas our data indicate that these fish play basal trophic roles in intertidal habitats, such as the grazing of algal turfs. The understanding of the trophic role of endemic species is fundamental to environmental planning and the evaluation of the conservation status of species or ecosystems (Keith *et al.* 2013).

4.2 Are the isotopic niches of the oceanic intertidal communities broader than those of the coastal communities?

The broader niches found in island communities initially led us to the general rules of Theory of Island Biogeography (TIB; *sensu* MacArthur & Wilson 1967), which predict that island populations or communities will have broader niches than mainland areas due to the competition release effect, which enables the exploitation of the resources available in vacant niches (MacArthur & Wilson 1967; Giller 1984). However, the TIB has been revisited by a number of authors (Losos & Ricklefs 2009; Jacquet *et al.* 2017), who have adapted or modified many approaches and hypotheses, based on novel observations of island floras and faunas (Losos & Ricklefs 2009; Pinheiro *et al.* 2017). In our study areas, in fact, Andrades *et al.* (Capítulo 3) did not observe any clear differences in species richness between coastal and oceanic sites or higher densities at the latter, which is

consistent with the results of other surveys of both plants and animals, worldwide (Helmus *et al.* 2014; Patiño *et al.* 2015). Marine habitats have received far less attention from the TIB approach, and many patterns are still unclear (Dawson 2016).

The broader niches found in the oceanic intertidal communities may be related to larger extent of the suitable reef habitat at these sites, which is presumably reflected in a greater supply of resources, which drives the higher trophic diversity and longer FCLs observed in our study. Intertidal reefs fringe most of the margins of the islands surveyed in the present study. At Rocas Atoll, all of the flat reef, with an area of 2.6 km² (c. 70% of the total territory of the atoll) can be considered to be an intertidal fringe, which is covered almost completely (c. 90%) during the flood tide, and emerges only when the tide ebbs. The coastal reefs are relatively small and sparse, by contrast, covering only 21 meters at Salinópolis, 300 m at Jericoacoara, and 58 m at Anchieta coastlines. In addition, the island reefs function as nursery grounds for juvenile fish, given the absence of estuaries and any substantial area of mangrove on the islands (Macieira *et al.* 2015; Capítulo 3), which influences all aspects of the trophic dynamics of the intertidal reefs at these sites.

Specific local factors also appear to have contributed to the observed patterns. At Salinópolis, for example, the reduced coverage of macroalgae and the lower fish species richness were influenced by the turbidity of the local estuarine waters, which limit algal growth and trophic diversity (Capítulo 3), resulting in a short FCL, and a relatively reduced community niche and $\delta^{13}\text{C}$ range. At Anchieta, by contrast, the longest FCLs of all sites were recorded, and the community niche width and $\delta^{13}\text{C}$ ranges were the highest among the coastal sites. This indicates that substrate type is a major factor influencing not only fish species richness and density, but also the diversity of food webs in intertidal reef environments (Arakaki *et al.* 2014). In fact, the structural complexity of the biogenic carbonate reefs found at Anchieta and the three islands probably provided a greater variety of suitable niches for consumers than the more homogeneous substrate of beach rocks found at Jericoacoara.

4.3 Which fish taxa are the most vulnerable in potential intraspecific and interspecific competitive interactions?

The fish taxa of intertidal waters, whether restricted or not to these environments, were identified as vulnerable when facing a high intensity of potential competitive interactions. Our findings indicated that the cryptobenthic resident reef fishes are the most vulnerable taxa (mainly to intraspecific competition). Cryptobenthic reef fishes are

characterized by relatively uncompetitive morphological (e.g., small size) and life-history traits, such as small life-territories and short life spans (Depczynski & Bellwood 2003; Jacquet *et al.* 2016; Goatley & Brandl 2017), which are partially compensated for by higher densities and patterns of microhabitat use (Depczynski & Bellwood 2004; Smith-Vaniz *et al.* 2006; Goatley & Brandl 2017), including intertidal habitats (Capítulo 3). Shorter FCLs were found in Salinópolis and Jericoacoara, where cryptobenthic species are less diverse and abundant (Capítulo 3). In fact, more structurally complex habitats tend to support higher densities and diversity of cryptobenthic fishes (Willis & Anderson 2003). In this sense, cryptobenthic reef fishes are one of the most abundant and diverse groups found in shallow reefs and were the principal reef fish taxa in our intertidal food chains. It seems reasonable to conclude that the higher niche metrics recorded in the biogenic carbonate reefs surveyed in the present study are related to the greater abundance of cryptobenthic fishes, which probably occupy single niches, supported by their small size and cryptic behavior.

Although cryptobenthic fish species can be found from intertidal to mesophotic reefs (Capítulo 3; Tornabene *et al.* 2013), in our study, many vulnerable taxa were restricted to the intertidal layers of only a few centimeters at depths of less than 1 m. These species include *Tomicodon* sp. (Trindade), *Storrsia olsoni* (Rocas Atoll), *Entomacrodus vomerinus* (Noronha), and *Gobiesox barbatulus* (Salinópolis), highlighting the unique importance of these species to the intertidal food chain. In a general competitive framework, we expected an increase in the use of resources by natural populations under high intraspecific pressure (Giller 1984; Svanback & Bolnick 2007), although intertidal cryptobenthic species have ecological traits (e.g. small body size and life territories) that limit their trophic flexibility (exploitation of large prey) and potential habitat use (subtidal habitats), and, in turn, their capacity to expand their niche in response to increased competition.

4.4 Do endemic island species present evidence of niche conservatism and density compensation in comparison with their mainland sister species?

We demonstrated that niche was partially retained by endemic species over evolutionary time, confirming the niche similarity hypothesis. *Scartella poiti* evolved from mainland species (*Scartella cristata*) during periods of reduced sea level in the Pleistocene, when the species probably dispersed through the intertidal habitats of emerged islands of the Vitória-Trindade Chain, which are now seamounts, through a stepping-stones process

(Macieira *et al.* 2015; Pinheiro *et al.* 2017). In addition to their niches, the trophic positions of the sister species were also conserved in the different intertidal communities, with *Scartella* invariably occupying the high layers of their communities. There was, however, no evidence of density compensation in the populations of the endemic species, as observed in reef fishes in previous studies (Hobbs *et al.* 2012). While some caveats need to be taken into account in the isotopic approach, including the imprecise definition of niche limits and the natural variation of the isotope signatures of different organisms, we observed a clear pattern in our data, with conservative modeling covering 95% of the predicted ellipses of the fish species, as well as the body sizes found most commonly at the intertidal study sites (Capítulo 3).

4.5 Concluding remarks

We used stable isotopes and the isotopic niche approach to construct an intertidal food chain and community niche framework for the investigation of ecological patterns between coastal and oceanic communities. The isotopic niche approach has been adopted widely in ecological studies, and the affinities with the ecological niche have been reinforced in many cases (Genner *et al.* 1999; Layman *et al.* 2007b; Brewster *et al.* 2016; Rader *et al.* 2017), which allows us to conclude that the intertidal oceanic reef environments have a rich food chain dominated by threatened endemic species in all layers. In addition, cryptobenthic resident species were the most vulnerable taxa in these environments, emphasizing the urgent need for the protection of this poorly-known fauna, which is in fact the most abundant group of vertebrates in reef environments (Goatley & Brandl 2017). The intertidal environments analyzed in the present study satisfy many of the criteria of the IUCN Red List of Ecosystems (Keith *et al.* 2013), and climate change and anthropogenic pressures are eroding the biological wealth of these ‘between the tides’ environments and their ecological services, which are being drowned, and may disappear forever.

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Table

Table 1: Niche metrics for the six intertidal reef communities: SEAc = Standard corrected ellipse area, CD = Mean distance to centroid, MNND = Mean nearest neighbour distance, SDNND = Standard deviation of the nearest neighbour distance, and CR = $\delta^{13}\text{C}$ range.

Metrics	Oceanic sites			Coastal sites		
	Rocas Atoll	Fernando de Noronha	Trindade	Salinópolis	Jericoacoara	Anchieta
SEAc	13.1	12.6	10.9	4.7	8.6	10.0
CD	2.6	2.6	2.5	1.6	1.9	2.1
MNND	1.0	0.9	0.9	0.5	0.6	0.8
SDNND	1.5	0.7	0.7	0.3	0.6	0.7
CR	11.9	11.2	10.0	3.8	6.6	7.4

Figures

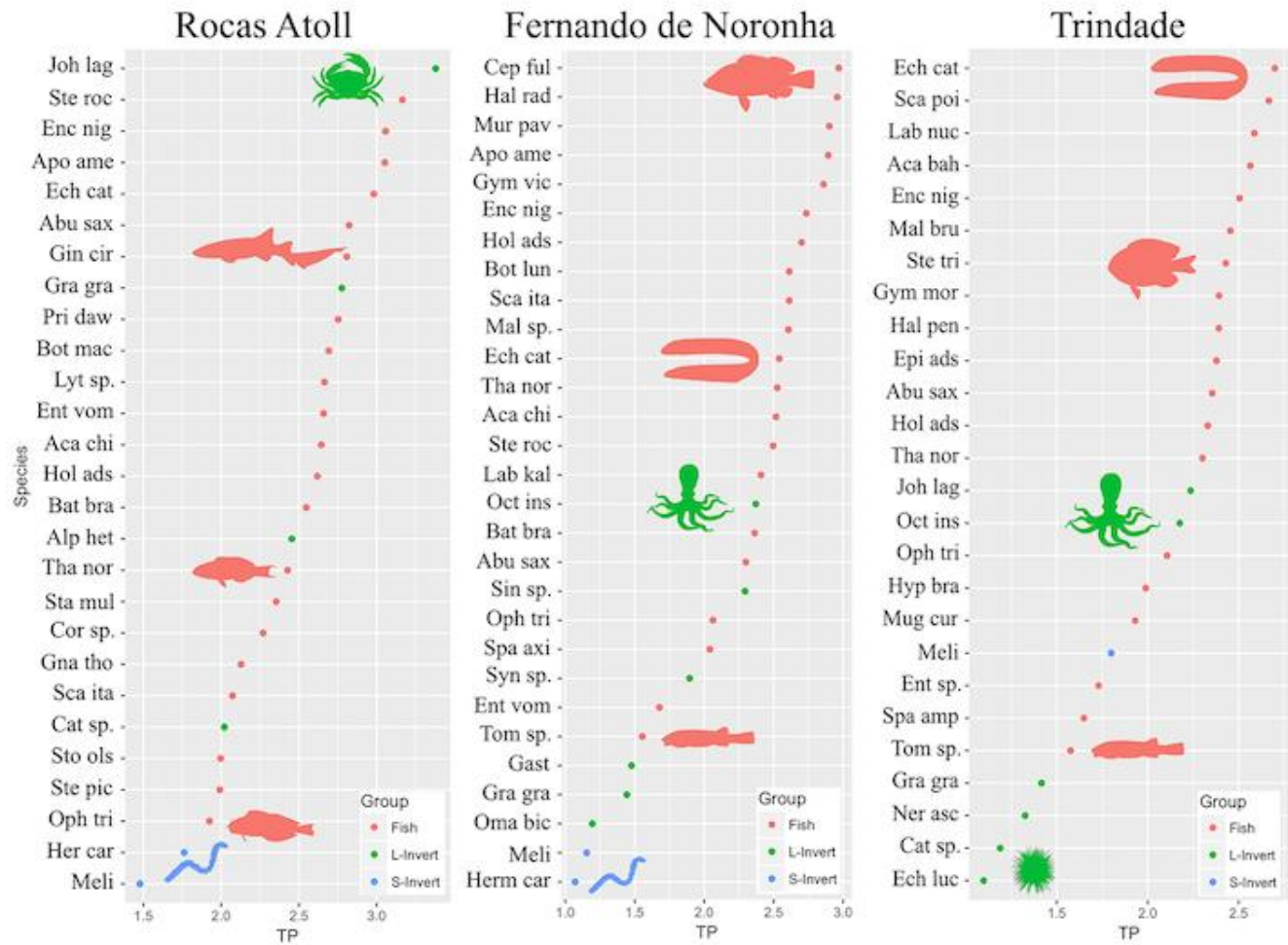


Figure 1: Species ranked by trophic position in the three oceanic intertidal environments. The acronyms of the different taxa are defined in Table S1. The trophic position (TP) is shown on the x-axis, and the species are ranked in increasing order on the y-axis.

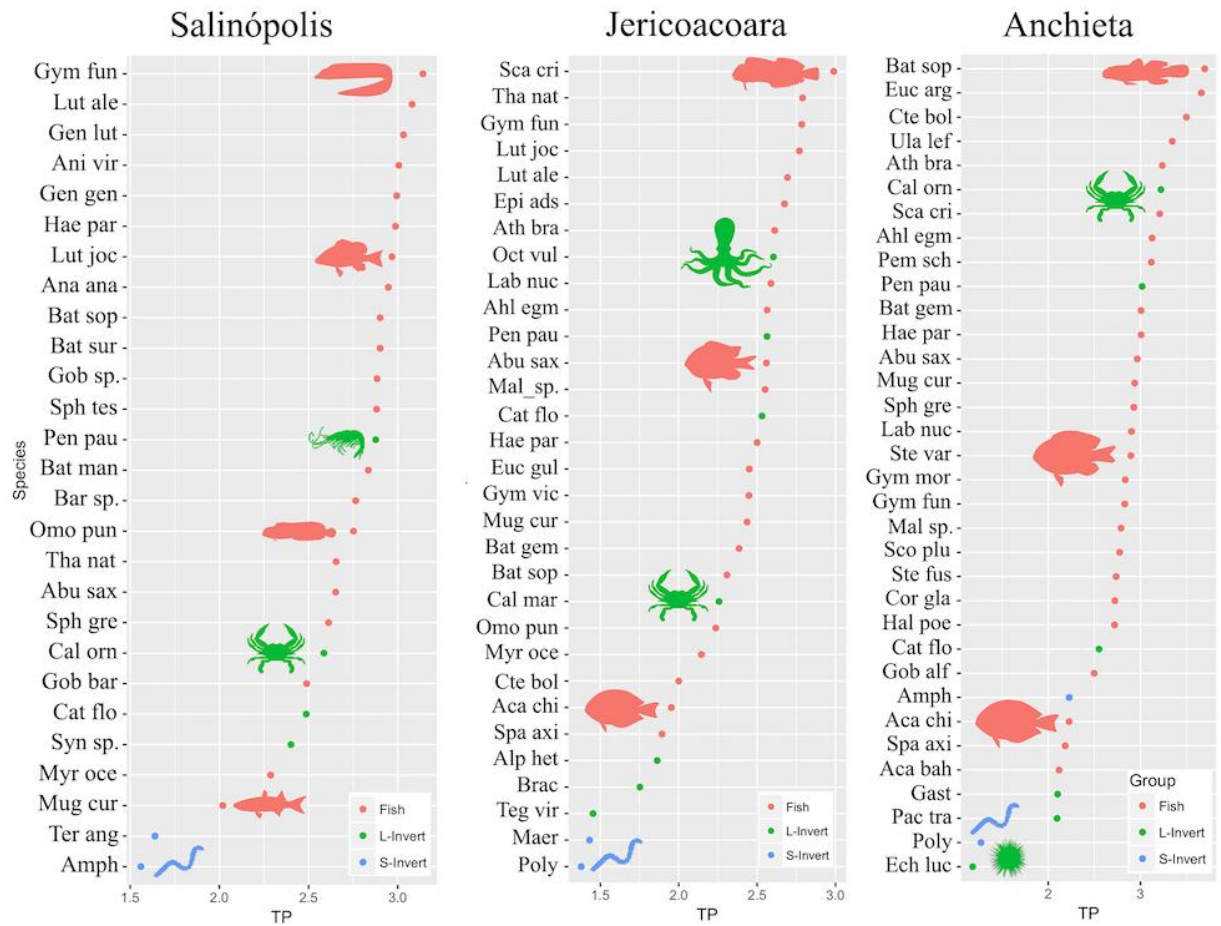


Figure 2: Species ranked by trophic position in the three coastal intertidal environments. The acronyms of the different taxa are defined in Table S1. The trophic position (TP) is shown on the x-axis, and the species are ranked in increasing order on the y-axis.

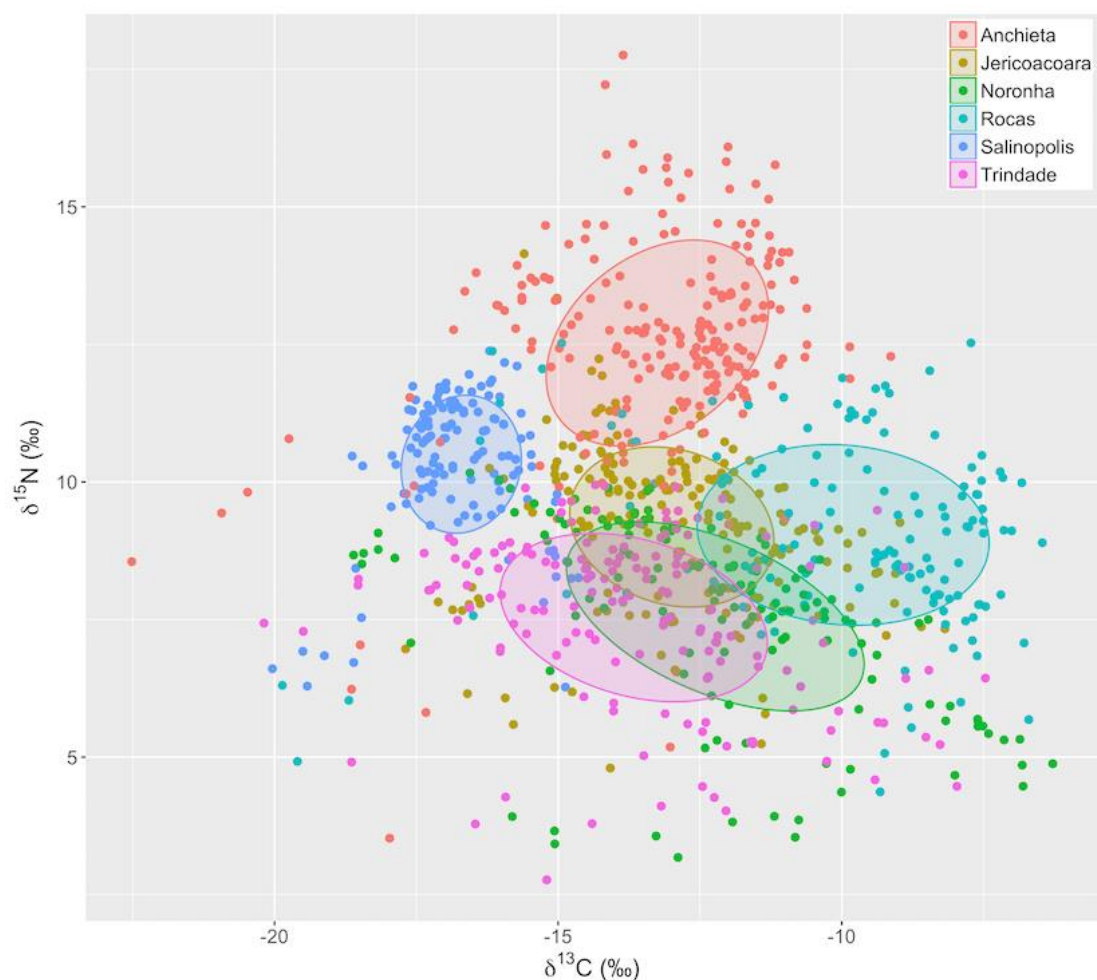


Figure 3: Standard ellipse areas (SEAc) calculated from the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of the consumers at three oceanic (Rocas, Noronha and Trindade) and three coastal (Salinópolis, Jericoacoara and Anchieta) intertidal environments. The consumer taxa are described in detail in Table S1.

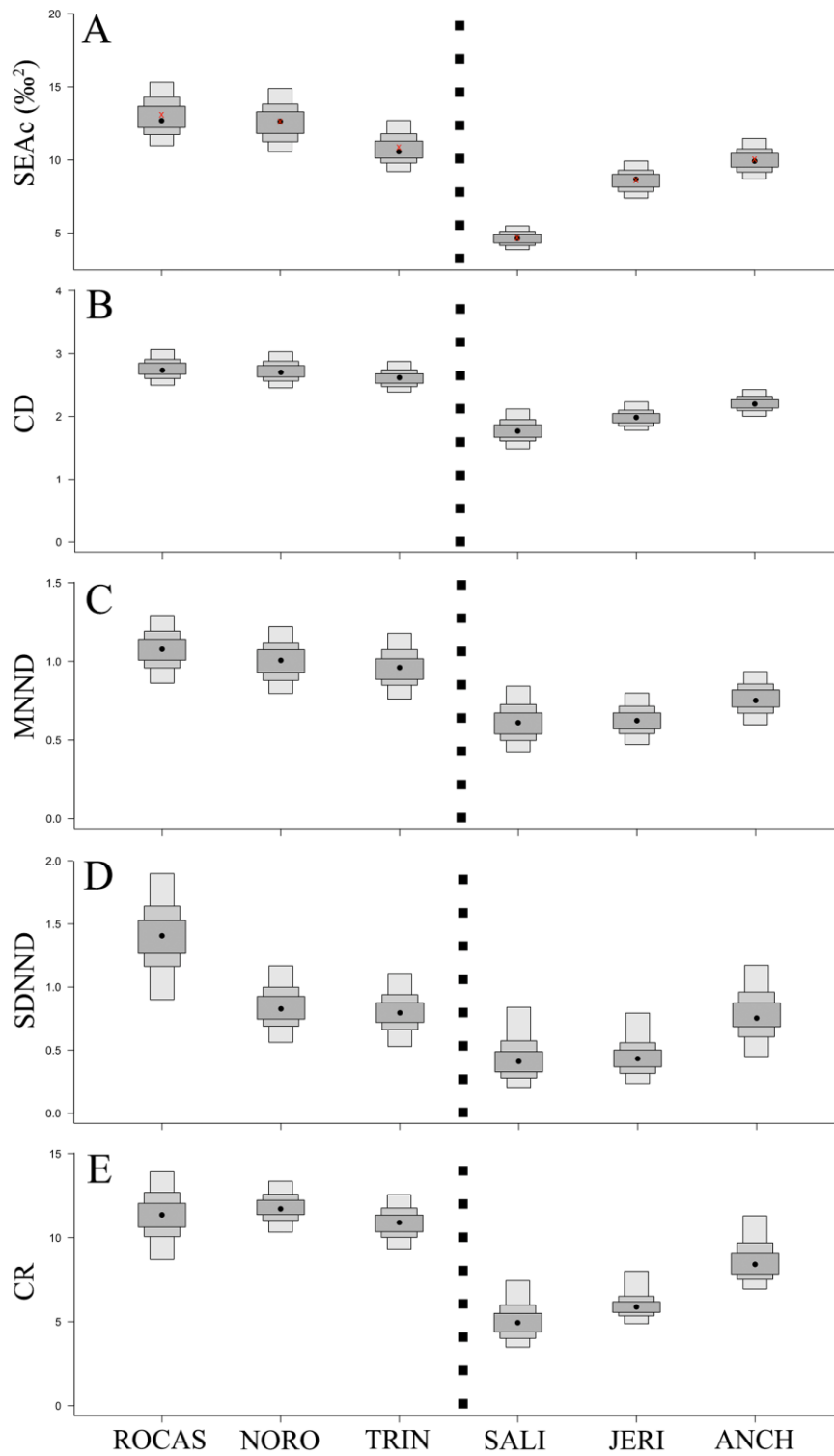


Figure 4: Isotopic niche metrics (A-E) calculated based by Bayesian Inference for the six intertidal environments (oceanic to the left and coastal to the right), ROCAS = Rocas Atoll, NORO = Fernando de Noronha, TRI = Trindade, SALI = Salinópolis, JERI = Jericoacoara and ANCH = Anchieta. A = Standard ellipse area (SEAc), B = Mean distance to centroid (CD), C = Mean nearest neighbour distance (MNND), D = Standard deviation of the nearest neighbour distance (SDNND) and E = $\delta^{13}\text{C}$ range (CR). The black dots represent the mode (%) and the boxes indicate the 50%, 75%, and 95% credibility intervals.

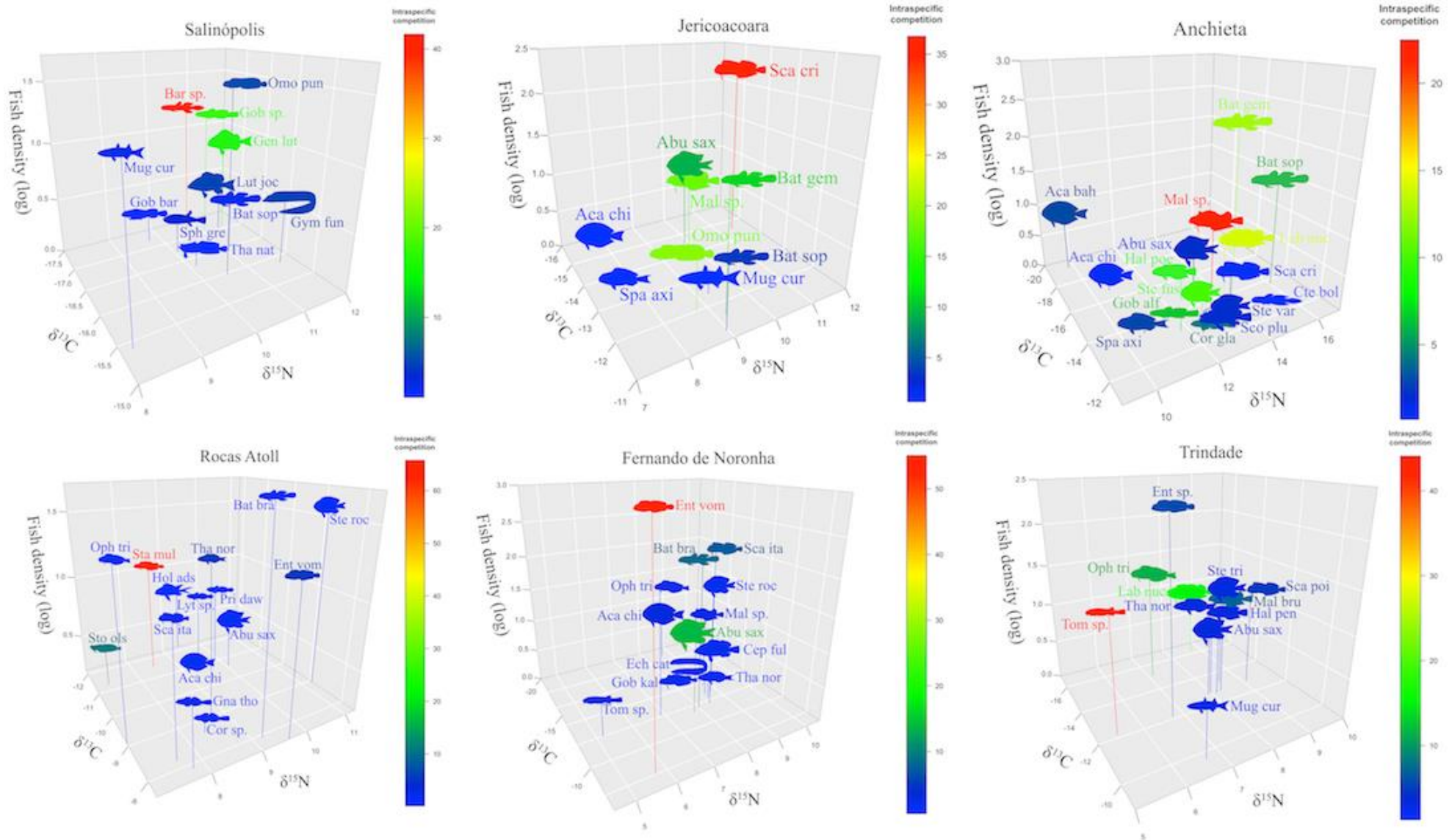


Figure 5: 3-D plots representing the fish density (ind.m^{-3}) on the z-axis, and the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures (on the x and y axes, respectively), showing the potential intraspecific interactions of the fish taxa in six intertidal environments. The acronyms of the different fish taxa are defined in Table S1. Fish colors denote the relative intensity of potential intraspecific competition within the populations of each site, as indicated by the color scale.

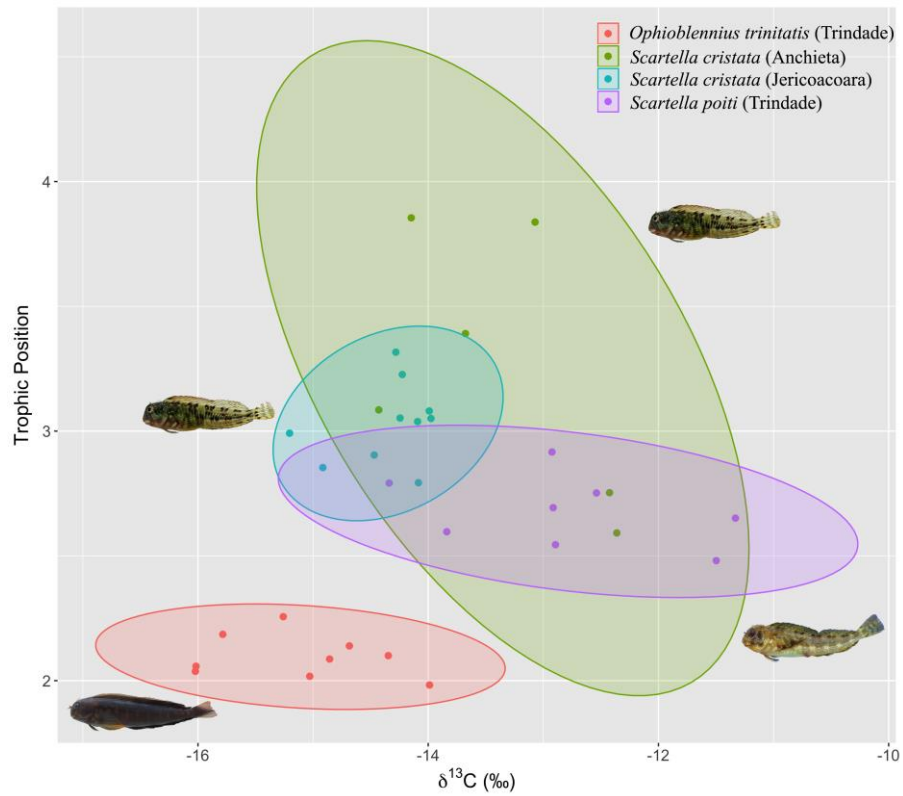


Figure 6: Overlap of the core isotopic niche ellipses (95% prediction intervals), representing the fundamental niche of the Trindade endemic *Scartella poiti* with their mainland sister species *Scartella cristata* (from Anchieta and Jericoacoara) and the sympatric blenniid *Ophioblennius trinitatis*.

Niche and competitive interactions in intertidal reefs: a stable isotopes approach

Ryan Andrades et al.

Supporting Information

Methods - Studied sites in the South Atlantic

Oceanic sites

Rocas Atoll (03°51' S; 33°49' W) is the only atoll in the South Atlantic far from 266 km of mainland (Rio Grande do Norte state) presenting an elliptical shaping and built primarily by coralline algae, vermetid gastropods and hermatypic corals. Tidal regime is semidiurnal mesotides with maximum height of 3.8 meters, which covers almost entire atoll, including all tidepools, during the high tides (Gherardi & Bosence 2001). The climate is Tropical with water temperature and salinities values in tidepools ranging from 28°C to 34°C and from 35 to 39, respectively (present study). Rocas Atoll probably poses as the most near-pristine area of the southwestern Atlantic being the first marine reserve established in Brazil (1978), however the effective monitoring only began in 1991 (Longo *et al.* 2015).

Fernando de Noronha Archipelago (03°50' S; 32°25' W) is located far 345 km from mainland (Rio Grande do Norte state) in the same volcanic ridge that shelters Rocas Atoll but comprises a set of islands, which has basaltic rocky shores dominating the intertidal environments. The present study was conducted in the main island, Fernando de Noronha, where phonolitic rocky intertidal reefs often occurring associated with biogenic carbonate substrate composed by encrusting coralline algae. Tidal regime is semidiurnal with mesotides reaching 3.2 meters of maximum height. The climate is Tropical with mean air temperature around 25°C and water temperature 27°C (Castro 2009). In tidepools, water temperature varied from 27°C to 35°C and water salinity from 35 to 40 (Capítulo 3). Most of Fernando de Noronha territory is included in a National Marine Park created in 1988 ensuring protection

from fishing activities and controlling tourism visitation. Also, in 2001 Fernando de Noronha and Rocas Atoll (named as Brazilian Atlantic Islands) were declared as a World Heritage Site by UNESCO (United Nations Educational, Scientific and Cultural Organization) due to poses an oasis to marine wildlife with productive waters and huge presence of endemic and endangered species such as seabirds, turtles and reef fish (UNESCO 2017).

Trindade Island (20°30' S; 29°20' W) is a tropical island located 1160 km off the coast of Espírito Santo state comprising the most isolated insular environment of Brazilian Province (*sensu* Briggs & Bowen 2012). Trindade and Martin Vaz Archipelago is the only emerged site and the eastern end of the Vitória-Trindade submarine chain (VTC). The VTC comprises a set of 17 volcanic seamounts sheltering rich fish fauna and benthic reef habitats, which has functioned as stepping-stones in order to connecting reef organisms along the VTC (Pinheiro, Joyeux & Moura 2014; Pinheiro *et al.* 2015). Among Brazilian oceanic islands, Trindade have the highest reef fish endemism rate (9.6%; Pinheiro *et al.* 2015), however is the youngest island dating from 3.7 Ma in contrast to oldest Fernando de Noronha-Rocas Atoll complex (12.3 Ma) and Saint Peter and Saint Paul's Archipelago (9 Ma) (Ferrari & Riccomini 1999; Hekinian *et al.* 2000; Castro 2009). The intertidal habitats of Trindade are encompassed by biogenic carbonate (mostly encrusting coralline algae) and phonolitic rocky substrates with semidiurnal microtidal regime reaching 1.7 maximum height (Macieira *et al.* 2015). In the present study, water temperature in tidepools varied from 27°C to 34°C and water salinities from 35 to 41. Since 1957 the Brazilian Navy occupies the island for military-strategic reasons, where is established a Navy Oceanographic Station (POIT – Posto Oceanográfico da Ilha da Trindade). Public visitation is restricted only to research and military purposes.

Coastal sites

Salinópolis (00°36' S; 47°21' W) is located in northern region of Brazil (Amazonian region, Pará state) under moderated influence of Amazonian river mouth and high influence of medium and small estuaries distributed along Pará coastline. In Salinópolis, intertidal reefs derived from Pirabas Formation (Early Miocene) comprising a biogenic carbonatic reefs composed mainly by coralline algae, corals, sponges and bryozoans (Távora, Neto & Maciel 2013) with relatively low coverage of macroalgae. Tidepools recorded water temperatures and salinities ranging from 31°C

to 35°C and from 36 to 41, respectively (Capítulo 3). Tidal regime is semidiurnal macrotides can reach up to 5 meters of maximum height (sometimes over it). Salinópolis is the main touristic beach-spot in the Pará coastline, mainly during the bathing season (Adrião 2006), which results in a higher human-related impacts on the beach such as organism removal and reef trampling.

Jericoacoara beach (02°47' S; 40°30' W) is situated in northeastern Brazil with less riverine influence and governed by semidiurnal mesotides with maximum height of 4 meters. Quartzite beach rocks with low complexity tidepools covered by dense fleshy macroalgae dominated the intertidal. Seasonally, harsh erosional events driven by sand-dune sediment occurred changing the intertidal-scape covering and uncovering tidepools. Water temperature and salinities in tidepools varied from 29°C to 32°C and from 39 to 41, respectively (Capítulo 3). The beach is inserted into Jericoacoara National Park created in 2002, an area of *ca.* 9 hectares comprised by sand dunes, mangrove areas, subtidal and intertidal shores, however public visitation is common and promoted.

Anchieta is a city of Espírito Santo state, southeastern Brazil, which shelters Castelhanos Beach (20°49' S; 40°36' W), a tropical carbonatic flat reef composed mainly by encrusting coralline algae and stony coral skeletons (Macieira & Joyeux 2011). Fleshy macroalgae and sessile animals (sea urchins and zoanthids) are abundant in tidepools. Water temperature and salinities varied from 24°C to 35°C and 36 to 41, respectively. Tidal regime is semidiurnal microtides can reaching up to 1.8 meters (Macieira & Joyeux 2011). As similar to aforementioned for coastal beaches, Castelhanos Beach is a touristic beach, which suffers several human-related impacts such as reef trampling, organism removal and fishing.

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Niche and competitive interactions in intertidal reefs: a stable isotopes approach

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Tables and figures - Supporting Information

Tables – Supporting Information

Table S1: Family (*or major group), taxa, taxa acronyms, size range (mm), $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ mean values (‰) and n sample size (**pooled individuals) of intertidal consumers collected in tropical environments. Body sizes in fish, polychaetes and shrimps taxa denote total length and crab taxa denote carapace width. Non-identified taxa are referred as ni.

Family*	Taxa	Acronyms	Body size (mm)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	n
ROCAS ATOLL						
Invertebrates						
Alpheidae	<i>Alpheus heterochaelis</i>	Alp het	20–41	-8.7	8.7	3
Amphinomidae	<i>Hermodice carunculata</i>	Her car	35–66	-9.6	6.6	3
Gecarcinidae	<i>Johngarthia lagostoma</i>	Joh lag	71–84	-15.6	12.1	4
Grapsidae	<i>Grapsus Grapsus</i>	Gra gra	83–98	-7.5	10.1	4
Melitidae	Melitidae ni	Meli		-19.4	5.8	3**
Xanthidae	<i>Cataleptodius</i> sp.	Cat flo	14–22	-8.5	7.1	3
Fish						
Acanthuridae	<i>Acanthurus chirurgus</i>	Aca chi	73–125	-11.3	9.6	10
Apogonidae	<i>Apogon americanus</i>	Apo ame	51–86	-13.9	11.0	3
Blenniidae	<i>Entomacrodus vomerinus</i>	Ent vom	82–96	-7.6	9.6	8
Blenniidae	<i>Ophioblennius trinitatis</i>	Oph tri	71–97	-9.1	7.1	6
Blenniidae	<i>Scartella itajobi</i>	Sca ita	32–46	-8.2	7.6	10
Bothidae	<i>Bothus maculiferus</i>	Bot mac	167	-10.2	9.9	1
Dactyloscopidae	<i>Storrsia olsoni</i>	Sto ols	22–25	-11.3	7.3	3
Ginglymostomatidae	<i>Ginglymostoma cirratum</i>	Gin cir	280	-12.1	9.4	1
Gobiidae	<i>Bathygobius brasiliensis</i>	Bat bra	52–74	-7.9	9.2	10
Gobiidae	<i>Coryphopterus</i> sp.	Cor sp.	42–60	-8.6	8.4	9
Gobiidae	<i>Gnatholepis thompsoni</i>	Gna tho	29–54	-7.9	7.8	10
Gobiidae	<i>Lythrypnus</i> sp.	Lyt sp.	15–19	-11.4	9.6	3
Gobiidae	<i>Priolepis dawsoni</i>	Pri daw	19–33	-11.1	9.9	3
Holocentridae	<i>Holocentrus adscencionis</i>	Hol ads	105–134	-12.2	9.4	10
Labridae	<i>Thalassoma noronhanum</i>	Tha nor	54–84	-9.1	8.8	10
Labrisomidae	<i>Starksia multileps</i>	Sta mul	24–27	-11.5	8.5	4
Muraenidae	<i>Echidna catenata</i>	Ech cat	490–562	-9.2	10.8	3
Muraenidae	<i>Enchelycore nigricans</i>	Enc nig	476	-16.4	10.7	1
Pomacentridae	<i>Abudefduf saxatilis</i>	Abu sax	58–84	-10.6	10.0	8
Pomacentridae	<i>Stegastes pictus</i>	Ste pic	33	-16.5	7.6	1
Pomacentridae	<i>Stegastes rocasensis</i>	Ste roc	51–75	-8.9	11.3	10
FERNANDO DE NORONHA						
Invertebrates						
Alpheidae	<i>Synalpheus</i> sp.	Syn sp.	37–40	-12.4	6.2	3
Amphinomidae	<i>Hermodice carunculata</i>	Her car	39–56	-12.3	3.4	3
Gastropoda	Gastropoda ni	Gast		-10.7	4.8	3
Grapsidae	<i>Grapsus Grapsus</i>	Gra gra	82–90	-7.0	4.7	4
Melitidae	Melitidae ni	Meli		-15.3	3.7	3**
Mithracidae	<i>Omalacantha bicornuta</i>	Oma bic	13–19	-11.3	3.9	3

	Octopodidae	<i>Octopus insularis</i>	Oct ins		-11.4	7.7	3
	Sicyoniidae	<i>Sicyonia</i> sp.	Sic sp.	28–34	-11.4	7.6	3
Fish							
	Acanthuridae	<i>Acanthurus chirurgus</i>	Aca chi	37–61	-18.2	8.5	7
	Apogonidae	<i>Apogon americanus</i>	Apo ame	51–86	-14.5	9.4	7
	Blenniidae	<i>Entomacrodus vomerinus</i>	Ent vom	51–79	-7.6	5.6	10
	Blenniidae	<i>Ophioblennius trinitatis</i>	Oph tri	73–78	-11.6	6.8	5
	Blenniidae	<i>Scartella itajobi</i>	Sca ita	48–67	-12.3	8.6	5
	Bothidae	<i>Bothus lunatus</i>	Bot lun	121–205	-15.0	8.7	2
	Epinephelidae	<i>Cephalopholis fulva</i>	Cep ful	43–58	-16.1	9.9	3
	Gobiesocidae	<i>Tomicodon</i> sp.	Tom sp.	20–23	-11.5	5.1	3
	Gobiidae	<i>Bathygobius brasiliensis</i>	Bat bra	51–80	-11.2	7.8	10
	Holocentridae	<i>Holocentrus adscensionis</i>	Hol ads	129–149	-12.8	8.9	5
	Labridae	<i>Halichoeres radiatus</i>	Hal rad	73	-13.9	9.3	1
	Labridae	<i>Sparisoma axillare</i>	Spa axi	82	-15.1	6.6	1
	Labridae	<i>Thalassoma noronhanum</i>	Tha nor	43–66	-11.8	8.4	10
	Labrisomidae	<i>Gobioclinus kalisherae</i>	Gob kal	38–72	-14.1	8.0	3
	Labrisomidae	<i>Malacoctenus</i> sp.	Mal sp.	40–53	-13.1	8.6	9
	Muraenidae	<i>Echidna catenata</i>	Ech cat	257–713	-12.2	8.4	11
	Muraenidae	<i>Enchelycore nigricans</i>	Enc nig	243–393	-13.3	8.8	2
	Muraenidae	<i>Gymnothorax vicinus</i>	Gym vic	477–556	-13.8	9.5	3
	Muraenidae	<i>Muraena pavonina</i>	Mur pav	228	-15.2	9.0	1
	Pomacentridae	<i>Abudefduf saxatilis</i>	Abu sax	45–81	-10.9	7.6	5
	Pomacentridae	<i>Stegastes rocasensis</i>	Ste roc	50–86	-11.3	8.2	10
TRINDADE							
Invertebrates							
	Echinometridae	<i>Echinometra lucunter</i>	Ech luc		-15.9	3.6	3
	Gecarcinidae	<i>Johngarthia lagostoma</i>	Joh lag	79–91	-19.2	7.8	4
	Grapsidae	<i>Grapsus Grapsus</i>	Gra gra	81–95	-9.2	4.9	4
	Melitidae	Melitidae ni	Meli		-14.2	6.0	3**
	Neritidae	<i>Nerita ascensionis</i>	Ner asc		-13.0	4.5	3
	Octopodidae	<i>Octopus insularis</i>	Oct ins		-14.0	7.3	3
	Xanthidae	<i>Cataleptodius</i> sp.	Cat sp.	15–21	-12.9	4.0	3
Fish							
	Acanthuridae	<i>Acanthurus bahianus</i>	Aca bah	91–124	-14.4	8.6	9
	Blenniidae	<i>Entomacrodus</i> sp.	Ent sp.	42–69	-10.3	6.0	10
	Blenniidae	<i>Hypleurochilus brasil</i>	Hyp bra	28	-15.6	7.2	1
	Blenniidae	<i>Ophioblennius trinitatis</i>	Oph tri	79–93	-15.1	7.1	9
	Blenniidae	<i>Scartella poiti</i>	Sca poi	43–70	-12.8	9.1	8
	Epinephelidae	<i>Epinephelus adscensionis</i>	Epi ads	90–99	-15.3	8.1	2
	Gobiesocidae	<i>Tomicodon</i> sp.	Tom sp.	11–21	-12.2	5.4	8
	Holocentridae	<i>Holocentrus adscensionis</i>	Hol ads	79–93	-16.6	8.0	10
	Labridae	<i>Halichoeres penrosei</i>	Hal pen	62–90	-12.6	8.1	6
	Labridae	<i>Sparisoma amplum</i>	Spa amp	63	-18.6	4.9	1
	Labridae	<i>Thalassoma noronhanum</i>	Tha nor	44–60	-12.8	7.9	10
	Labrisomidae	<i>Labrisomus nuchipinnis</i>	Lab nuc	135–157	-16.3	8.7	10

Labrisomidae	<i>Malacoctenus bruno</i>	Mal bru	38–47	-13.3	8.5	10
Mugilidae	<i>Mugil curvidens</i>	Mug cur	42–68	-9.7	6.7	6
Muraenidae	<i>Echidna catenata</i>	Ech cat	365–658	-15.0	9.1	8
Muraenidae	<i>Enchelycore nigricans</i>	Eng nig	655–762	-15.8	8.6	2
Muraenidae	<i>Gymnothorax moringa</i>	Gym mor	618	-16.4	8.4	1
Pomacentridae	<i>Abudefduf saxatilis</i>	Abu sax	47–74	-12.7	8.0	7
Pomacentridae	<i>Stegastes trinidadensis</i>	Ste tri	48–83	-12.7	8.3	10

SALINÓPOLIS

Invertebrates

Alpheidae	<i>Synalpheus</i> sp.	Syn sp.	34–36	-16.8	9.4	3
Amphipoda	Amphipoda ni	Amph		-19.2	6.6	3**
Penaeidae	<i>Penaeus paulensis</i>	Pen pau	25–29	-16.9	11.0	3
Porcellanidae	<i>Petrolisthes galathinus</i>	Pet gal		-18.7	6.8	3
Portunidae	<i>Calinectes ornatus</i>	Cal orn	55–69	-15.9	10.1	4
Trichobranchidae	<i>Terebellides anguicomus</i>	Ter ang	25–41	-19.2	7.0	3
Xanthidae	<i>Cataleptodius floridanus</i>	Cat flo	47–58	-15.5	9.6	4

Fish

Anablepidae	<i>Anableps anableps</i>	Ana ana	70–111	-16.7	11.2	8
Ariidae	<i>Genidens genidens</i>	Gen gen	81	-16.4	11.7	1
Batrachoididae	<i>Batrachoides manglae</i>	Bat man	320	-16.0	11.0	1
Batrachoididae	<i>Batrachoides surinamensis</i>	Bat sur	155	-16.0	11.5	1
Batrachoididae	<i>Thalassophryne nattereri</i>	Tha nat	100–123	-16.3	10.1	3
Blenniidae	<i>Omobranchus punctatus</i>	Omo pun	57–79	-16.0	10.5	9
Gobiesocidae	<i>Gobiesox barbatulus</i>	Gob bar	53–73	-17.2	9.8	10
Gobiidae	<i>Barbulifer</i> sp.	Bar sp.	23–30	-17.3	10.8	6
Gobiidae	<i>Bathygobius soporator</i>	Bat sop	54–78	-16.4	11.0	10
Gobiidae	<i>Gobiosoma</i> sp.	Gob sp.	25–38	-17.1	11.1	8
Haemulidae	<i>Anisotremus virginicus</i>	Ani vir	69	-17.6	11.3	1
Haemulidae	<i>Genyatremus luteus</i>	Gen lut	93–130	-17.1	11.5	10
Haemulidae	<i>Haemulon parra</i>	Hae par	81	-16.1	11.1	1
Lutjanidae	<i>Lutjanus jocu</i>	Lut joc	108–128	-17.0	11.4	8
Lutjanidae	<i>Lutjanus alexandrei</i>	Lut ale	143	-17.1	11.7	1
Mugilidae	<i>Mugil curema</i>	Mug cur	26–34	-15.4	8.2	10
Muraenidae	<i>Gymnothorax funebris</i>	Gym fun	280–649	-15.9	11.7	4
Ophichthidae	<i>Myrichthys ocellatus</i>	Myr oce	432	-16.0	9.5	1
Pomacentridae	<i>Abudefduf saxatilis</i>	Abu sax	64–81	-17.9	10.4	6
Tetraodontidae	<i>Sphoeroides greeleyi</i>	Sph gre	69–110	-16.7	10.1	9
Tetraodontidae	<i>Sphoeroides testudineus</i>	Sph tes	137	-17.4	10.7	1

JERICOACOARA

Invertebrates

Alpheidae	<i>Alpheus heterochaelis</i>	Alp het	18–20	-13.0	7.4	3
Brachyura n.i.	Brachyura ni	Brac		-12.7	6.9	3
Maeridae	Maeridae ni	Maer		-15.6	6.0	3**
Octopodidae	<i>Octopus vulgaris</i>	Oct vul		-13.0	9.7	2
Penaeidae	<i>Penaeus paulensis</i>	Pen pau	21–31	-12.4	9.7	3

	Polychaeta	Polychaeta n.i.	Poly	21–37	-15.1	5.7	3
	Portunidae	<i>Callinectes marginatus</i>	Cal mar	63–67	-11.2	8.6	4
	Tegulidae	<i>Tegula viridula</i>	Teg vir		-11.4	5.7	3
	Xanthidae	<i>Cataleptodius floridanus</i>	Cat flo	23–38	-13.5	9.7	4
Fish							
	Acanthuridae	<i>Acanthurus chirurgus</i>	Aca chi	41–74	-15.6	7.7	10
	Atherinopsidae	<i>Atherinella brasiliensis</i>	Ath bra	93–130	-14.5	9.9	10
	Batrachoididae	<i>Thalassophryne nattereri</i>	Tha nat	150	-14.9	10.1	1
	Blenniidae	<i>Omobranchus punctatus</i>	Omo pun	43–54	-11.9	8.7	3
	Blenniidae	<i>Scartella cristata</i>	Sca cri	58–78	-14.3	11.3	10
	Epinephelidae	<i>Epinephelus adscensionis</i>	Epi ads	123–188	-12.1	10.2	8
	Gerreidae	<i>Eucinostomus gula</i>	Euc gul	91–111	-11.3	9.4	10
	Gobiidae	<i>Bathygobius geminatus</i>	Bat gem	39–60	-11.5	9.1	10
	Gobiidae	<i>Bathygobius soporator</i>	Bat sop	44–84	-11.1	8.9	10
	Gobiidae	<i>Ctenogobius boleosoma</i>	Cte bol	24–36	-9.0	7.5	5
	Haemulidae	<i>Haemulon parra</i>	Hae par	61–97	-12.9	9.6	8
	Labridae	<i>Sparisoma axillare</i>	Spa axi	65–81	-13.6	7.6	10
	Labrisomidae	<i>Labrisomus nuchipinnis</i>	Lab nuc	75–106	-14.5	9.7	2
	Labrisomidae	<i>Malacoctenus</i> sp.	Mal sp.	32–59	-14.1	9.8	10
	Lutjanidae	<i>Lutjanus alexandrei</i>	Lut ale	94–131	-12.3	10.2	10
	Lutjanidae	<i>Lutjanus jocu</i>	Lut joc	90–136	-13.4	10.5	10
	Mugilidae	<i>Mugil curema</i>	Mug cur	84–103	-12.2	9.2	10
	Muraenidae	<i>Gymnothorax funebris</i>	Gym fun	137–821	-13.1	10.5	6
	Muraenidae	<i>Gymnothorax vicinus</i>	Gym vic	110–220	-12.7	9.3	3
	Ophichthidae	<i>Ahlia egmontis</i>	Ahl egm	240	-13.4	9.1	1
	Ophichthidae	<i>Myrichthys ocellatus</i>	Myr oce	273–410	-13.4	8.2	2
	Pomacentridae	<i>Abudefduf saxatilis</i>	Abu sax	42–80	-14.3	9.8	9
ANCHIETA							
Invertebrates							
	Amphipoda	Amphipoda ni	Amph		-14.4	10.5	3**
	Echinometridae	<i>Echinometra lucunter</i>	Ech luc		-18.2	6.4	3
	Gastropoda	Gastropoda ni	Gast		-11.0	9.3	1
	Grapsidae	<i>Pachygrapsus transversus</i>	Pac tra	13–16	-12.0	9.7	3
	Penaeidae	<i>Penaeus paulensis</i>	Pen pau	23–26	-11.3	13.1	3
	Portunidae	<i>Callinectes ornatus</i>	Cal orn	59–89	-11.7	13.7	3
	Xanthidae	<i>Cataleptodius floridanus</i>	Cat flo	26–49	-12.5	11.6	4
Fish							
	Acanthuridae	<i>Acanthurus bahianus</i>	Aca bah	78–128	-18.5	9.6	5
	Acanthuridae	<i>Acanthurus chirurgus</i>	Aca chi	61–95	-16.0	10.4	9
	Atherinopsidae	<i>Atherinella brasiliensis</i>	Ath bra	70–102	-15.1	13.9	10
	Blenniidae	<i>Scartella cristata</i>	Sca cri	38–57	-13.4	13.9	6
	Gerreidae	<i>Eucinostomus argenteus</i>	Euc arg	93–107	-11.5	15.2	3
	Gerreidae	<i>Ulaema lefroyi</i>	Ula lef	107–126	-11.1	13.9	10
	Gobiidae	<i>Bathygobius geminatus</i>	Bat gem	38–51	-11.8	12.9	10
	Gobiidae	<i>Bathygobius soporator</i>	Bat sop	48–73	-13.2	15.5	9
	Gobiidae	<i>Coryphopterus glaucofrenum</i>	Cor gla	24–38	-12.0	12.0	10

Gobiidae	<i>Ctenogobius boleosoma</i>	Cte bol	30–49	-12.1	14.7	9
Gobiidae	<i>Gobiosoma alfiei</i>	Gob alf	16–25	-12.5	11.5	10
Haemulidae	<i>Haemulon parra</i>	Hae par	64–83	-12.3	13.1	4
Labridae	<i>Halichoeres poeyi</i>	Hal poe	70–97	-14.0	12.3	9
Labridae	<i>Sparisoma axillare</i>	Spa axi	65–92	-13.0	10.5	6
Labrisomidae	<i>Labrisomus nuchipinnis</i>	Lab nuc	102–126	-12.4	12.9	10
Labrisomidae	<i>Malacoctenus</i> sp.	Mal sp.	44–51	-12.2	12.4	10
Mugilidae	<i>Mugil curema</i>	Mug cur	85	-9.1	12.3	1
Muraenidae	<i>Gymnothorax funebris</i>	Gym fun	100–490	-12.6	12.4	5
Muraenidae	<i>Gymnothorax moringa</i>	Gym mor	220–573	-13.1	12.6	3
Ophichthidae	<i>Ahlia egmontis</i>	Ahl egm	129–235	-13.2	13.3	2
Pempheridae	<i>Pempheris schomburgkii</i>	Pem sch	60–79	-15.4	13.5	9
Pomacentridae	<i>Abudefduf saxatilis</i>	Abu sax	44–63	-14.6	13.1	10
Pomacentridae	<i>Stegastes fuscus</i>	Ste fus	43–74	-12.5	12.2	10
Pomacentridae	<i>Stegastes variabilis</i>	Ste var	45–55	-12.7	12.9	9
Scorpaenidae	<i>Scorpaena plumieri</i>	Sco plu	80–161	-12.0	12.3	5
Tetraodontidae	<i>Sphoeroides greeleyi</i>	Sph gre	80–136	-14.7	13.0	10

TableS2: Stable isotopes mean values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and sample size (n) of primary producers collected in intertidal studied sites

Site		$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	n
ROCAS ATOLL				
MACROALGAE				
	Ochrophyta	-13.3	5.1	3
	Rhodophyta	-13.7	3.0	3
POM				
	Particulate organic matter	-18.5	3.9	6
FERNANDO DE NORONHA				
MACROALGAE				
	Cholophyta	-17.1	3.1	3
	Ochrophyta	-14.4	3.4	3
	Rhodophyta	-11.9	2.7	3
POM				
	Particulate organic matter	-20.7	3.4	6
TRINDADE				
MACROALGAE				
	Cholophyta	-14.7	1.9	3
	Ochrophyta	-15.8	3.6	3
	Rhodophyta	-17.6	3.3	3
	Turf algae	-15.0	4.3	6
POM				
	Particulate organic matter	-21.6	3.7	6
SALINÓPOLIS				
MACROALGAE				
	Cholophyta	-17.1	3.8	3
	Rhodophyta	-18.4	5.8	3
POM				
	Particulate organic matter	-25.0	4.9	6
JERICOACOARA				
MACROALGAE				
	Cholophyta	-12.0	5.1	3
	Ochrophyta	-18.4	4.0	3
	Rhodophyta	-12.4	4.8	3
	Turf algae	-23.8	3.5	6
POM				
	Particulate organic matter	-23.8	3.5	6
ANCHIETA				
MACROALGAE				
	Cholophyta	-15.7	6.7	3
	Ochrophyta	-13.3	6.8	3
	Rhodophyta	-16.6	6.1	3
	Turf algae	-12.9	6.9	6
POM				
	Particulate organic matter	-22.7	4.7	6

Figures – Supporting Information

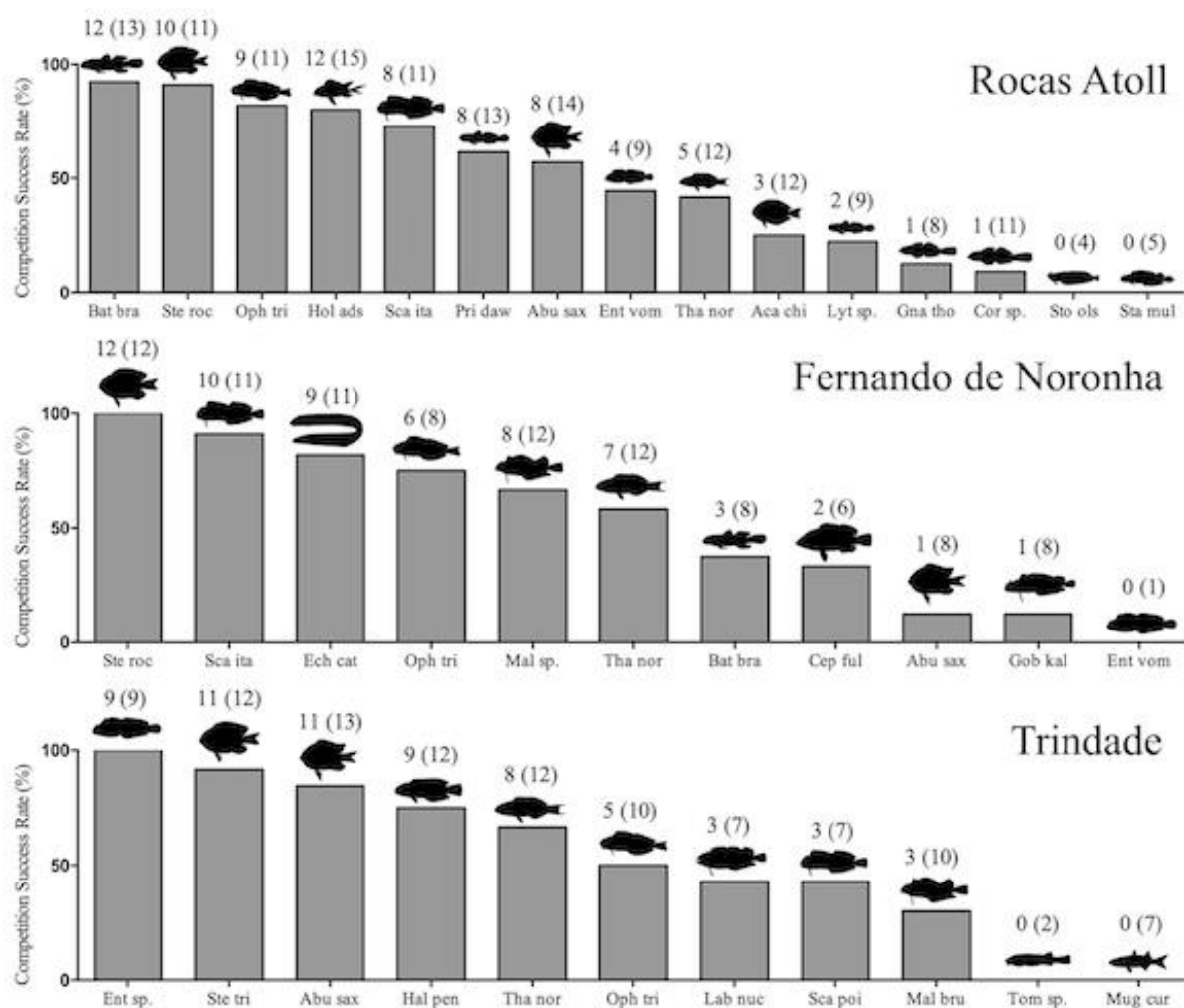


Figure S1: Potential competition success rate among oceanic intertidal taxa. Numbers above fish draws denote number of successful interactions between potential competitors and numbers into the parentheses denote numbers of potential competitors of each species showed through the isotopic niche overlap in a δ -space plot. Potential pairwise interactions were calculated via species competition proxy.

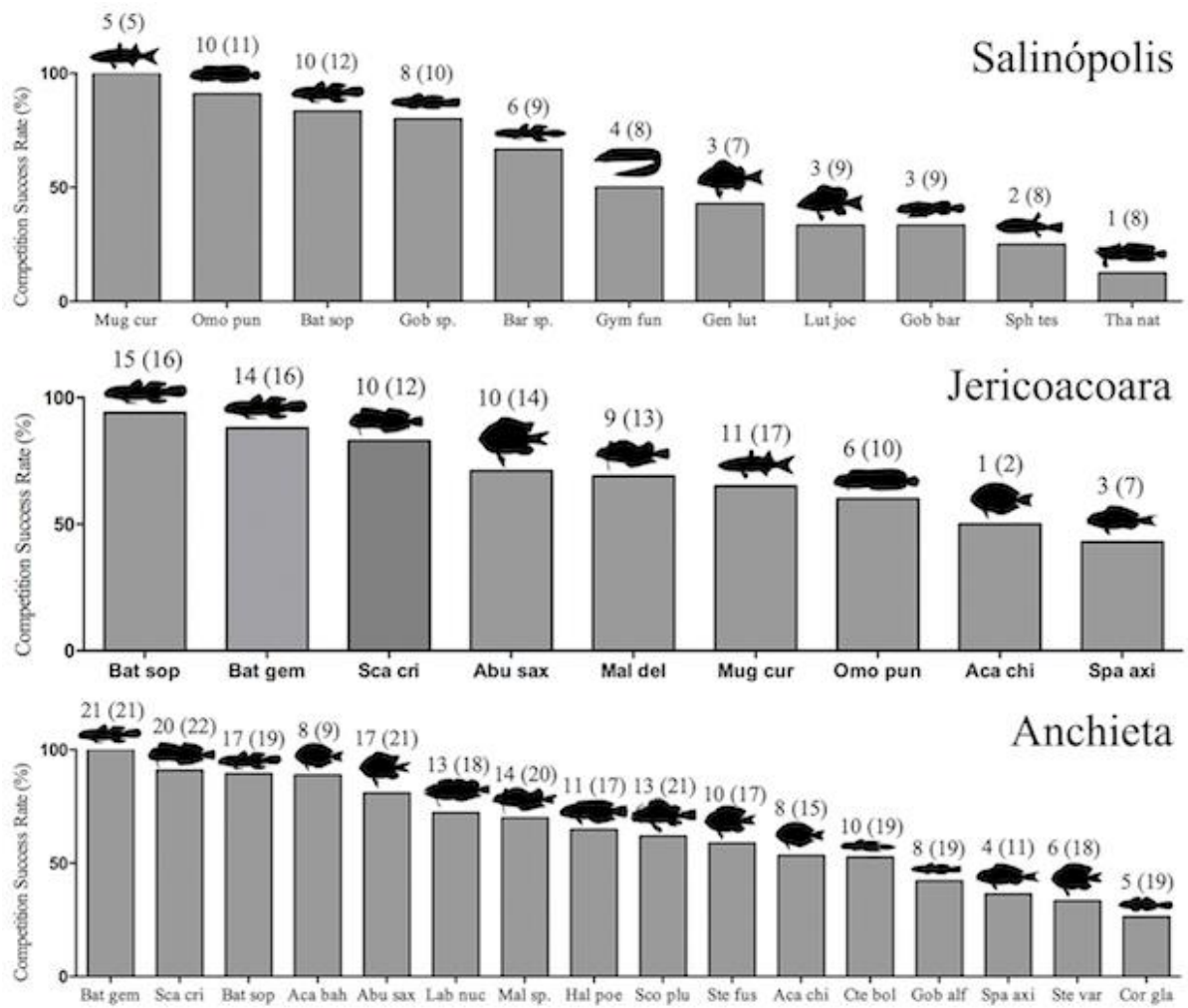


Figure S2: Potential competition success rate among coastal intertidal taxa. Numbers above fish draws denote number of successful interactions between potential competitors and numbers into the parentheses denote numbers of potential competitors of each species showed through the isotopic niche overlap in a δ -space plot. Potential pairwise interactions were calculated via species competition proxy.

CAPÍTULO 5

ARE ISLAND INTERTIDAL ENDEMIC FISHES VULNERABLE TO POTENTIAL IMPACTS FROM AN INVASIVE FISH?

*Artigo a submeter ao periódico *Marine Ecology Progress Series**

Are island intertidal endemic fishes vulnerable to potential impacts from an invasive fish?

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Abstract

Historically, human-made introductions are one of the most harmful causes of island species declining. In this scenario, endemic species are particularly at risk of disappearance due to their inherent restricting distributions and other ecological traits. Here, we studied the trophic ecology of the invasive *Omobranchus punctatus* using gut contents and stable isotopes and simulated its impact through competition interaction model in Brazilian intertidal island communities to verify whether endemic island species are weak competitors in a hypothetical invasion of *O. punctatus* by ballast water. Gut contents and stable isotope mixed models evidenced an omnivorous feeding habit of *O. punctatus* consuming mostly detrital mass, and algae and crustaceans in minor importance. Most of intertidal species were weak competitors in a direct competition simulation using $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and fish density data. The main concerns falls into the natural vulnerability of island endemic species, which mostly are restricted to shallow layers of intertidal and subtidal waters such as *Lythrypnus* sp., *Storrsia olsoni* and *Malacoctenus* spp.. Currently, Fernando de Noronha island is the destiny of many cruise ships, which may act as a vector of *O. punctatus* dispersion through Brazilian islands since the species is well-established in Brazilian coast.

1. Introduction

Purposeful species introductions by humans first occurred *ca.* 8,000 years ago, mainly for food and game (Reichard & White 2001, Yan et al. 2001, Lockwood et al. 2007). However, even small intentional or unintentional introductions can be greater in two or three orders of magnitude than the background rate (Gaston et al. 2003), thus potentially multiplying impacts on natural ecosystems. In this context, islands are particularly vulnerable to invasions, and competition and predation by invasive species are major concerns since they can lead native island species to extinction (Sax et al. 2002, Sax & Gaines 2008). Several island invasion events have been readily documented on the long term. One of the most iconic case occurred in the island of Guam, where thriving invaders triggered the disappearance of native species and niche replacements in the food web of the whole island (Savidge 1987, Fritts & Rodda 1998, Richmond et al. 2014).

Ecological traits inherent to island endemic species, such as small populations and restricted distribution area, place them at high risk of extinction face to an invasion. For this reason, endemism *per se* functions as an indicator of invasion vulnerability (Berglund et al. 2009). Small-sized intertidal endemics, restricted to few centimeters depth, may be especially at risk. Intertidal environments, and their endemics, are under pressure due to habitat loss, climate changes and, also, invasive species (Thompson et al. 2002, Andrades et al. 2017). On the Atlantic coast of Central and South America, invasive species have been suppressed endemic species by predation (e.g. lionfishes *Pterois* spp.; Rocha et al. 2015) or competition for space (e.g. sun corals *Tubastrea* spp., Creed 2006, Silva et al. 2014).

In this study, we selected the muzzled blenny *Omobranchus punctatus* to evaluate the potential effects of invasion in oceanic intertidal environments. Originating from the Indo-Pacific, *O. punctatus* is well-established in shallow coastal and estuarine habitats of the central and south-western Atlantic (Gerhardinger et al. 2006, Lasso-Alcalá et al. 2011). Although the first known invasion, at Trinidad, probably predates 1915 (Lasso-Alcalá et al. 2011), the species' presence in oceanic islands remains unreported. In the Caribbean region, cruise tourism has brought diverse and dramatic impacts (Lester & Weeden 2004, Wilkinson 2017). In the last years, touristic cruises were permitted landing at Fernando de Noronha, the only inhabited oceanic Brazilian island, possibilitating introduction via ship transportation

(Lasso-Alcalá et al. 2011). In order to better define a scenario for an *O. punctatus* island invasion and to understand the impacts such invasion could generate, we divided the present study in two sections: (i) a definition of the invasive species trophic ecology using gut contents and stable isotopes analysis; and (ii) an evaluation of the potential impacts of its presence on intertidal fish communities in oceanic islands, focusing on endemic species.

2. Materials and Methods

2.1 Study areas

The three largest islands (Rocas Atoll, Fernando de Noronha and Trindade) of the Brazilian Province (*sensu* Briggs & Bowen 2012) were chosen to evaluate the potential impact of *Omobranchus punctatus* in Atlantic oceanic intertidal reefs. Rocas (03°51' S; 33°49' W) is the only atoll in the South Atlantic. Located 266 km off the continent (state of Rio Grande do Norte), it is primarily built by coralline algae, vermetid gastropods and hermatypic corals. Rocas probably poses as the most near-pristine area of the southwestern Atlantic and is a Biological Reserve. On the same volcanic ridge, Fernando de Noronha (hereafter Noronha; 03°50' S; 32°25' W) is located farther east 345 km from mainland. The small archipelago presents phonolitic rocky intertidal reefs often associated with biogenic carbonate substrate composed of encrusting coralline algae. Since 1988, most of Noronha is a National Marine Park to ensure protection from fishing activities (to 50 m depth) and controlling (not prohibiting) urbanization and tourism visitation. Rocas and Noronha are a World Heritage Sites by UNESCO (United Nations Educational, Scientific and Cultural Organization) (UNESCO 2017).

Trindade (20°30' S; 29°20' W), located 1,160 km off the coast of the state of Espírito Santo, is the most isolated insular environment of the Brazilian Province. Intertidal reefs are made of biogenic carbonate (mostly encrusting coralline algae) and phonolitic rocky substrates. Since 1957, the Brazilian Navy occupies the island and visitation is restricted to research and military purposes.

2.2 Sampling procedure

Individuals of *Omobranchus punctatus* were collected from intertidal reefs of Salinópolis, northern coast of Brazil (00°36' S, 47°21' W), to determinate gut contents and conduct stable isotopes analysis. The sampling area was chosen due to the high

densities of *O. punctatus*, the most abundant fish species on Brazilian northern intertidal reefs and a strong competitor in comparison to native fish species (Capítulo 3 e 4). Community composition, density and stable isotopes sampling procedures of consumers and sources are detailed in Andrades et al. (Capítulo 4).

2.3 Data analysis

2.3.1 Trophic Ecology

The trophic ecology of *O. punctatus* was defined through dietary and stable isotopes analysis. Twenty individuals (10 juveniles and 10 adults) were selected based on age estimated following Ismail & Clayton (1990). Age 1+ individuals (juveniles) showed a mean total length (TL) of 41.6 mm and adults of age 2+ and 3+ measured 61.2 mm mean TL. We examined the anterior 1/3 of the digestive tract, as suggested for combtooth blennies (Hundt et al. 2014, 2017), and ingested items were identified. Results are expressed as weight (%W) and occurrence (%F) frequency. Stable isotopes analysis were ran over fish muscular tissue and preys commonly reported in feeding habits studies (Kanou et al. 2004, Hundt et al. 2014) that had been collected at Salinópolis at the time of sampling. Sixteen individuals, seven juveniles (37 mm mean TL) and nine adults (67.4 mm mean TL), were selected. The relative contribution of food sources to juvenile and adult stages were estimated through the Bayesian mixing model *simmr* (Stable Isotope Mixing Model in R; Parnell 2016). Since no trophic enrichment factor (TEF) for *O. punctatus* is available, standard TEF values of $0.4 \pm 1.3\text{‰}$ for $\delta^{13}\text{C}$ and $3.4 \pm 1.0\text{‰}$ for $\delta^{15}\text{N}$ (Post 2002) were adopted for juveniles and adults and used in the model. Potential food sources considered in the mixing model were small invertebrates (polychaetes + amphipods), macroalgae (green + red algae), phytoplankton (POM) and sedimentary biofilm. As suggested by Phillips et al. (2014), isotopic signatures of polychaetes and amphipods were combined after comparison did not showed significant differences of isotopic signatures (Mann-Whitney paired tests; $p > 0.05$). Furthermore, we calculated the isotopic niche of *Omobranchius punctatus* using the SIBER (Stable Isotope Bayesian Ellipses in R; Jackson et al. 2011) multivariate ellipse-based model and rescaled (see next section) overlapping it on the isotopic niches of main trophic groups of each oceanic intertidal communities to verify what trophic groups can compete to resources with the invader. All analysis were made using R statistical computing package (R Core Team 2017).

2.3.1 Potential impacts in oceanic intertidal reefs

We rescaled *O. punctatus* stable isotope signatures to best estimate its isotopic niche in oceanic communities. Natural systems present natural enrichments and variation in their food web, which manifest in their isotope signatures of primary sources, even when these belong to the same taxa. Rescaling used the absolute difference between average isotope values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of individual *O. punctatus* and main primary sources (macroalgae) at Salinópolis. Differences were then added to stable isotope signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of primary sources (macroalgae) for each oceanic site. Stable isotope values of primary consumers were acquired from Andrades et al (Capítulo 4).

Interspecific competition was estimated to evaluate potential interactions between *O. punctatus* and other fish species in oceanic intertidal communities. Fish density data and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of each species were used into the species competition proxy built to determine the overlap in isotopic niche between two species in relation to the density of the focal species (Capítulo 4), as follows:

$$SCP_i = \frac{\text{Ellipses95c}_i}{FD_i \times (\text{Ellipses95c}_i - \text{Ov}_{ij})}$$

Where FD_i is the mean fish density ($\text{ind} \cdot \text{m}^{-3}$) of species *i* (*O. punctatus*), Ellipses95c_i is the small sample size cored (i.e. core isotopic niche ellipses) of species *i*, containing 95% prediction ellipse interval, and Ov_{ij} is the overlap of the area of the corrected standard ellipse between *O. punctatus* and other species (*j*) that corresponds to the overlap of the maximum likelihood standard ellipse area within the 95% prediction ellipse interval.

3. Results

The gut content analysis and four-source mixing model evidenced an omnivore diet. Detritus (amorphous animal and vegetal digested mass) was the main food resource consumed by juvenile and adult in both weight and occurrence frequency (Table 1). Mixing models runs showed a tendency toward a larger ingestion of small invertebrates than macroalgae in early life (medians of 54 vs. 26%, respectively) and an increase in herbivory in adulthood (41 vs. 45%, respectively; Figure 1; Table 2). The isotopic niche of *O. punctatus* overlapped that of all trophic groups (carnivores, omnivores and herbivores) of oceanic intertidal fishes (Fig. 2)

reinforcing the omnivore ecology of invader and the wide spectrum of potential resources used by species.

Interspecific competition simulations revealed a potentially strong influence of *O. punctatus* on oceanic intertidal communities, including interactions with endemic species (Fig. 3). We observed a potential impact of *O. punctatus* on island native species with the invader may competing successfully over the main intertidal species, from small cryptobenthic endemic species such as *Lythrypnus* sp. in Rocas Atoll to large moray eels such as *Echidna catenata* in Noronha and Trindade islands.

4. Discussion

4.1. Trophic Ecology

Diet and stable isotopes analyses evidenced here new facets of the trophic ecology of the invasive species *Omobranchus punctatus*. Investigations performed in native and invaded sites have described *O. punctatus* as herbivore (Soares et al. 2013, Hundt et al. 2014). However, detritus have been commonly identified as the main ingested item in gut content analysis (Kanou et al. 2004; present study). Detritus reveal little about the trophic ecology of a species, especially in *Omobranchus* since species of that genus can present omnivore, herbivore or molluscivore feeding habits (Hundt et al. 2014). We corroborated and followed Ismael and Clayton (1990) report showing *O. punctatus* as an opportunistic omnivore grazer. Their conclusions was based on a year-round investigation and more than 200 individuals instead of the 10 individuals examined in others studies (Kanou et al. 2004, Soares et al. 2013, Hundt et al. 2014, present study). In accordance, our isotopic niche modeling and mixing model were built on a miscellaneous diet and the contribution of various food items although we cannot infer on what source (animal or vegetal) contributed more to the species energetic intake. Currently, one of the greatest challenges in isotope ecology is to unweave the uncertainty around omnivores species and the importance of preys in their diet (Caut et al. 2009, Galván et al. 2012, Phillips et al. 2014). The first step, however, to construct robust estimations is to determine the trophic discriminations factors of the target species, which is unknown for mostly species, including *O. punctatus*. Compared to a snapshot dietary analysis, stable isotopes is more reliable a tool to infer about trophic ecology despite the caveats still existing in isotope mixing models, mainly when complemented with classical gut content analysis (Davis et al. 2012).

4.2. Potential impacts in oceanic intertidal reefs

From the invader perspective there are a series of filters involving ballast water transportation before successful establishment into a new area. Briefly, a species needs to survive the three stages of transportation: loading into the ballast tanks, voyage and then the discharge in the recipient area (Carlton 1996, Wonham et al. 2001). *O. punctatus* has proven to withstand this three-stage process and its capacity to acclimation and dispersion along the Atlantic coasts is well-established (Lasso-Alcalá et al. 2011). Our central hypothesis was confirmed partially, since the simulated competitive interactions demonstrated strong competitive impact of both juvenile and adult *O. punctatus* over most intertidal fishes, including but not limited to endemic species. In fact, although *O. punctatus* can compete with a wide range of species on islands, its impact would likely affect functionally-related species (Case et al. 2016) such as Blenniidae and other small-sized fishes, which are essentially represented by the endemic species *Scartella poiti*, *S. itajobi*, *Malacoctenus* sp., *M. brunoi*, *Starksia multilepis*, *Lythrypnus* sp. and *Storrsia olsoni*. Others species (e.g. *Abudefduf saxatilis*, *Acanthurus* spp., *Stegastes* spp. and *Holocentrus adscensionis*) commonly occurred at larger body sizes (Capítulo 3) and while their isotopic niches overlapped with *O. punctatus*, these species probably explore preys from similar groups but over different sizes (Pimentel 2012).

Charles Elton in his seminal work on invasion ecology suggested that competitive interactions are the main force and defense to repel the spread of an invasive species (Elton 1958). However our results suggest that oceanic intertidal communities might not be able to repel *O. punctatus*, which could result in extirpation of endemic species presenting as weak competitors in the simulated presence of *O. punctatus*. Another factor attenuating the resistance to invasion is the absence of piscivorous species (i.e. predation pressure) in tidepools of Brazilian oceanic islands to control the invader's population growth (Capítulo 3). The wide distribution of *O. punctatus* along the Brazilian coast, from 0° to 26°S latitude, and the diversity of habitats it occupies, mangroves, ports, coastal mariculture fields and tidepools (Gerhardinger et al. 2006, Lasso-Alcalá et al. 2011) demonstrate its capacity to withstand harsh conditions and to spread into available areas.

4.3. Conclusions

Obviously, it is not possible to estimate accurately when or whether *O. punctatus* will invade an island, nor what response the impact would induce on island communities (Simberloff & Holle 1999, Ruokonen et al. 2012, Ramus et al. 2017). However, is important to consider their invasion and warn the governance about potential impacts. If negative, the impact on the intertidal environments tends to be extremely harmful to biodiversity at all, since oceanic intertidal reefs shelters higher fish endemism rates than subtidal habitats representing an endemic reservoir in these ‘remote worlds’ (Andrades et al. 2017). Here, we verified that generalist *O. punctatus* may compete for resources with many endemic Brazilian island species, which suggests negative impacts on tidepools communities. In this respect, we strongly suggest an effective and efficient control and enforcement for ballast water treatments of cruise ships visiting the Caribbean and the Brazilian (Fernando de Noronha) islands.

5. Acknowledgments

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Tables

Table 1. Gut contents composition of juvenile (N = 10) and adult (N = 10) individuals of the invasive *Omobranchus punctatus* in the Atlantic coast (Salinópolis, Brazil). The %W and %F acronyms denote weight and occurrence frequencies, respectively.

Food items	%W		%F	
	Juvenile	Adult	Juvenile	Adult
MACROALGAE				
Filamentous algae	8	—	30	60
Leathery algae	—	—	—	10
CRUSTACEA				
Amphipoda	6	—	20	10
DETRITUS				
Detrital mass	86	100	90	100

Table 2. Source contribution of food resources to juvenile and adult *Omobranchus punctatus* trophic ecologies based on the Bayesian mixing model analysis.

	Juvenile				
	2.5%	25%	50%	75%	97.5%
Small invertebrates	0.028	0.219	0.539	0.759	0.927
Macroalgae	0.017	0.098	0.261	0.585	0.891
Phytoplankton	0.009	0.036	0.068	0.122	0.351
Biofilm	0.007	0.025	0.044	0.076	0.193
	Adult				
	2.5%	25%	50%	75%	97.5%
Small invertebrates	0.013	0.116	0.413	0.746	0.927
Macroalgae	0.017	0.133	0.454	0.787	0.944
Phytoplankton	0.007	0.025	0.046	0.082	0.226
Biofilm	0.005	0.018	0.032	0.052	0.125

Figures

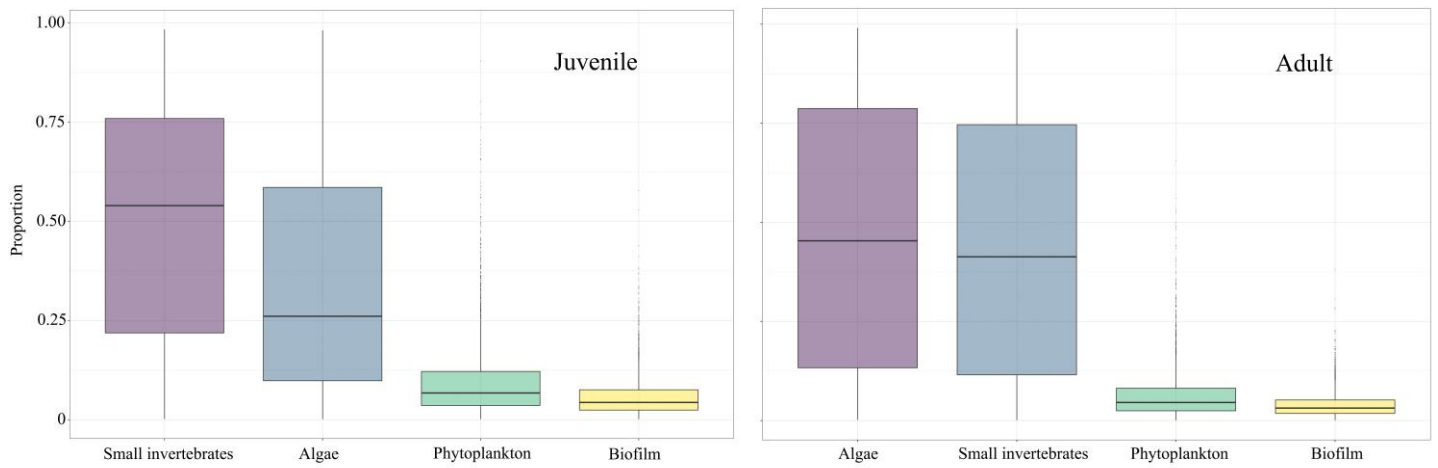


Fig. 1. Stable Isotopes mixing models for different estimated food resources proportion to juvenile and adult *O. punctatus* diet.

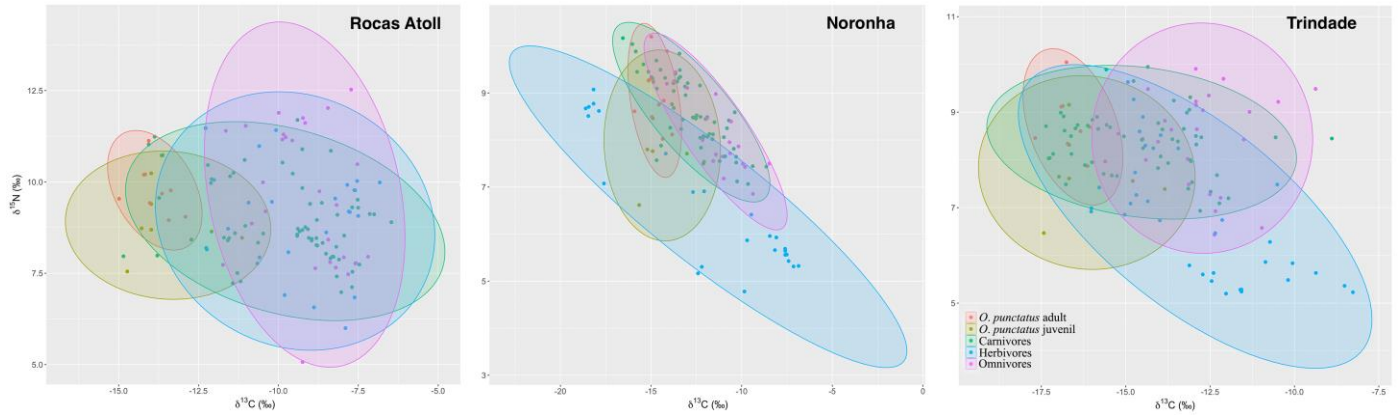


Fig. 2. Simulations of the invasive species niche overlap between *O. punctatus* and trophic groups of native oceanic fish communities. Standard ellipse areas (SEAc) were calculated from the rescaled $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of juvenile and adult *O. punctatus* and different fish consumers of oceanic island communities.

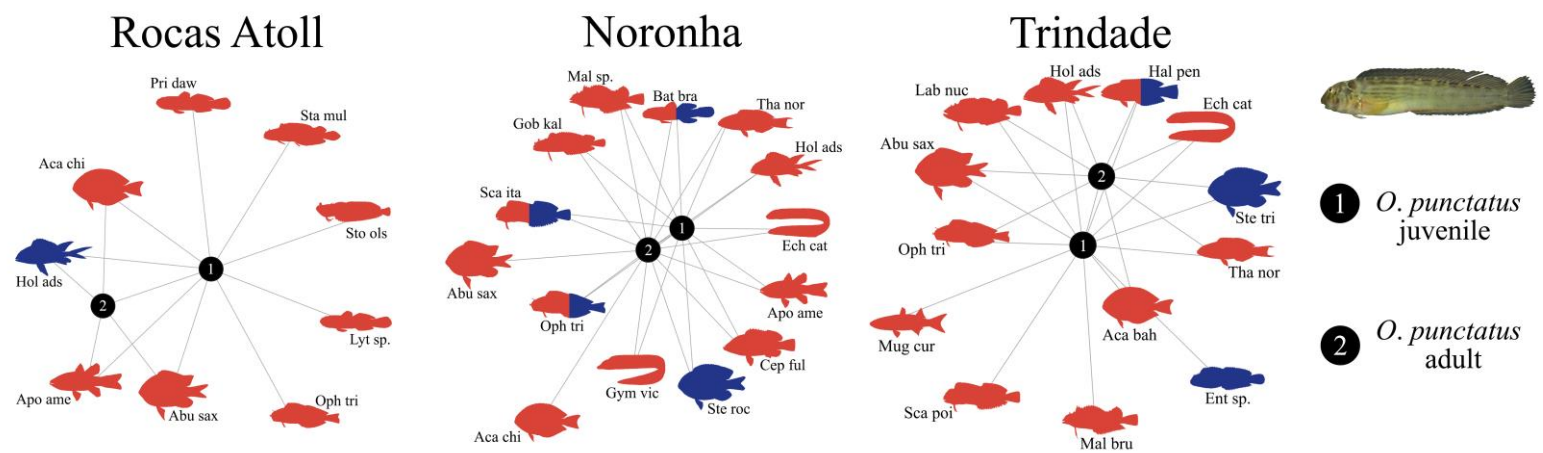


Fig. 3. Competitive interactions between *O. punctatus* and native oceanic intertidal fish communities estimated from the interspecific competition proxy. Red and blue colored shapes denotes respectively weak and strong competitors in simulated *O. punctatus* invasion. Half red-blue colored indicates relationships which native species are strong competitors in relation to adult *O. punctatus* and weak competitors in relation to juvenile *O. punctatus*. Starting from Rocas Atoll, fish species are *Priolepis dawsoni* (Pri daw), *Starksia multilepis* (Sta mul), *Storrsia olsoni* (Sto ols), *Lythrypnus* sp. (Lyt sp.), *Ophioblennius trinitatis* (Oph tri), *Abudefduf saxatilis* (Abu sax), *Apogon americanus* (Apo ame), *Holocentrus adscensionis* (Hol ads) and *Acanthurus chirurgus* (Aca chi). In Noronha, previously unlisted species are *Bathygobius brasiliensis* (Bat bra), *Thalassoma noronhanum* (Tha nor), *Echidna catenata* (Ech cat), *Cephalopholis fulva* (Cep ful), *Stegastes rocasensis* (Ste roc), *Gymnothorax vicinus* (Gym vic), *Scartella itajobi* (Sca ita), *Gobioclinus kalisherae* (Gob kal) and *Malacoctenus* sp. (Mal sp.). In Trindade, species not listed above are *Halichoeres penrosei* (Hal pen), *Stegastes fuscus trinidadensis* (Ste tri), *Malacoctenus bruno* (Mal bru), *Scartella poiti* (Sca poi), *Mugil curema* (Mug cur), and *Labrisomus nuchipinnis* (Lab nuc).

CAPÍTULO 6

TRAPPED IN THEIR OWN ‘HOME’: UNEXPECTED RECORDS OF INTERTIDAL FISH DESICCATION DURING LOW TIDES

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Short communication

Trapped in their own ‘home’: unexpected records of intertidal fish desiccation during low tides

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Introduction

Intertidal fishes are recognized mainly by some extraordinary morphological, physiological and behavioural adaptations that allow them to occupy intertidal environments (Gibson and Yoshiyama, 1999; Martin and Bridges, 1999; White and Brown, 2013). Tidal cycles generate two distinct ecological scenarios for intertidal fishes. During the flood tide, large predators and other non-resident fishes (from the subtidal habitat) visit the intertidal habitat and increase the risk of predation and competition with the resident fishes. In contrast, for many fish species during the ebb tide the intertidal habitat is restricted to isolated tidepools, which may have extreme environmental conditions (e.g. high salinity, temperature). Thus, adaptations of resident species to intertidal life increases the competition for resources as well as the resistance to physicochemical variations of water characteristics during the ebb tide, in the absence of subtidal predators and competitors (Gibson, 1986; Gibson and Yoshiyama, 1999).

Some resident species live in two or more tidepools in order to better exploit the resources (e.g. food, shelter and nesting sites) or to avoid adverse conditions during reef emersion (Gibson, 1999; Thyssen et al., 2014). Often, fishes that live in naturally harsh habitats such as tidepools, exhibit a wide range of sensory mechanisms for spatial mapping (Gibson, 1999; Braithwaite and De Perera, 2006) and several studies have described the noteworthy site fidelity and homing performance of intertidal fishes (e.g. Griffiths, 2003; White and Brown, 2013, 2014). Occurrences of residents and opportunists of intertidal fish species trapped in tidepools during low tides (i.e. exposed to air and desiccated) in two sites in the Atlantic Ocean (Brazil) are reported here, and the ecological and behavioural aspects of these events are discussed.

Materials and methods

The intertidal sites studied were Rocas Atoll (03°51'S; 33°49'W), an oval-shaped oceanic atoll 266 km off the Brazilian coast and dominated by a mesotidal regime (up to

3.8 m; Gherardi and Bosence, 2001), and a coastal flat reef at Castelhanos Beach (20°49'S; 40°36'W), located in south-eastern Brazil and under the influence of a microtidal regime (up to 1.8 m; Macieira and Joyeux, 2011). Dead fishes were unexpectedly found in tidepools during low tides in August (Castelhanos Beach) and September (Rocas Atoll) of 2014 during a scientific survey of the intertidal environment at these sites. Physicochemical parameters (water temperature, pH and salinity) in neighbouring tidepools during the period of records were also measured. Fishes were collected, measured (total length, 1 mm precision) and classified in relation to their degree of residency as Permanent Resident (PR) or Opportunist (O), adapted from Macieira and Joyeux (2011) and Macieira et al. (2015). All individuals were externally examined and deposited in the fish collection of the Universidade Federal do Espírito Santo (CIUFES; <http://splink.cria.org.br/>).

Results

Fourteen specimens belonging to five species (five families; 11 permanent residents and three opportunists; Table 1) were found trapped in tidepools: 13 in Rocas Atoll and one in Castelhanos Beach in the spring tide periods. On the occurrence dates, differences in water levels between high and low tides were 2.1 m in Rocas Atoll and 1.4 m at Castelhanos Beach. Individuals were found highly desiccated at 00:10, 01:08, 01:58, 02:08 hours after peak low tide in depressions 2–5 m from the nearest (filled) tidepool. In Rocas Atoll, where 93% of the fish were found, mean water temperature in neighbouring tidepools during the sampling period was 30.9°C. Mean water pH and salinity were 8.4 and 37, respectively. External examination evidenced no anomaly, pathology or predation wound in any specimen.

Discussion

Blenniidae and Gobiidae are the most abundant families in intertidal fish communities and which display emergence behaviours to avoid desiccation, such as skipping or hopping

Table 1

Fish family and species, sites, dates, time, residency status and number of individuals found dead in this study. Family order follows Nelson (2006). Fish were deposited at the fish collection of Universidade Federal do Espírito Santo (CIUFES; <http://splink.cria.org.br/>). Species were classified according to degree of residency in tidepools (Residency status) based on Macieira and Joyeux (2011) and Macieira et al. (2015). Residency status correspond to Permanent resident (PR) and Opportunist (O)

Family / Species	Site	Date	Time	Residency status	Number of specimens	Voucher number CIUFES
Pomacentridae						
<i>Stegastes rocasensis</i> (Emery, 1972)	Rocas Atoll	26/IX/2014	14:00	PR	1	3247
Labridae						
<i>Thalassoma noronhanum</i> (Boulenger, 1890)	Rocas Atoll	24/IX/2014	10:58	O	2	3248
Blenniidae						
<i>Ophioblennius trinitatis</i> Miranda Ribeiro 1919	Rocas Atoll	24/IX/2014	10:58	PR	9	3250
Gobiidae						
<i>Bathygobius geminatus</i> Tornabene, Baldwin & Pezold 2010	Castelhanos Beach	14/VIII/2014	13:49	PR	1	3251
Acanthuridae						
<i>Acanthurus chirurgus</i> (Bloch, 1787)	Rocas Atoll	25/IX/2014	13:40	O	1	3249



Fig. 1. Intertidal fish trapped in crevices of a tidepool in Rocas Atoll, 2014. Scale reference: *Thalassoma noronhanum* individual (white belly) total length is 47 mm. White arrows = crevices. Note that fish were pushed out of the crevices for the photographic record. Photo by R. Andrades.

to adjacent pools (Aronson, 1951; Martin and Bridges, 1999) or by seeking refuge in small humid crevices or under small algae patches (Ikebe and Oishi, 1997; Braithwaite and De Perera, 2006; White and Brown, 2013). However, fishes of these two families (and others) were trapped in small crevices (Fig. 1), which suggests that they were seeking suitable refuge, whereby the depression dried up, an occurrence that is by itself uncommon.

Resident tidepool fishes perform daily movements and return to their home pools during ebb tides using complex spatial navigation abilities (Bshary et al., 2001; Braithwaite and De Perera, 2006; Jorge et al., 2012). Although homing failure is probably uncommon in resident species, we hypothesize that the fishes could not find their home pools and were stranded in dry depressions not having usable outlets. However, it is unlikely that several individuals would suffer the same fate at the same place, particularly

because they were of different species (as in Fig. 1), unless high-tide movements were involving cohesive multi-species groups or following behaviour. Alternatively, predators such as sharks and piscivorous teleosts of all sizes gain access to intertidal habitats to forage during high tide (e.g. Castro and Rosa, 2005; Wetherbee et al., 2007; both at Rocas Atoll). Tidepool fishes seek refuge in shallow pools and occasionally may emerge to avoid predation (Gibson, 1999). The foraging or simple presence of potential predators could have forced tidepool fish to escape to unsuitably dry areas, precluding their return to their home tidepool. Neither hypothesis appears wholly convincing, and we suspect stranding of tidepool fishes results from a variable conjunction of factors that include, but are not limited, to those discussed. Among these plausible reasons are the drying out of carbonate pools due to sudden habitat alteration.

Desiccation in intertidal habitats can affect vagile as well as sessile organisms (Grant and McDonald, 1979; Sebens, 1982; Ji and Tanaka, 2002), but the former in particular exhibit complex behavioural adaptations to withstand stresses associated with low tide levels (Finke et al., 2007; Dabruzzi et al., 2011). Here, the evidence of tidepool fish desiccation highlights the inter-play between biological interactions and pressure in shaping natural populations and intertidal fish communities.

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CAPÍTULO 7

Filling the gap: Length–weight and length–length relationships of intertidal endemic fishes of the Brazilian Province Oceanic Islands

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Filling the gap: Length–weight and length–length relationships of intertidal endemic fishes of the Brazilian Province Oceanic Islands

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Summary

Length-weight and length-length relationships were determined for nine fish species of Rocas Atoll, Fernando de Noronha and Trindade Island. Samples were conducted in 2014 (Rocas) and 2015 (Noronha and Trindade) in tidepools using anaesthetic clove oil and hand nets to collect fish fauna. Four species (*Stegastes rocasensis*, *Scartella itajobi*, *Starksia multilepis* and *Bathygobius brasiliensis*) are endemic from the Noronha-Rocas ridge, two are endemic from the Trindade-Martin Vaz insular complex (*Scartella poiti* and *Malacoctenus bruno*), and three species have a widespread distribution. All relationships are novel for science.

1 | INTRODUCTION

A very common method in marine ecology to survey reef fish community structure is visual censuses during which a trained diver records the abundance and total length of each species (Luckhurst & Luckhurst, 1978; St. John, Russ, & Gladstone, 1990). Thus, fish biomass estimations are commonly made using length–weight relationships (LWRs) (e.g., Pinheiro, Ferreira, Joyeux, Santos, & Horta, 2011) to result in more species variables to compare among and within communities. In this context, endemic and cryptic reef species of isolated areas are rarely accounted for due to limited sampling, detection or data. Lack of simple weight and length data often requires the use of surrogates, often sister or congener species (e.g., Longo et al., 2015; Pinheiro et al., 2011), a procedure that is not recommended (see Froese, 2006) and may misrepresent and/or confound conservation strategies as well as studies of populational interest. Here, we present

LWRs and length-length relationships (LLRs) for six endemic species and three typically intertidal and shallow-water reef species (two LLRs) from three Oceanic Islands of the Brazilian Province: Rocas Atoll, Fernando de Noronha and Trindade Island.

2 | MATERIALS AND METHODS

Intertidal fishes of the three largest Oceanic Islands of the Brazilian Province (sensu Briggs & Bowen, 2012), Rocas Atoll (03°51'S; 33°49'W), Fernando de Noronha (03°50'S; 32°25'W) and Trindade Island (20°30'S; 29°20'W) were surveyed during the dry seasons of 2014 (Rocas) and 2015 (Noronha and Trindade). Fish were sampled using hand nets (0.1 and 0.2 cm mesh size) after application of the anaesthetic clove oil (40 ml/L) in tidepools and reef crevices of the intertidal zone. Immediately after collection fish were

frozen at -20°C . In the laboratory, fish were thawed and total length (TL, in cm) and standard length (SL, in cm) measurements were taken using calipers (0.1 mm) and weight (W, in g) measured with a digital balance (0.01 g). Voucher specimens were fixed in formalin solution (10%), preserved in 70% ethanol and deposited in the Ichthyological Collection of Federal University of Espírito Santo (CIUFES). Presence of outliers for each species was identified graphically using $\ln(\text{TL})$ vs. $\ln(\text{WT})$ plots (Froese & Binohlan, 2000), and obvious outliers removed. Relationships were built based on the growth equation model

$$W = a \text{ TL}^b, \quad (1)$$

where a is a constant and b the allometric coefficient (Froese, 2006). Parameters a and b were estimated from the linear relationship between \log_e -transformed variables

$$\ln(W) = q + b \ln(TL), \quad (2)$$

with b the slope and q the intercept of the linear equation and, thus, in Eq. (1) $a = e^q$. Length-length relationships and parameters were estimated based on formula

$$TL = a + b SL, \quad (3)$$

with b and a the parameters (slope and intercept) of the equation.

3 | RESULTS

Length-weight and length-length relationships and their metrics are summarized in Tables 1 and 2. A total of 248 specimens belonging to six families were analysed; LLR was not estimated for the

TABLE 1 Descriptive statistics and length-weight relationship parameters for 9 intertidal species of Brazilian Oceanic Islands sampled in 2014 (Rocas) and 2015 (Noronha and Trindade)

Family/ <i>taxa</i>	Site	<i>n</i>	TL (cm)		W (g)		Regression parameters		<i>r</i> ²
			Min.	Max.	Min.	Max.	<i>a</i> (95% CI)	<i>b</i> (95% CI)	
Muraenidae									
<i>Echidna catenata</i> (Bloch, 1795)	T	8	25.7	71.3	32.62	1,004	0.0006 (0.0004–0.0009)	3.3475 (3.2370–3.4579)	.999
Mugilidae									
<i>Mugil curvidens</i> Valenciennes, 1836	T	6	4.2	23.2	0.90	109.84	0.0156 (0.0126–0.0192)	2.8434 (2.7492–2.9375)	.999
Pomacentridae									
<i>Stegastes rocasensis</i> (Emery, 1972) ^b	N, R	45	1.6	9.8	0.09	20.04	0.0236 (0.0226–0.0246)	2.9214 (2.8935–2.9494)	.999
Blenniidae									
<i>Ophioblennius trinitatis</i> Miranda Ribeiro, 1919	N, T	17	4.6	10.2	0.89	9.36	0.0112 (0.0103–0.0122)	2.8815 (2.8353–2.9278)	.999
<i>Scartella itajobi</i> Rangel & Mendes, 2009 ^b	N, R	74	1.3	6.7	0.03	3.91	0.0120 (0.0117–0.0123)	3.0557 (3.0333–3.0781)	.999
<i>Scartella poiti</i> Rangel, Gasparini & Guimarães, 2004 ^a	T	5	4.0	8.8	0.82	7.59	0.0169 (0.0107–0.0266)	2.8122 (2.5481–3.0762)	.997
Labrisomidae									
<i>Malacoctenus bruno</i> Guimarães, Nunan & Gasparini, 2010 ^a	T	10	3.6	5.2	0.46	1.39	0.0094 (0.0084–0.0106)	3.0390 (2.9615–3.1164)	.999
<i>Starksia multilepis</i> Williams & Mounts, 2003 ^b	N, R	7	1.2	3.2	0.02	0.24	0.0127 (0.0119–0.0135)	2.5642 (2.4794–2.6491)	.999
Gobiidae									
<i>Bathygobius brasiliensis</i> Carvalho-Filho & De Araújo, 2017 ^{b,c}	N	76	1.4	9.7	0.04	13.47	0.0129 (0.0124–0.0135)	3.0472 (3.0166–3.0778)	.998

T, Trindade; N, Noronha; R, Rocas; n, number of individuals. Minimum and maximum total length and wet weight are given. Constant (a) and allometric coefficient (b) of the LWR are furnished with their 95% confidence intervals. r^2 , coefficient of determination. Family order follows Nelson, Grande, and Wilson (2016).

^aTrindade Island endemic species.

^bNoronha-Rocas endemic species.

^cThis species is not listed in FishBase database due to its recent description (Rodríguez-Rey, Carvalho Filho, De Araújo, & Solé-Cava, 2017).

TABLE 2 Total length–standard length relationship parameters for 8 intertidal species of Brazilian Oceanic Islands sampled in 2014 (Rocas) and 2015 (Noronha and Trindade)

	Regression parameters		
Family/taxa	a (95% CI)	b (95% CI)	r ²
Mugilidae			
Mugil curvidens Valenciennes, 1836	-0.0268 (-0.2792-0.2256)	1.2628 (1.2391-1.2865)	.999
Pomacentridae			
Stegastes rocasensis (Emery, 1972) ^b	-0.1852 (-0.3033 to -0.0672)	1.3088 (1.2805-1.3370)	.995
Blenniidae			
Ophioblennius trinitatis Miranda Ribeiro, 1919	-0.3060 (-0.5472 to -0.0648)	1.2812 (1.2375-1.3249)	.996
Scartella itajobi Rangel & Mendes, 2009 ^b	0.0180 (-0.0406-0.0765)	1.1788 (1.1556-1.2020)	.993
Scartella poiti Rangel, Gasparini & Guimarães, 2004 ^a	-0.1390 (-0.8659-0.5878)	1.2257 (1.0805-1.3709)	.996
Labrisomidae			
Malacoctenus brunoí Guimarães, Nunan & Gasparini, 2010 ^a	-0.3375 (-0.7531-0.0780)	1.2767 (1.1664-1.3870)	.989
Starksia multilepis Williams & Mounts, 2003 ^b	-0.1592 (-0.3635-0.0452)	1.2694 (1.1583-1.3806)	.994
Gobiidae			
Bathygobius brasiliensis Carvalho-Filho & De Araújo, 2017 ^{b,c}	-0.0740 (-0.1438 to -0.0042)	1.2321 (1.2130-1.2512)	.996

T, Trindade; N, Noronha; R, Rocas. Number of individuals and minimum and maximum total length as mentioned in Table 1. Intercept (a) and slope (b) of the LLR are furnished with their 95% confidence intervals. r^2 : coefficient of determination. Family order follows Nelson et al. (2016).

^aTrindade Island endemic species.

^bNoronha-Rocas endemic species.

^cThis species is not listed in FishBase database due to its recent description (Rodríguez-Rey et al., 2017).

Anguilliform *Echidna catenata*. Species size (TL) ranged from 1.2 (*Starksia multilepis*) to 71.3 cm (*E. catenata*) and body mass ranged from 0.020 (*S. multilepis*) to 1,004 g (*E. catenata*). All LWRs were strongly significant ($p < .001$) with a coefficient of determination (r^2) ranging between .997 (*Scartella poiti*) and .999. The allometric coefficient b ranged from 2.56 for *S. multilepis* to 3.34 for *E. catenata* (Table 1). LLRs were strongly significant ($p < .001$) for all species examined, with r^2 ranging from .989 (*M. bruno*i) to .999 (*M. curvidens*) (Table 2). New maximum lengths (SL) are provided for four species: *Ophioblennius trinitatis* (8.3 cm SL), *Scartella itajobi* (5.6 cm SL), *S. multilepis* (2.6 cm SL) and *Malacoctenus bruno*i (4.4 cm SL).

4 | DISCUSSION

Diversity, evolution or ecology of intertidal oceanic island reefs are poorly known despite the interest and relative easiness to access these environments compared to oceanic subtidal reef habitats (Andrades et al., 2017; Prochazka, Chotkowski, & Buth, 1999). The southern Atlantic follows the rule and no data are available for a number of

parameters relevant to community studies, including LWRs and LLRs. Herein are provided 9 novel LWRs, 8 LLRs and 4 maximum body sizes for endemic and a few non-endemic intertidal fishes of the Brazilian Oceanic Islands.

The a -values for *Bathygobius brasiliensis*, *Scartella poiti*, *S. itajobi* and *Mugil curvidens* LWRs were close to 0.01, as expected for fusiform species, while the lowest a -value was computed for the eel *Echidna catenata* (see Froese, 2006). Two species (*Stegastes rocasensis*, and *Malacoctenus bruno*i) are currently listed as Vulnerable in the Brazilian Red List of Threatened Species (MMA, 2014). However, to date the Brazilian government has failed to regulate and implement the list due to opposition from the fisheries industry sector (Di Dario et al., 2015). Overall, for all species the values of parameters b remained within the expected range of 2.5–3.3 (Froese, 2006). Endemic species reported here are restricted to shallow and intertidal reefs (<12 m depth). Apart to small life-territory, their endemism *per se* would argue for high vulnerability to, among others, local impacts such as sewage, habitat fragmentation or invasive species. Globally, intertidal environments are one of the most impacted marine habitats (Halpern et al., 2008), and call for urgency in conservation planning from Government Environmental agencies (Andrades

et al., 2017). We hope that the present data help future investigations to produce robust biomass estimations of oceanic intertidal fish fauna.

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