Universidade do Estado do Rio de Janeiro

Centro Biomédico

Instituto de Biologia Roberto Alcântara Gomes

Larissa Marques Pires Teixeira

Bioinvasão marinha e mudanças na comunidade: Análises de diversidade, caracterização trófica e nicho isotópico

Rio de Janeiro

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Tese apresentada, como requisito parcial para obtenção do título de Doutora, ao Programa de Pós-Graduação em Ecologia e Evolução, da Universidade do Estado do Rio de Janeiro.

Orientador: Prof. Dr. Joel Christopher Creed

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CATALOGAÇÃO NA FONTE

UERJ/ REDE SIRIUS/ CTC-A

T266 Teixeira, Larissa Marques Pires.
Bioinvasão marinha e mudanças na comunidade: análises de diversidade, caracterização trófica e nicho isotópico/ Larissa Marques Pires Teixeira. – 2021.
258 f.: il.

Orientador: Joel Christopher Creed
Coorientador: Vinicius Neres-Lima
Tese (Doutorado em Ecologia e Evolução) - Universidade do Estado do Rio de Janeiro, Instituto de Biologia Roberto Alcantara Gomes.

1. Ecologia marinha - Teses. 2. Bioinvasão - Teses. 3. Espécies exóticas - Teses. I. Creed, Joel Christopher. II. Neres-Lima, Vinicius. III. Universidade do Estado do Rio de Janeiro. Instituto de Biologia Roberto Alcântara Gomes. IV.Título.

CDU 594.1:574.3

Patricia Bello Meijinhos CRB-7/ 5217- Bibliotecária responsável pela elaboração da ficha catalográfica

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Assinatura Data

Larissa Marques Pires Teixeira

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Aprovada em 16 de Setembro de 2021.

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Instituto Brasileiro de Biodiversidade - BrBio

Rio de Janeiro
2021

DEDICATÓRIA

Aos que lutam pela ciência e resistem ao desmantelamento das instituições de pesquisa brasileira. Aos que acreditam em uma educação pública, gratuita e de qualidade. Aos que sonham com um Brasil sem fome e com um mundo socialmente justo. Para lutadores, resistentes e sonhadores, esse trabalho é dedicado a vocês.

AGRADECIMENTOS

Reconheço e sou eternamente grata a todas e todos que tornaram essa experiência possível.Concluir os objetivos a que me propus durante meus anos de doutorado só foi possível porque me apoiei sobre os ombros de gigantes, aos quais agradeçoa seguir:

Agradeço à CAPES - Coordenação de Aperfeiçoamento de Pessoal de Nível Superior pela bolsa de doutorado concedida. À Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (JCC, FAPERJ E-26 / 010.003031 / 2014 e E26 / 203.002 / 2017)e Conselho Nacional de Desenvolvimento Científico e Tecnológico (JCC, CNPq- 305924 / 2018-4) pelo financiamento para logística de trabalho de campo e análise isotópica.Ao Instituto Brasileiro deBiodiversidade (BrBio) no âmbito do Projeto Coral-sol financiado por meio do Compromisso de CondutaAcordo de Ajuste assinado pela Chevron Brasil com o Ministério Público Federal Brasileiro(Ministério Público Federal), com implantação pelo Fundo Brasileiro para a Biodiversidade (FUNBIO) pelo empréstimo de material e apoio em campo.

Agradeço à professora Drª. Helena de Godoy Bergallo por dispor do seu tempo e aceitar revisar o presente trabalho.

Agradeço às professoras e professores que aceitaram contribuir para o aperfeiçoamento deste trabalho participando da banca avaliadora: Dr. Carlos Eduardo Rezende, Drª. Fernanda Araujo Casares, Drª, Gisela Mandali de Figueiredo, Dr. Joel Creed, Dr. Bruno Pereira Masi e Drª. Eugenia Zandonà.

Agradeço especialmente ao meu orientador Dr. Joel Creed, com quem tive o prazer de trabalhar nos últimos dez anos. Grande parte do conhecimento que adquiri ao longo dos anos trabalhando como pesquisadora veio dos seus ensinamentos, acompanhamento e orientação que são para mim uma inspiração. Obrigada pela dedicação, pela autonomia concedida durante o doutorado, pela disponibilidade para discussões, por aceitar e incentivar minhas ideias, pelas correções certeiras. Agradeço também a compreensão, empatia, incentivo e puxões de orelha necessários.

Agradeço imensamente ao meu também orientador Dr. Vinicius Neres-Lima, que foi fundamental para o desenvolvimento deste trabalho e com quem eu tenho imensa alegria em poder trabalhar. Vinicius tem o dom de transmitir conhecimento com uma fala lúcida e inspiradora e poder receber seus ensinamentos diretamente durante meu mestrado e doutorado foi um privilégio. Sou grata também pelas reuniões que se transformaram em conversas e discussões políticas e foram essenciais para amenizar a saudade que eu sinto de estar na UERJ presencialmente e a solidão em tempos de isolamento social.

Sem a minha família, que é também minha rede de apoio, seria no mínimo enlouquecedor conciliar o doutorado com as demandas que surgiram quando me tornei mãe. Ao meu companheiro Danillo, que é também o responsável por deixar meu coração mais colorido e minha vida mais leve, sou extremamente grata por dividir os cuidados com a Maya, por me incentivar diariamente e acreditar no meu potencial, não posso deixar de agradecer também por ser apoio em campo, macerar amostras e assistir apresentações. Agradeço à minha mãe que além de achar incrível e me incentivar em tudo o que eu faço é também o respiro que eu tanto necessito e que só é possível acontecer durante suas visitas prolongadas na minha casa. Agradeço às minhas tias Gelci e Lena e ao meu tio Luiz que gentilmente cederam suas casas quando precisei de um lugar calmo e silencioso para escrever, realizar análises e me reunir com meus orientadores. Por último o mais importante agradecimento vai para minha filha Maya, que nasceu de surpresa interrompendo meu cronograma e tem o sorriso mais lindo que já vi, minha companheira de todos os momentos, motivo de todo o meu esforço e dedicação e com quem aprendo diariamente fazem dois anos.

Agradeço à todas as professoras e professores do Programa de Pós-Graduação em Ecologia e Evolução da Universidade do Estado do Rio de Janeiro (PPGEE-UERJ) pelos ensinamentos dentro e fora de sala de aula, pelas trocas e discussões ao longo desses anos. Agradeço também às secretárias Verusca e Sonia por contribuírem para o funcionamento do PPGEE mesmo em períodos conturbados.

Meu muito obrigada atodas e todos que me auxiliaram nos trabalhos de campo e tornaram esse trabalho não só possível mas muito prazeroso: Amanda Guilherme, Augusto Machado, Bruno Masi, Herick Simas, Edson Faria, KatiaCapel, Marcello Mantellato, Vanessa Bettcher e Vinícius Kerr. Meus agradecimentos para Juliana Magalhães Araujo, que pesou parte das amostras enquanto eu estava de licença maternidade e me auxiliou na identificação das macroalgas. Agradeço também ao amigo Humberto Fortunato que me auxiliou na identificação dos poríferos.

Minha imensa gratidão a todos que tornaram possível o projeto de extensão, parte deste trabalho, “Projeto Pra Que Serve?”. Agradeçoàs professoras Elizabeth Lourenço e Luciana Costa que durante a disciplina Ações extensionistas, educação e popularização da ciência me direcionaram e me inspiraram na missão de levar ciência para além dos muros da universidade. Agradeço especialmente a Juliana Magalhães Araujo, que pensou todo o Projeto junto comigo, desenvolveu os materiais, esteve presente nas oficinas e foi essencial para elaboração e publicação do artigo que é parte do capítulo 5 dessa tese. Meu muito obrigada ao meu orientador Joel Creed que abraçou e financiou a ideia e nos deu autonomia para desenvolver o Projeto. Agradeço aos colegas que participaram das oficinas e foram fundamentais para a realização desse trabalho: Amanda Guilherme, Beatriz Dutra, Carolina Amorim, Erika Mamede, Fernanda Araujo Casares, Mariana Pinto Aguiar e Rafael Santos.

Agradeço aos colegas do Laboratório de Ecologia Marinha Bêntica (LEMB) e Laboratório de Ecologia Marinha Química (LEMARQUI) por compartilharem ideias, discussões e muitas risadas que definitivamente tornaram os anos de doutorado mais divertidos. Agradeço especialmente à Mariana Pinto Aguiar por compartilhar diariamente o mesmo caminho de ida e volta para o laboratório e tornar esse ritual um estímulo diário para cumprirmos nossos objetivos e metas.

Agradeço à toda a equipe do Centro de Energia Nuclear na Agricultura – USP (CENA) que me receberam, me auxiliaram e realizaram as análises isotópicas, em especial Dr. Plínio Barbosa, Marcelo, Fabiana e Roberta.

Meus amigos são parte essencial que tornaram esses anos de doutorado mais leve e divertido e grande parte da minha gratidão é dedicada a eles. Especialmente àLarissa Akiko que mesmo com adistânciafísica está sempre presente na minha vida, compartilhando ensinamentos, planos, alegrias, conquistas, incertezas e receitas bem gostosas. Juliana Magalhães Araujo, que é mais que uma amiga, mas uma companheira de sonhos e ideais. Agradeço também à minha amiga, comadre e futura doutra em linguística Renata Martins que compartilha comigo as alegrias e frustaçõesacadêmicas.

RESUMO

TEIXEIRA, Larissa Marques Pires. *Bioinvasão marinha e mudanças na comunidade:* análises de diversidade, caracterização trófica e nicho isotópico. 2021. 260 f.Tese (Doutorado em Ecologia e Evolução) – Instituto de Biologia Roberto Alcântara Gomes, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, 2021.

A bioinvasão marinha representa um dos impulsionadores diretos de mudanças na natureza com maior impacto global, levando a perda de diversidade biológica e de funções ecossistêmicas. Ainda que as consequências causadas pela introdução de uma espécie exótica invasora (EEI) sejam incertas, elas podem causar efeitos quase imperceptíveis até a completa dominação e deslocamento de comunidades nativas. Os mecanismos por trás do sucesso de uma EEI são determinados tanto por características da espécie como da comunidade, contudo, ainda não existe um consenso a respeito do que torna uma EEI bem-sucedida. O presente trabalho, dividido em 5 capítulos, tem como objetivo principal avaliar o efeito de EEI marinhas na diversidade e estrutura trófica em comunidades bentônicas de costão rochoso e divulgar os conceitos relacionados ao estudo da bioinvasão marinha e da ciência marinha para além da academia. Inicialmente reunimos informações atualmente disponíveis sobre as EE marinhas no Brasil e observamos que entre o período de 1950 a 2010, o número de EE marinhas dobrou pelo menos a cada década, o que mostra que o Brasil deve se empenhar de forma mais eficiente no combate a introdução de EE e utilizar ferramentas mais efetivas, por exemplo, umbanco de dados nacional para monitorar tendências nas introduções EE marinhas. No segundo capítulo, nós usamos a abordagem de ajuste e seleção de modelos de distribuição de abundância de espécies, índices de diversidade taxonômica e índices de diversidade funcional baseados em matrizes de agrupamento hierárquico para avaliar os efeitos de quatro espécies marinhas invasoras na diversidade biológica e funcional em costões rochosos ao longo do litoral do estado do Rio de Janeiro. Consideramos que os índices de diversidade taxonômica e funcional são ferramentas úteis para identificar processos que determinam a diversidade biológica, contudo, as características funcionais das espécies refletiram melhor o número e a biomassa de EEI. No terceiro capítulo, utilizamos valores de $\delta^{13}C$ e $\delta^{15}N$ e métricas de nicho isotópico para investigaras relações tróficas em costões rochosos invadidos pelos corais *Tubastraea tagusensis* e *T. coccinea*. Ambos se revelaram competidores alimentares de sucesso que ocupam um nicho específico dentro do nicho ocupado por outras espécies funcionalmente equivalentes Ainda utilizando análise de $\delta^{13}C$ e $\delta^{15}N$, no quarto capítulo nós fornecemos a primeira caracterização de uma teia trófica em um costão rochoso de uma área invadida pelo coral mole invasor *Sansibia* sp., corroborando observações documentadas em campo de um possível predador, também identificamos mudanças desde o último levantamento realizado em 2017 (ano de introdução) e um aumento na abundância e distribuição da EEI para áreas mais favoráveis. O quinto e último capítulo representa um trabalho de extensão universitária desenvolvido em paralelo ao projeto de doutorado onde analisamos diferentes dimensões de atuação do projeto e a resposta daqueles que participaram das oficinas, mostrando a importância de levar informações e debates restritos á academia para além da universidade.

Palavras-chave: Comunidade. Diversidade Funcional. Espécies Exóticas Invasoras. Índices de Diversidade. Relações Tróficas.

ABSTRACT

TEIXEIRA, Larissa Marques Pires. *Marine bioinvasion and community changes:* analysis of diversity, trophic characterization and isotopic niche. 2021. 260 f. Tese de Doutorado em Ecologia e Evolução– Instituto de Biologia Roberto Alcântara Gomes, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, 2021.

Marine bioinvasion represents one of the direct drivers of changes in nature with the greatest global impact, leading to the loss of biological diversity and ecosystem functions. Although the consequences caused by the introduction of a non-native species (NS) are uncertain, they can cause almost imperceptible effects up to the complete domination and displacement of native communities. The mechanisms behind the success of a NS are determined by both species and community characteristics, however, there is still no consensus on what makes a NS successful. The present work, divided into 5 chapters, has as main objective to evaluate the effect of marine NS on the diversity and trophic structure in benthic communities of rocky shore and to disseminate the concepts related to the study of marine bioinvasion and marine science beyond the academy. We initially gathered information currently available on marine NS in Brazil and noted that between 1950 and 2010, the number of marine NS doubled at least every decade, which shows that Brazil should be more efficient in combating introduction of NS and use more effective tools, for example a national database to monitor trends in marine NS introductions. In the second chapter, we use the fit and selection approach of species abundance distribution models, taxonomic diversity indices, and functional diversity indices based on hierarchical cluster matrices to assess the effects of four invasive marine species on biological and functional diversityon rocky shores along the coast of the state of Rio de Janeiro. We consider that the taxonomic and functional diversity indices are useful tools to identify processes that determine biological diversity, however, the functional characteristics of the species better reflected the number and biomass of NS. In the third chapter, we use $\delta^{13}C$ and $\delta^{15}N$ values and isotopic niche metrics to investigate trophic relationships in rocky shores invaded by the corals *Tubastraea tagusensis* and *T. coccinea*. Both proved to be successful food competitors occupying a specific niche within the niche occupied by other functionally equivalent species. Still using $\delta^{13}C$ and $\delta^{15}N$ analysis, in the fourth chapter we provide the first characterization of a food web on a rocky shore of an area invaded by invasive soft coral *Sansibia* sp., corroborating field-documented observations of a possible predator, we also identified changes since the last survey conducted in 2017 (year of introduction) and an increase in NS abundance and distribution to more favorable areas. The fifth and last chapter represents a university extension work developed in parallel to the doctoral project where we analyze different dimensions of the project's performance and the response of those who participated in the workshops, showing the importance of taking information and debates restricted to academia beyond the university.

Keywords: Community. Diversity indices.Functional diversity. Nonnative species.Trophic relationships.

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LISTA DE ABREVIATURAS E SIGLAS

1-λ	Índice de Simpson
AS	*Alien species*
AT	Área Total
BIG	Baía da Ilha Grande
CDB	Convenção sobre Diversidade Biológica
CONABIO	Conselho Nacional de Biodiversidade
C	Carbono
d	Índice de Margalef
DAS	Distribuição de abundância de espécies
DC	Distância média do centróide
DT	Diversidade Taxonômica
DF	Diversidade Funcional
DO	Oxigênio Dissolvido
df	Grau de Liberdade
EE	Espécie Exótica
EEI	Espécie Exótica Invasora
FEve	Uniformidade Funcional
FDis	Dispersão Funcional
FDiv	Divergência Funcional
FRic	Riqueza Funcional
H’	Índice de Shannon
IA	Ilha de Âncora
IC	Ilhas Comprida
IG	Ponta do Bananal
J’	Equitabilidade de Pielou
MNND	Desvio padrão da distância do vizinho mais próximo
N	Nitrogênio
NIS	*Non-indigenous species*
NS	*Non-native species*
NND	Distância média do vizinho mais próximo

RaoQ	Entropia Quadrática de Rao
PB	Praia da Baleia
PSU	Unidade de Salinidade Prática
PV	Praia Vermelha
RR	*Response ratio*
SD	*Standard deviation*
RJ	Rio de Janeiro
SEA	Área de elipse padrão
SEAc	Área de elipse padrão corrigida
SP	São Paulo
UC	Unidade de Conservação

LISTA DE SÍMBOLOS

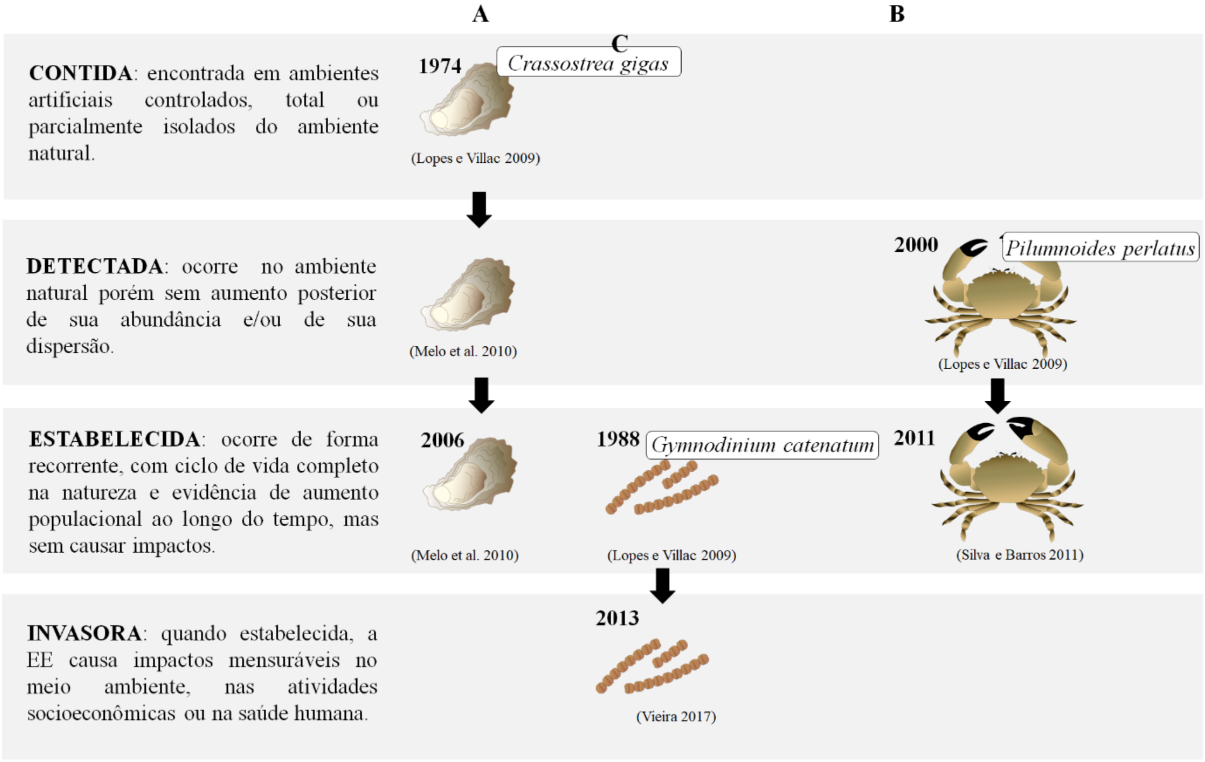
$\delta^{13}C$	Isótopo de Carbono
$\delta^{15}N$	Isótopo de Nitrogênio
%	Porcentagem
λ	Lambda
±	Mais ou menos
×	Multiplicação
km	Quilômetro
≥	Maior ou igual
>	Maior
≤	Menor ou Igual
<	Menor
mL	Mililitro
m	Metros
°C	Graus Celcius
rpm	Rotações por minuto
α	Alfa
∩	Intersecção

SUMÁRIO

INTRODUÇÃO GERAL

O oceano, ainda que cubra a maior parte da superfície terrestre e atue na manutençãoclimática, sustentando a vida na Terra e o bem-estar humano, está seriamente degradado e continuamente sendo ameaçado por atividades antrópicas (Pereira e Soares-Gomes 2009; Solan et al. 2012; Simcock 2017). Entre as ameaças que levama perda de biodiversidade marinha e de funções ecossistêmicas, a bioinvasão é considerada uma das mais caras em termos de danos econômicos e ecológicose um dos impulsionadores diretos de mudanças na natureza com maior impacto global (Occhipinti-Ambrogi e Savini 2003; Rilov and Crooks 2009, IPBES 2019).De acordo com a Convenção sobre Diversidade Biológica (CDB, 2016) os impactos ecológicos da bioinvasão podem ser tão severos que são considerados um dos principais responsáveis pela perda de biodiversidade em todo o mundo. Bioinvasão ou invasão biológica é o ato ou efeito de um ou mais organismos invadirem e se estabelecerem em ambientes onde não havia registros anteriores para a espécie, que após a introdução passa a ocorrer fora da sua distribuição natural, em locais onde não seria possível chegar sem a interferência das atividades humanas (Pereira e Soares-Gomes 2009; Souza et al. 2009). A espécie introduzida, conhecida como espécie exótica (EE), segue uma hierarquia de status de acordo com a condição em que ela se encontra após a chegada no novo ambiente: 1) Contida: quando a presença da EE foi detectada apenas em ambientes artificiais controlados, total ou parcialmente isolados do ambiente natural; 2) Detectada: quando foi detectada a presença da EE no ambiente natural, mas sem posterior aumento em sua abundância e dispersão ou, alternativamente, sem maiores informações sobre a situação da população da espécie; 3) Estabelecida: quando a EE foi detectada de forma recorrente, com seu ciclo de vida completo na natureza e evidência de aumento populacional ao longo do tempo em uma região restrita ou ampla, mas sem impactos ecológicos ou socioeconômicos aparentes; 4) Invasora: quando a EE tem abundância ou dispersão geográfica que interfere na capacidade de sobrevivência de outras espécies em uma ampla região geográfica ou mesmo em uma área específica ou quando a espécie estabelecida causa impactos mensuráveis nas atividades socioeconômicas ou na saúde humana (Lopes et al. 2009; Teixeira e Creed 2020) (Figura 1).

Figura 1 – Diagrama conceitual exemplificando os quatro estágios de um processo de bioinvasão: contida, detectada, estabelecida e invasora, de três espécies exóticas (EE) (A, B e C) após a introdução



Legenda: A– Inicialmente introduzida no Brasil na década de 70 para consumo humano, o bivalve *Magallana gigas* (Thunberg, 1793)ampliou sua distribuição para além dos tanques de cultivo e deixou de ser uma EE contida, sendo detectada ocorrendo em ambiente natural e após expandir sua distribuição é atualmente considerada uma EE estabelecida; B– O dinoflagelado *Gymnodinium catenatum* H.W.Graham, 1943foi detectado em 1988 ocorrendo de forma recorrente, em 2013 ocorreram três alertas de concentração e detecção de toxinas paralisantes para essa espécie, que atualmente possui o status de espécie invasora; C–Até 2011, o caranguejo *Pilumnoides perlatus* (Poeppig, 1836)possuía apenas um registro para o Brasil sendo considerada uma EE detectada, em 2011 registrada em um novo local é atualmente considerado uma EE estabelecida (Texeira e Creed 2020)

Nota: Adaptado de Lopes e Villac 2009; DesenhosThe IAN symbol libraries (https://ian.umces.edu/projects/ian-symbol-libraries/)

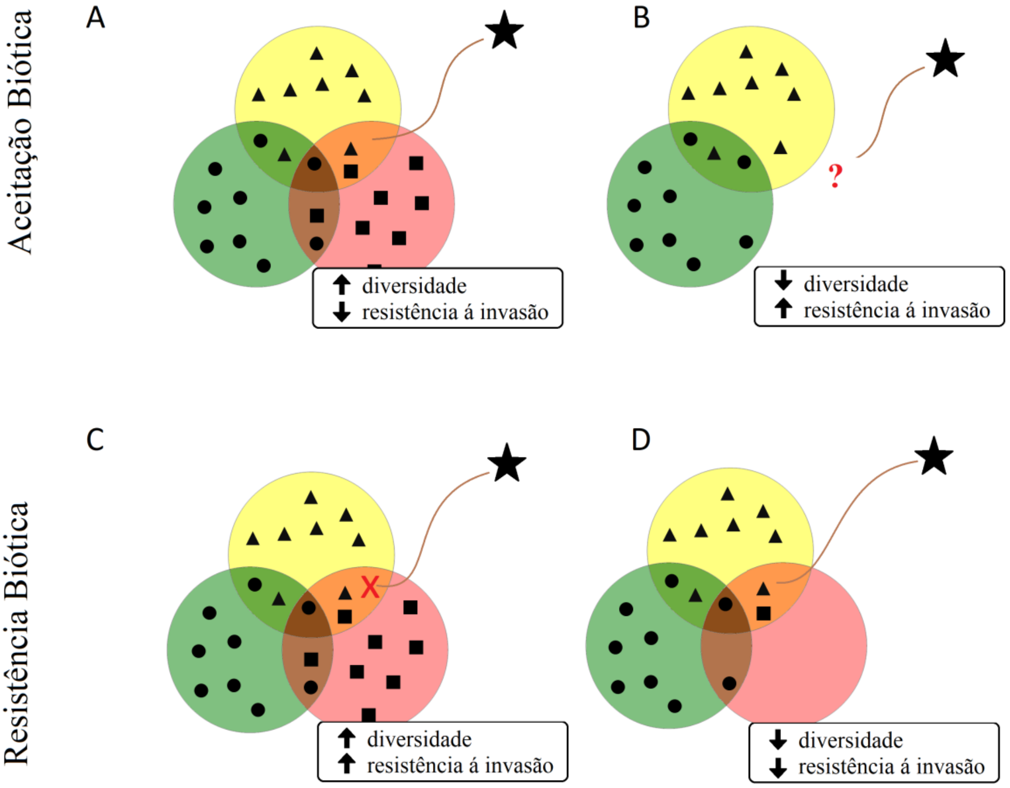
Fonte: A autora, 2021.

Ainda que as consequências causadas pela introdução de uma espécie exótica invasora (EEI) sejam incertas, elaspodem causar efeitos quase imperceptíveis até a completa dominação e deslocamento de comunidades nativas, equando detectado, muitas vezes de forma tardia, são impactos difíceis de serem revertidos (Ruiz et al. 1997; Simberloff et al. 2012; Giakoumi et al. 2016). Em uma revisão recente, Salimi et al. (2021) destacou que os impactos causados por EEI em ecossistemas marinhos tropicais ocorrem principalmente por meio da competição, predação, alteração do habitat e doença. Pimentel et al. (2001) estima que os impactos causados por EEI em diferentes países, incluindo o Brasil, cause um prejuízo de mais de US$ 314 bilhões por ano. Só no Brasil US$ 105,53 bilhões foram gastos em 35 anos (1984–2019), dos quais US$

104,33 bilhões foram devidos a danos e perdas causados por EEI, enquanto apenas US$ 1,19 bilhão foram investidos em seu manejo (prevenção, controle ou erradicação) (Adelino et al. 2021). Um exemplo de EEI que impacta a dinâmica do ecossistema e a estrutura das comunidades nativassão os corais do gênero *Tubastraea*, EEI introduzidas no Mar do Caribe em cascos de navios e no Golfo do México e no Atlântico sudoeste brasileiro por plataformas de petróleo (Creed et al. 2017). No Brasil, *Tubastraea* spp. foi documentado competindo com espécies nativas e facilitando a introdução de outras EE (Lages et al. 2010; Moreira e Creed 2012; Santos et al. 2013; Hoeksema e Harry 2017; Luz et al. 2019; Guilhem et al. 2020).

Embora não exista um consenso no que se refere ao sucesso de uma espécie introduzida que se torna um EEI, determinadas características tanto da espécie como da comunidade podem favorecer o estabelecimento de uma nova espécie após a chegada em um novo local.O estabelecimento bem-sucedido de uma EE depende de um propágulo introduzido em um local altamente adequado, o que de certa forma envolve não somente os traços funcionais da EE, frequentemente características biológicas diferentes das espécies nativas, como por exemplo, maior potencial reprodutivo (Meister et al. 2005; Sax e Brown 2000; Van Kleunen et al. 2010; Zhan et al. 2015). Um processo de invasão bem-sucedidoenvolve tambémparticularidades da comunidade invadida, como a falta de inimigos naturais (Mack et al. 2000;Troost 2010). A comunidade receptora que atua como uma barreira à invasão, previne o estabelecimento da EE, ou quando o estabelecimento ocorre são as interações ecológicas que regulam o crescimento subsequente e a disseminação das populações invasoras (Stachowicz et al. 1999; Levine et al. 2004; Rivera et al. 2005; Kimbro et al. 2013). Esse processo em que a comunidaderepelea invasão de EE é o cerne da “Hipótese de Resistência Biótica” (Elton 1958), em que a riqueza de espécies de uma comunidade atua impedindo que novas espécies se estabeleçam, já que em comunidades ricas os recursos e/ou nichos estão sendo amplamente usados e portanto, estão pouco disponíveis para novas espécies, ou seja, quanto maior a diversidade, maior é a capacidade de resistência a invasão (Byers e Noonburg 2003; Kennedy et al. 2002; Rivera et al. 2005; Fridley et al. 2007; Jeschke et al. 2018). Embora muitos ecologistas corroborem que a resistência biótica é um processo forte capaz de repelir invasões de EE, outra possibilidade, que está por trás da “Hipótese de Aceitação Biótica”, é que se o ambiente é adequado para sustentar uma grande diversidade de espécies nativas, também o será para o estabelecimento de EE, ou seja, os padrões de riqueza de espécies nativas são em grande parte resultado das condições ambientais, que são universalmente desejáveis tanto para espécies naturalmente existentes na comunidade quanto para as espécies introduzidas (Brown e Peet 2003; Stohlgren 2006). Ambas as hipóteses, que se contradizem, representam o “Paradoxo da Invasão” (Fridley et al. 2007), e apontam que o papel da diversidade de espécies como barreira para bioinvasão ainda é discutível.

Figura 2 – Diagrama conceitual demonstrandocomo as mudanças na diversidade se relacionam com a invasibilidade da comunidade receptora e representam um paradoxo da invasão.



Legenda: Aceitação Biótica: A – comunidades mais diversas possuem maior diversidade de nichos (círculos coloridos) para receber espécies exóticas (EE, estrela), consequentemente são menos resistentes à invasão; B – comunidades menos diversas possuem menor oferta de nicho que diminuem as chances de uma EE encontrar um nicho adequado, logo, são mais resistentes à invasão. Resistência Biótica: C – comunidades mais diversas possuem maior número de nichos ocupados por espécies nativas, o que diminui a disponibilidade de nichos vagos para EE e aumenta a resistência a invasão; D - comunidades menos diversas possuem maior número de nichos vagos disponíveis para EE e consequentemente são menos resistentes à invasão.

Fonte: A autora, 2021.

No que se refere ao combate às EE, agir para prevenir novas introduções é reconhecida como a ação principal, sem descartar que simultaneamente as EE já introduzidas sejam gerenciadas, controladas e em última análise, erradicadas(Rilov and Crooks 2009). Majoritariamente, as pesquisas envolvendo bioinvasão marinha incluem o gerenciamento de introduções que já aconteceram, o que é compreensível já que na maioria das situações as invasões se tornam aparentes apenas quando os efeitos e presença da EEI são visíveis (Anil 2006). Contudo, recomendações eficientes para a prevenção de novas introduções ainda são negligenciadas no Brasil, como por exemplo, políticas públicas eficientes sobretudo no ambiente marinho e um banco de dados nacional de EE marinhos (Sliwa et al. 2009; Zanella 2015; Bai e Cheng 2019). AConvenção sobre Diversidade Biológica (CDB, 2016), que engloba tudo o que se refere direta ou indiretamente à biodiversidade, estabelece que os países participantes, entre eles o Brasil, devem impedir, controlar ou erradicar EE que ameacem os ecossistemas, habitats ou espécies nativas. Em 2002, o Decreto nº 4.339/02, que instituiprincípiose diretrizes para a implementação da Política Nacional da Biodiversidade, especificou medidas de combate ás EE, entre elas: Inventariar e mapear as EEI e ecossistemas em que foram introduzidas para nortear estudos dos impactos gerados e ações de controle; promover e apoiar pesquisas para subsidiar a prevenção, erradicação e controle de EEI; articular ações com o órgão responsável para impedir a entrada no país de EEI, principalmente em áreas de Unidade de Conservação (UC); promover a prevenção, a erradicação e o controle de EEI e apoias ações com esse objetivo; monitorar os impactos causado pela introdução de EEI; apoiar estudos dos impactos da introdução de EE potencialmente invasoras. Contudo, somente em 2009 o Conselho Nacional de Biodiversidade (CONABIO) instituiu um documento que trata exclusivamente do combate a EEI, a Resolução nº 05/09, que aprova a Estratégia Nacional sobre Espécies Exóticas Invasoras.

Introdução de espécies e mudanças na diversidade

O número de invasões marinhas documentadas está aumentando ao longo dos anos (Bailey et al. 2020) e as consequências para a comunidade nativa e os mecanismos subjacentes ao sucesso ou fracasso das invasões variam enormemente (Mack et al. 2000; Stachowicz et al. 2002).Entre ameaças causadas por EEI, alterar a diversidade das comunidades invadidas representa um dos maiores impactos e mais difíceis de serem revertidos (Mack et al. 2000; Bax et al. 2003; Simberloff 2005; Salimi et al. 2021). Por exemplo, na Baía da Ilha Grande (BIG), Rio de Janeiro, sudeste do Brasil,após a introdução da alga verde *Caulerpa scalpelliformis* (R. Brown ex Turner) C.Agardh, 1817, foram observadas mudanças significativas na estrutura da comunidade de macroalgas, incluindo diminuiçãodrástica da alga parda *Sargassum vulgare*

C.Agardh, 1820 e a dominação dos substratos rochosos e arenosos por *C. scalpelliformis*(Falcão e Széchy 2005).

A diversidade pode ser medida de diferentes maneiras, entre as medidas de diversidade, a diversidade taxonômica (DT) expressa a variedade de espécies em uma comunidade. Na busca por padrões de diversidade, muitos ecologistas concentraram seus esforços para medir a diversidade a nível de espécie, seja pela riqueza de espécies, definida como o número de espécies em uma comunidade, pela abundância, definida pela quantidade de indivíduos ou pela equitabilidade, que se refere a distribuição do número de indivíduos entre as espécies (Magurran 2013). O posterior desenvolvimento de índices de DT surgiu como uma necessidade para incorporar informações sobre as medidas de diversidade, e enfatizam diferentes aspectos da diversidade (Tabela 1).

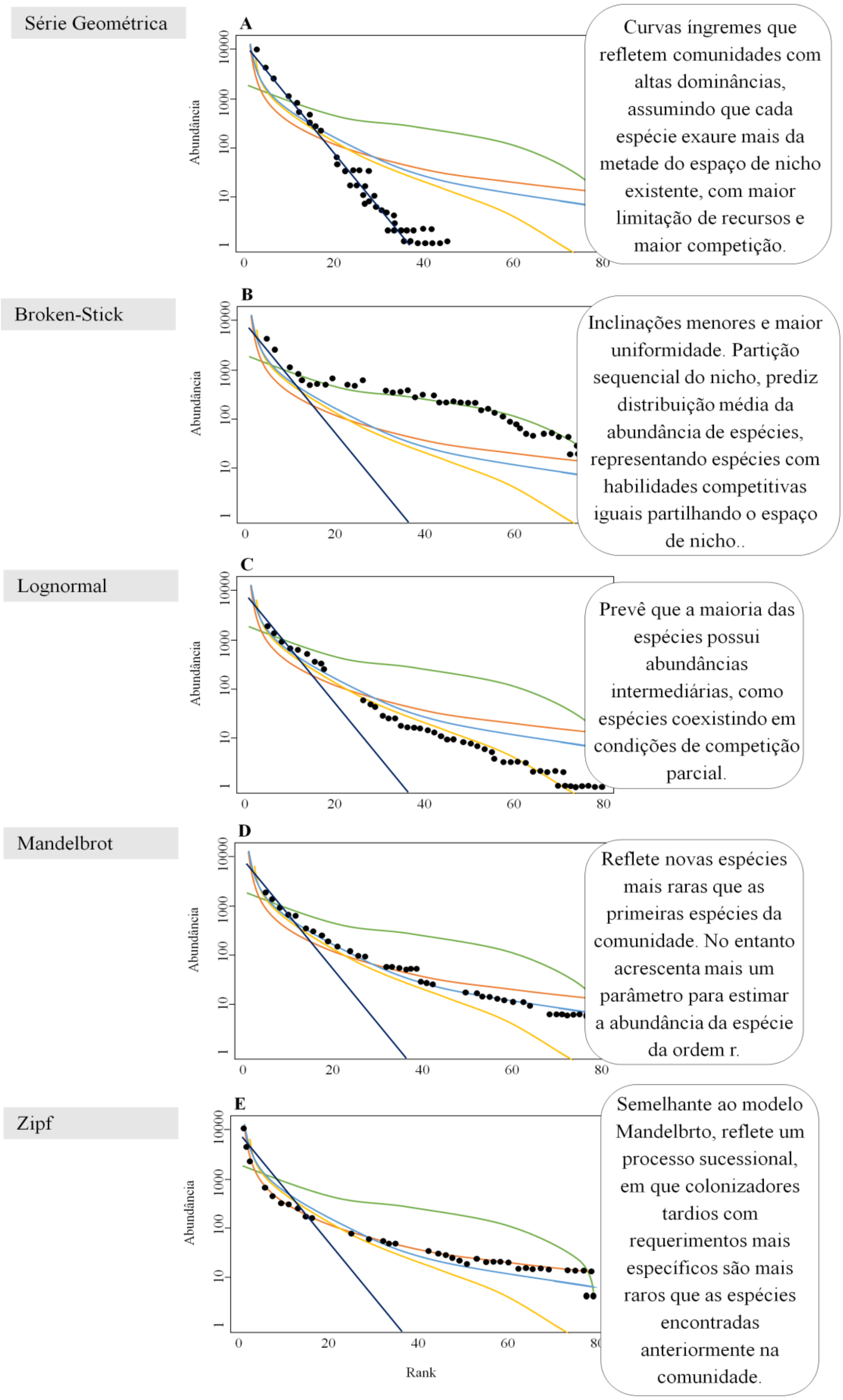
Tabela 1 - Índices de diversidade taxonômica (DT) utilizados neste estudo

Índices	Descrição	Cálculo	Referencia
Índice de Simpson (D)	Calcula a probabilidade de dois indivíduos retirados aleatoriamente de uma comunidade pertencerem a mesma espécie e captura a variância da distribuição da abundância das espécies.	$D=\Sigma p_i^2$ em que p^i é a proporção relativa	Simpsom (1949); Magurran (2004)
Índice de Shannon (H’)	Assume que indivíduos são amostrados aleatoriamenteem uma comunidade ou sub-comunidade de interesse.	$H' = -\Sigma p_i \text{Log} p_i$ em que p_i é a proporção de indivíduos encontrados em relação ao número total de espécies	Shannon e Weaver (1949); Krebbs (1999); Magurran (2004)
Índice de Fisher	Ajusta a distribuição de uma série logarítima, relaciona o número de espéciesao número de indivíduos em uma comunidade e é pouco influenciado pelo tamanho daamostra ou pelaabundância das espécies mais comuns.	$S = \alpha \ln (1 + n/\alpha)$	Fisher et al. (1943)
Equitabilidade de Pielou (J’)	Indica se as diferentes espécies possuem abundâncias semelhantes ou diferentes e permite representar a uniformidade da distribuição dos indivíduos entre as espécies da comunidade.	$J' = H'/H_{max}$ onde $H_{max} = \text{Log}(S)$ em que S é o número total de espécies amostradas e H’ é o Índice de Shannon	Pielou (1966)
Índice de Margalef (d)	Estima a diversidade da comunidade baseado na distribuição numérica dos indivíduos das diferentes espécies em função do número total de indivíduos presentes na amostra	$d = (S-1)/\text{Log}(n)$onde S = número de espécies e n = número total de indivíduos da amostra	Margalef (1951); Moreno (2000)

Fonte: A autora, 2021.

Outra forma de analisar a diversidade e descrever dados de abundância de espécies é através de modelos matemáticos, como a distribuição de abundância de espécies (DAS), uma ferramenta amplamente utilizada em ecologia que permite identificar processos que determinam a diversidade biológica de uma comunidade, partindo do pressuposto que a abundância de uma espécie é na maioria das vezes reflexo do seu sucesso em competir por recursos limitados (Magurran 2013; Rosindell e Cornell, 2013; Drake et al. 2014; Morri et al. 2019). Esses modelos utilizam o conjunto total dos valores de importância de cada espécie e a relação entre o rank de abundância, onde as espécies são apresentadas em ordem decrescente da sua abundância no eixo x, e a abundância no eixo y. A linha que melhor se ajusta aos pontos é o modelo que explica a diversidade. O uso de DAS pode ilustrar mudanças após um impacto ambiental, apresentar padrões contrastantes de riqueza de espécies, informações referentes às abundâncias relativas mesmo que as espécies sejam poucase destacar diferenças na uniformidade entre comunidades (Magurran 2007; Mc Gill et al. 2007; Lyashevska e Farnsworth 2012) (Figura 3).

Figura 3 - Diagrama conceitual exemplificando os modelos de distribuição de abundância de espécies (DAS) nos gráficos de ranking/ abundância.



Curvas íngremes que refletem comunidades com altas dominâncias, assumindo que cada espécie exaure mais da metade do espaço de nicho existente, com maior limitação de recursos e maior competição.

Inclinações menores e maior uniformidade. Partição sequencial do nicho, prediz distribuição média da abundância de espécies, representando espécies com habilidades competitivas iguais partilhando o espaço de nicho..

Prevê que a maioria das espécies possui abundâncias intermediárias, como espécies coexistindo em condições de competição parcial.

Reflete novas espécies mais raras que as primeiras espécies da comunidade. No entanto acrescenta mais um parâmetro para estimar a abundância da espécie da ordem r.

Semelhante ao modelo Mandelbrto, reflete um processo sucessional, em que colonizadores tardios com requerimentos mais específicos são mais raros que as espécies encontradas anteriormente na comunidade.

Legenda: A – Série Geométrica; B – Broken-Stick; C – Lognormal; D – Mandelbrot; E – Zipf.
Nota: Dados hipotéticos.
Fonte: A autora, 2021.

Medidas de diversidade são baseadas apenas na identidade taxonômica e partem do pressuposto de que todas as espécies são equivalentes em seus papéis ecológicos, e não consideram as diferenças morfológicas, bioquímicas, fisiológicas, estruturais, fenológicas e comportamentais dos indivíduos (Bengtsson 1998; Schleuter et al. 2010). Não considerar o papel de cada espécie nos ecossistemas ou nas respostas das espécies às condições ambientais fornece uma visão incompleta debiodiversidade (Villéger et al. 2010). Ainda assim, mesmo não levando em conta as muitas funções ecológicas diferentes das espécies que compõem a comunidade, aDT continua a ser usada como medida de biodiversidade (Jarzyna e Jetz 2018). Nos últimos anos, muitos ecólogos têm utilizado medidas de diversidade complementares e que possibilitem também analisar as interações que ocorrem no ecossistema utilizando abordagens baseadas nas características das espécies e assim revelar o efeito de impactos, como a introdução de uma EEI, sobre o funcionamento da comunidade (Lambdon et al. 2008; Lyashevska e Farnsworth 2012; Gomes et al. 2018; Takács et al. 2021). Um exemplo é o uso de medidas de diversidade funcional (DF) que refletem a diversidade através de característicasmorfológicas, fisiológicas e traços ecológicos encontrados nas espécies (Tilman 2001).

Partindo da premissa que as espécies não possuem características ecológicas iguais e contribuem de forma diferente nos processos ecossistêmicos, a DF utiliza os valores e a amplitude dos atributos das espécies para incorporar as diferenças nos papéis desempenhados pelas espécies, suas contribuições para as relações de diversidade e funcionamento do ecossistema e a complementaridade no uso de recursos e diferenciação dos nichos (Díaz e Cabido 2001; Tilman 2001; Laureto 2015; Goswami et al. 2017). É justamente por medir a diversidade a partir de características (denominadas traços funcionais), morfológicas, fisiológicas ou ecológicas mensuráveis em nível individual de cada espécieque a escolha adequada dos traços é um ponto importante nas análises de DF (Dalerum et al. 2012; Tsianou et al. 2016). Quando falamos em traços funcionais estamos nos referindo as características das espécies que são mensuradas, enquanto que os atributos funcionais se referem ao valor de um traço qualquer em um dado lugar e tempo (Petchey et al. 2009; Laureto et al. 2015). Estimativas corretas da DF dependem principalmente da escolha de características ecologicamente significativas, que podem ser divididas em traços de efeito, que determinam como as espécies afetam as funções do ecossistema, e traços de resposta, que revelam como as espécies respondem ao seu ambiente (Lavorel e Garnier, 2002; Vandewalle et al. 2010; Laureto et al. 2015). Para caracterizar a diversidade funcional e funções ecológicas selecionadas de comunidades de invertebrados bentônicos marinhos na escala do ecossistema e avaliar as contribuições relativas da filtragem ambiental, incluindo pesca de contato com o fundo e interações competitivas para a montagem da comunidade bentônica, Murillo et al. (2020) selecionou um conjunto de sete características biológicas com base em sua suposta importância para a estrutura e funcionamento dos ecossistemas bentônicos (características de efeito) ou por sua sensibilidade a perturbações ou mudanças no ambiente (características de resposta), entre eles tamanho, longevidade, método reprodutivo, dispersão de propágulo, mobilidade, grau de agregação e tipo de alimentação. Micheli e Halpern (2005) usaram dois conjuntos de dados distintos, um de florestas de *kelps* e outro de uma síntese global de reservas marinhas, para testar diretamente como a variação na diversidade de espécies se traduz em mudanças na diversidade funcional, e para isso usou apenas três características funcionais baseadas no conhecimento biológico das características das espécies que são fundamentais para determinar seu papel nas comunidades marinhas costeiras e suas respostas à perturbação, entre elas, grupo trófico, tamanho e mobilidade. Assim sendo, traços irrelevantes devem ser excluídos das análises, de modo que os traços selecionados estejam diretamente ligados aos objetivos da pesquisa, e sejam válidos para identificar e quantificar os atributos funcionais para predição de espécies e respostas da comunidade às mudanças ambientais. (Petchey and Gaston 2006;Rosado et al. 2013; Chao et al. 2019).

Além da escolha dos traços, selecionar o índice apropriado para medir a DF também é fundamental. Quatro componentes principais da diversidade funcional são descritos em cinco índices - riqueza funcional (FRic), uniformidade funcional (FEve), divergência funcional (FDiv), dispersão funcional (FDis) e Entropia Quadrática de Rao (RaoQ) (Botta-Dukát 2005; Mason et al. 2005; Villéger et al 2008; Pla et al. 2012) e cada um dos componentes fornece informações independentes sobre a distribuição das espécies no espaço das características funcionais, sendo que um índice separado é necessário para quantificar cada componente (Mouchet et al. 2010; Mason et al. 2013; Schleuter et al. 2010) (Tabela 2).

Tabela 2 - Índices de diversidade funcional (DF) utilizados neste estudo

Índices	Descrição	Cálculo	Referências
Riqueza Funcional (FRic)	Mede a quantidade de espaço de funcional preenchido na comunidade, considerando o número de grupos funcionais presentes.	Baseado no conceito de casco convexo. O casco convexo mínimo que inclui todas as espécies consideradas e corresponde ao volume contido neste casco, calculado após a projeção de cada espécie de acordo com seus valores de traços em um espaço multidimensional onde cada dimensão representa um traço funcional.	Villéger et al. 2008; Legras et al. 2018
Uniformidade Funcional (FEve)	Mede a regularidade da distribuição de abundância e dissimilaridades dos traços médios das espécies no espaço funcional.	Baseado na árvore geradora mínima que liga todos os pontos, aqui representado por espécies, contidos em um espaço multidimensional com a soma mínima dos comprimentos dos ramos, que representam a distância funcional entre as espécies. Em seguida, para cada ramo da árvore o comprimento é dividido pela soma das abundâncias das duas espécies ligadas por este ramo.	Villéger et al. 2008; Mouillot et al. 2013; Legras et al. 2018
Divergência Funcional (FDiv)	Mede o grau em que a abundância de uma comunidade é distribuída em direção às extremidades da ocupação no espaço funcional utilizando os valores de traços mais extremos, independente do volume de espécies.	É calculada a média não ponderada entre as espécies que formam os vértices do casco convexo e então é aplicada uma série de equações para comparar a soma observada das distâncias euclidianas ponderadas pela abundância das espécies a partir do centro de gravidade em relação ao valor máximo possível.	Mason et al. 2005; Levin 2013
Dispersão Funcional (FDis)	Mede a distância média de cada espécie no espaço funcional multidimensional em relação ao centroide de todas as espécies presentes na comunidade.	A partir da média ponderada pela abundância para cada traço é encontrado o centroide do grupo ponderado pela abundância. Em seguida, é somado o desvio ponderado pela abundância desse centroide entre as espécies. A diferença em relação aos outros índices é que ele não está limitado entre 0 e 1.	Laliberté and Legendre 2010; Levin 2013
Entropia Quadrática de Rao (RaoQ)	Incorpora tanto a abundância relativa de espécies quanto uma medida das diferenças funcionais aos pares entre as espécies. É um índice de dispersão que mede a abundância específica e as diferenças funcionais entre pares de espécies em uma comunidade.	Soma as distâncias em pares ponderadas pela abundância entre as espécies no espaço de traços funcional.	Botta-Dukát 2005; Levin 2013

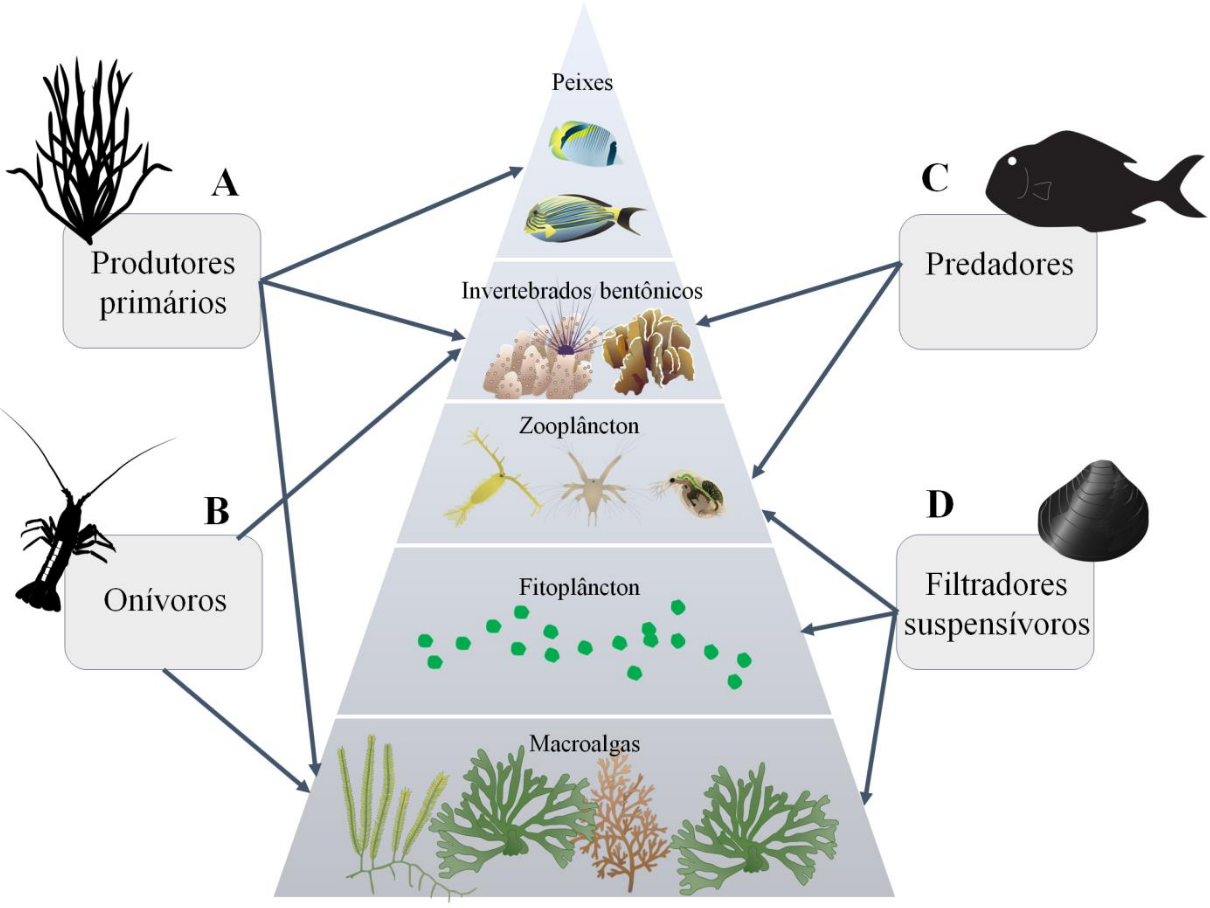
Fonte: A autora, 2021.

Da mesma forma que os efeitos de uma EEI aumentam com sua abundância, eles também variam com seus atributos funcionais. Portanto, se inicialmente, a chegada de uma nova espécie pode trazer novos atributos para um ecossistema, e aparentemente representar um aumento na riqueza de espécies, a permanência das EEI pode mudar esse cenário (Thomsen et al. 2011; Gallardo et al. 2015). Uma nova espécie pode se estabelecer em uma comunidade invadida ao ocupar um nicho diferente das espécies já existentes naquela comunidade e/ou utilizar recursos diferentes (Catford et al. 2009; Strayer et al. 2006). Por exemplo, Hejda e Bello (2013) usaram índices de DF para mostrar que as plantas invasoras costumam introduzir novas combinações de características para as comunidades de plantas invadidas. Da mesma forma, Emery (2007) ao analisar comunidades de plantas herbáceas mostrou que os invasores se saem melhor nas comunidades dominadas por uma espécie que pertence a um grupo funcional diferente das espécies nativas. Por outro lado, EEI funcionalmente semelhante às espécies já existentes na comunidade invadida podem competir mais fortemente com as espécies residentes da comunidade (Riva et al 2019). Ainda, a dominação de uma comunidade invadida pela EEI pode resultar na homogeneização taxonômica (Olden et al. 2004; Dar e Reshi 2014) e consequentemente na redução da variedade de traços, afetando a diversidade funcional das áreas invadidas. Essa premissa testada por Milardi et al. (2019), foi confirmada em comunidades de peixes de água doce, onde um alto grau de invasão correspondeu a uma menor diversidade funcional.

Introdução de espécies e mudanças tróficas

A introdução de EEI, que muitas vezes constitui mudanças na diversidade e adição de novos componentes funcionais na comunidade invadida, também implica em impactos ecológicos que podem se propagar ao longo da cadeia trófica (Strayer 2010). Em ecossistemas marinhos costeiros as invasões podem aumentar de maneira considerável o número de consumidores filtradores, detritívoros, depositívoros e outros consumidores primários (Byrnes et al. 2007).De modo geral, os impactos causados por EEI estão relacionados com a posição trófica do invasor, estratégia de alimentação e a capacidade de modificar o habitat e são resultado de interações ecológicas diretas, como predação, competição, pastoreio, e impactos indiretosmediados por mudanças nas condições físico-químicasdos habitats (Thomsen et al. 2014; Maggi et al. 2015; Gallardo et al. 2015; David et al. 2017; Flood et al. 2020). São eles: (1) Produtores primários invasores podem mudar as condições ambientaisde seu entorno através da produção de detritos, captura de sedimentosou modificação de complexidade estrutural/ tridimensionalidade do habitat afetando a utilização do habitat por peixes e invertebrados bentônicos(Carniatto et al. 2013; Angeler e Johnson 2013), reduzir a diversidade de macrófitas aquáticas através de competição e alteração do habitat (Angeloni et al. 2006) (Figura 4A); (2) Consumidores onívoros podem reduzir a abundância de macroalgas (Angeler2001; Matsuzaki et al. 2007) e invertebrados bentônicos através do consumo direto,perturbação do habitat ao ressuspender sedimentos e destruição de macroalgas durante o forrageamento (Matsuzaki et al. 2009; Lodge et al. 2012) (Figura 4B); (3) Consumidores predadores seletivos, podem reduzir a abundância de peixes, invertebrados bentônicos e zooplâncton, e consequentemente aumentar a abundância do fitoplâncton (Power 1990;Brett e Goldman 1996;Simon e Townsend 2003; Stoks et al. 2003; Kadye e Booth 2012) e aumentar a pressão de seleção sobre espécies nativas para desenvolver defesas (Freeman e Byers2006) (Figura 4C). (4) Consumidores filtradores suspensívoros podem predar e competir em mais e um nível trófico,exercendo um impacto particularmente negativo nas comunidades planctônicas por filtragem direta ea alteração indireta das condições do habitat, reduzindo a concentração de nutrientes necessários para a produção de fitoplâncton (Higgins e Zanden2010). Também podem consumir o pequeno zooplâncton e afetar a disponibilidade de recursos para o zooplâncton maior (Bowen e Johannsson 2011), aumentando a biomassa de macroalgas em função do aumento da clareza da água (Karatayev 1992), modificando a estrutura complexa do substrato que causa um aumento na abundância de invertebrados bentônicos (Higgins e Zanden 2010; Bazterrica et al. 2012) (Figura 4D).

Figura 4 – Impactos tróficos causados por espécies exóticas invasoras marinhas.



Legenda: As setas refletem os impactos resultado de uma combinação de impactos ecológicos diretos e impactos físico-químicos indiretos de espécies invasoras.
Nota:Adaptado de Gallardo et al. 2015; Desenhos The IAN symbol libraries (https://ian.umces.edu/projects/ian-symbol-libraries/)
Fonte: A autora, 2021.

Uma ferramenta útil para descrever as relações em teias tróficas, como a relação predador-presa, é a análise isotópica de produtores e consumidores (Peterson 1999). Além de ser utilizada para examinar aspectos da estrutura de teias tróficas, como fontes de energia, ligação trófica e posição trófica,as razões de isótopos estáveis, principalmente as de carbono, ^{13}C:^{12}C ($\delta^{13}C$), e nitrogênio, ^{15}N:^{14}N ($\delta^{15}N$), nos últimos anos têm sido usadas como uma forma poderosa para investigar nichos ecológicos(Layman et al. 2007; Newsome et al. 2007). Enquanto a transferência de $\delta^{13}C$ ao longo da teia trófica permanece conservada, $\delta^{15}N$ são fracionados consistentemente, dessa forma $\delta^{13}C$ é usado como ferramenta para traçar a origem do recurso alimentar basal, enquanto $\delta^{15}N$ possibilita inferências sobre o nível trófico ocupado pela espécie (Fry 2007).A teoria do nicho sugere que sea competição por recursos é alta, as espécies serão levadas afaixas de nicho mais estreitas e especialização para permitir a coexistência (Pianka 1974).Nas análises de nicho isotópico, $\delta^{13}C$ e $\delta^{15}N$ são usados para explorar questões tradicionalmente trabalhadas no domínio da teoria de nicho mas em um espaço isotópico, que é a área que contém as coordenadas dos valores isotópicos no espaço bidimensional ou mais diretamente no espaço das contribuições proporcionais por recursos (Newsome et al. 2007). A partir de uma abordagem analítica para calcular medidas da estrutura trófica de uma comunidade usando razões de isótopos estáveis é possível avaliar onicho ocupado pelas espécies utilizando métricas. Conhecidas como métricas de Layman ou métricas de nicho isotópico, essas medidas fornecem respostas quantitativasque refletem características especificas da estrutura trófica (Layman et al. 2007; Jackson et al. 2011) (Tabela 3).

Tabela 3 – Métricas isotópicas que refletem aspectos importantes da estrutura tróficaque são utilizadas neste estudo.

Métrica	Descrição	Cálculo
N_range	É a representação vertical dentro de uma teia trófica, onde intervalos maiores geralmente sugerem mais níveis tróficos e maior grau de diversidade trófica.	Distância entre as duas espécies com os valores máximos e mínimos de $\delta^{15}N$ (ou seja, máximo $\delta^{15}N$ - mínimo $\delta^{15}N$).
C_range	Intervalos maiores são esperados em comunidades com maior diversidade de recursos basais.	Distância entre as duas espécies com os valores máximos e mínimos de $\delta^{13}C$ (ou seja, máximo $\delta^{13}C$ - mínimo $\delta^{13}C$).
Área total (AT)	Mede a quantidade total de espaço de nicho ocupado,e, portanto, um proxy para a extensão total da diversidade tróficadentro de uma teia alimentar.	Área do casco convexo englobada portodas as espécies no espaço bidimensional $\delta^{13}C$ - $\delta^{15}N$.
Distância média do centróide (DC)	Distâncias mais altas sugerem alto grau médio de diversidade trófica dentro da cadeia alimentar.	Distância euclidiana média de cada espécie em relação ao centróide $\delta^{13}C$ - $\delta^{15}N$,onde o centróide é o valor médio $\delta^{13}C$ e $\delta^{15}N$ paratodas as espécies na cadeia alimentar.
Distância média do vizinhomais próximo (NND)	Valores baixos sugerem teias tróficas com espécies caracterizadas por ecologias tróficas semelhantes e alta redundância trófica.	Média das distâncias euclidianas até o vizinho mais próximo de cada espécie no espaço bidimensional e, portanto, uma medida da densidade geral do empacotamento de espécies.
Desvio padrão da distância do vizinho mais próximo (SDNND)	Valores baixos sugerem distribuição mais uniforme do nicho trófico.	Medida da uniformidade do empacotamento de espécies no espaço bidimensional que é menos influenciada do que o NND pelo tamanho da amostra
Área de elipse padrão (SEA)	Medida do nicho isotópico médio da população central que é robusto à variação no tamanho da amostra.	É calculada a partir da variância e covariância dos dados no espaço isotópico e contém aproximadamente 40% dos dados, insensível ao tamanho da amostra ao revelar a área de nicho central.
Área de elipse padrão corrigida (SEAc)	Representa um valor de SEA corrigido para contornar o viés que surge quando os tamanhos das amostras são pequenos e permite que o grau de sobreposição de nicho isotópico seja calculado, o qual pode então ser usado como uma medida quantitativa da similaridade alimentar entre as populações.	É uma versão corrigida do tamanho da amostra deSEA utiliza uma correção (n-2) no denominador no lugar do padrão (n-1) ao calcular as variâncias.

Fonte: A autora, 2021.
Nota: Adaptado de Layman et al. 2007; Jackson et al. 2011

Inicialmente utilizada para descrever a dieta de EEI, atualmente as análises de isótopos estáveis fornecem múltiplas informações sobre estrutura trófica de áreas invadidas, tais como:comparação de dietas no espaço e no tempo;teias alimentares em diferentes estágios de invasão;quantificação da competição por recursos entre espécies nativas eEEI; questões específicas relacionadas aos modos de dispersão e mecanismos de estabelecimento (Marshall et al. 2019). Contudo, a eficácia das métricas de Laymanem ecossistemas marinhos é praticamente inexplorada, assim como a utilização de análises isotópicas para estimar o impacto de invasores em ecossistemas marinhos (Mancinelli e Vizzini, 2015).Partindo da premissa que EEI bem-sucedidas possuem nichos mais amplos e são mais plásticas do que espécies não invasoras, Olsson et al. (2009) usou valores de $\delta^{13}C$ e $\delta^{15}N$ para comparar as larguras de nicho de espécies nativas e EEI de lagostins em córregos, mostrando que em nível de espécie o lagostim invasor tinha duas vezes a largura de nicho do lagostim nativo, o que sugere maior plasticidade no que diz respeito à utilização do habitat e alimentação em EEI. Karlson et al. (2015) usou as métricas de Laymande $\delta^{13}C$ e $\delta^{15}N$ e observou que o nicho ocupado por uma EEI de depositívoro marinho é diferente do nicho ocupado por espécies nativas com o mesmo hábito alimentar, sugerindo uma competiçãolimitada por recursos entre as espécies e a ocupação do nicho vago pela EEI. Quando a EEI é uma produtora primária, as métricas de Layman de $\delta^{13}C$ e $\delta^{15}N$ podem ser utilizadas para avaliar se a introdução representa a adição de um novo recurso basal que pode causar umaampliação do nicho trófico dentro da cadeia alimentar marinha (Alomar et al. 2016).

Modelo de estudo e espécies exóticas invasoras estudadas

Descrita como a interface entre dois ambientes distintos, o ambiente marinho e o terrestre, a zona costeira está entre os ambientes marinhos mais produtivos do planeta, recebendo não só a energia de produtores primários marinhos, como as algas e o fitoplâncton, mas também da vegetação terrestre que fica próxima desses locais (Mann 1982; Pereira e Soares-Gomes 2009; Pires 2016).Os ambientes costeiros também são locais de alimentação, crescimento e reprodução de diferentes espécies, o que está relacionado com a grande disponibilidade de alimento e confere aos costões rochosos uma alta riqueza de espécies de grande importância ecológica e econômica (Pereira e Soares-Gomes 2009).A grande diversidade de organismos e a importância econômica e ecológica dos costões rochosos contrastam com as numerosas ameaças que esses ambientes sofrem, sobretudo pelos impactos antrópicos (Kendall et al. 2004; O’Connor 2013; Mendez et al. 2017), entre eles, a introdução de EEI, que estão modificando costões rochosos em todo o mundo (Grosholz 2002; Caro et al. 2011; Lages et al. 2011; Sadchatheeswaran et al. 2015, 2018; Guilhem et al. 2020).

Podemos observar os costões rochosos ao longo de quase toda a costa brasileira, desde o Rio Grande do Sul até o Maranhão, principalmente na costa sudeste, devido à proximidade da serra com o Oceano Atlântico.Da extensão de 7.408 km do litoral brasileiro, o principal trecho da costa em que os costões rochosos são considerados os ecossistemas mais importantes compreende Cabo Frio (RJ) até o Cabo de Santa Marta (SP), região com composição específica de característica sub-tropical, com uma alta diversidade de espécies(Coutinho 2002).

Nossa área de estudo compreende costões rochosos localizados em cinco locais distintos ao longo de cerca de 280 km da costa do estado do Rio de Janeiro, Brasil (Figura 5), uma região que recebeu múltiplas invasões ao longo dos últimos 40 anos:

a) *Caulerpa scalpelliformis* (R.Brown ex Turner) C.Agardh, 1817na Praia da Baleia (PB): Localizada na Baía da Ilha Grande (BIG), Angra dos Reis (23º01'63"S, 44º14'18"W), PB é um local protegido contra ondas com águas rasas (<5 m) onde recifes rochosos se misturam com manchas arenosas. Introduzida em 2001, a alga verde *C. scalpelliformis* é considerada uma EEI neste local (Falcão e Széchy 2005; Lopes et al. 2009; Vasconcelos et al. 2011). *C. scalpelliformis* é amplamente distribuída em águas tropicais e subtropicais no Mar Vermelho, Oceanos Índico e Pacífico, Mar do Caribe e Oceano Atlântico (Ilhas do Atlântico, Atlântico Ocidental e América do Sul desde a Venezuela ao sul até o Estado do Espírito Santo, Brasil) (Lopes et al. 2009). É considerada não nativa no Mar Mediterrâneo e no Brasil na localidade estudada devido à sua distribuição disjunta em uma região muito bem estudada, onde pode crescer tanto na areia como em blocos isolados(Vasconcelos et al. 2011) (Figura 6A). Embora o acesso a PB seja restrito por um condomínio privado e um caminho íngreme, a praia costuma receber embarcações recreativas e barcos de pesca comercial devido à sua localização protegida. Entre os possíveis vetores de introdução e dispersão desta espécie estão o transporte marítimo (âncoras de incrustação e equipamentos de pesca em barcos que utilizam o local para pesca e passeios recreativos) e a aquariofilia (descarte irregular de espécies de aquários por comerciantes ou aquaristas) (Vasconcelos et al. 2011).

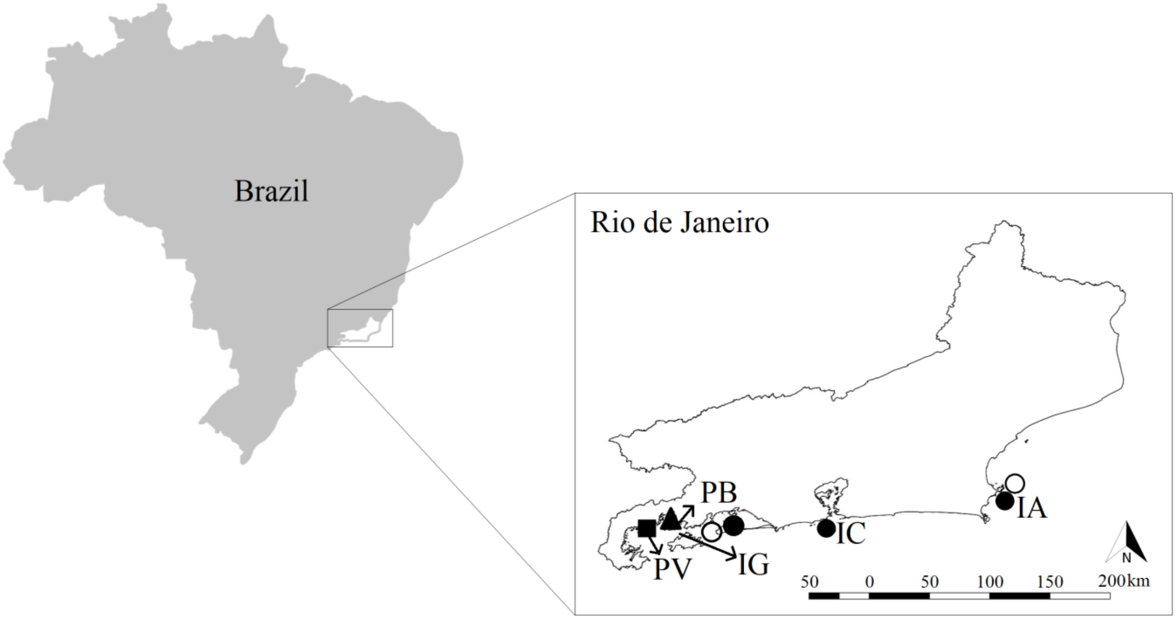
b) *Sansibia* sp. na Praia Vermelha (PV): Localizada em Angra dos Reis, na parte interna da BIG (23º01'34"S, 44º30'05"W), este local possui águas calmas e rasas, com costões rochosos se estendendo a uma profundidade entre 4 e 7m até uma planície de areia. As principais atividades locais são o turismo náutico e a pesca. Em 2017, três espécies de coral mole foram detectadas na costa rochosa, inicialmente*Clavularia* cf. *viridis* e *Sansibia* sp., e posteriormente *Erythropodium caribaeorum*. Ambas as espécies são de origem indo-pacífica e nunca foram registradas no Atlântico e pouco se sabe sobre a biologia e ecologia de*Sansibia*sp. descrito recentemente (Alderslade 2000). Após ações para remover as EEI da PV, *C. viridis* foi erradicado, contudo, *Sansibia* sp. expandiu seu alcance desde então (Mantelatto et al. 2018; Carpinelli et al. 2020). Como todas as espécies detectadas são usadas por aquaristas, é altamente provável que a introdução tenha sido pelo descarte de um aquário doméstico (Mantelatto et al. 2018) ou uma estratégia de cultivo de corais *in situ*(Carpinelli et al. 2020) (Figura 6B).

c) *Tubastraea tagusensis* Wells, 1982 na Ilha Comprida (IC): Localizada a cerca de 5 km do Rio de Janeiro (23º02'15"S, 43º12'17"W), IC é uma das cinco ilhas e duas ilhotas que compõemo Arquipélago das Cagarras, umaUnidade de Conservação (UC) marinha de proteção integral. O local de estudo na IC está posicionado no interior do arquipélago abrigado da ação das ondas. A profundidade máxima do costão rochoso é de 40m e o local sofre o impacto da eutrofização da cidade do Rio de Janeiro, além de receber constantemente visitas turísticas (mergulho e passeios recreativos de barco) (Creed et al. 2020; Machado et al. 2021). O coral azooxantelado *T. tagusensis* é endêmico e nativo do Arquipélago de Galápagos, onde é relatado como abundante e forma um importante componente da fauna coralínea. Foi introduzido no Brasil através de plataformas de petróleo na década de 1980 junto com seu congênere *T. coccinea*(Creed et al. 2017). *Tubastraea tagusensis* também foi documentado na Índia, Palau e no Golfo Pérsico, embora a identificação da espécie nesses locais seja discutida (Creed et al. 2017). No Arquipélago das Cagarras, *T. tagusensis* foi detectado e removido manualmente em 2004, mas em 2011 a espécie foi novamente relatada no local (Creed et al. 2017)(Figura 6C, D).

d) *Tubastraea coccinea* Lesson, 1829 e*T. tagusensis* Wells, 1982 na Ilha de Âncora (IA): IA é uma ilha localizada 8km da costa noroeste em Armação dos Búzios (22º46'16"S, 41º47'08"W). É também um ponto de mergulho popular na região, com águas transparentes, calmas e rasas (profundidade <22 m)(Creed et al. 2020). IA está sujeita a uma ressurgência sazonalvinda do Atlântico Sul Central, caracterizada pelo aporte de nutrientes (nitrato até 18µM) e baixas temperaturas (até 14ºC) (Coelho-Souza et al. 2012). Além de *T. tagusensis*, IA também foi invadida por umaEEI do mesmo gênero,*T. coccinea*, que foi registrado pela primeira vez em 2011 (Santos et al. 2019). *Tubastraea coccinea* tem uma distribuição natural em todo o Indo-Pacífico tropical e subtropical e invadiu algumas ilhas no Atlântico, Mar do Caribe, Golfo do México e no Atlântico sudoeste (Brasil) (Creed et al. 2017) (Figura 6C, D).

e) *Tubastraea coccinea* Lesson, 1829 e *T. tagusensis* Wells, 1982 na Ponta do Bananal (IG): localizada na parte interna da BIG (23°05'55"S 44°15'34"W), é uma região de intenso tráfego marítimo de navios e plataformas de petróleo, incluindo o Ancoradouro do Bananal, onde plataformas de petróleo param para reparos e manutenção ou enquanto aguardam atracação no estaleiro BrasFels (Silva et al. 2014). IG é caracterizado por águas rasas e claras, e indicado como o primeiro ponto de introdução de *Tubastraea* spp. em ecossistemas naturais no Brasil (Creed et al. 2017)(Figura 6C, D).

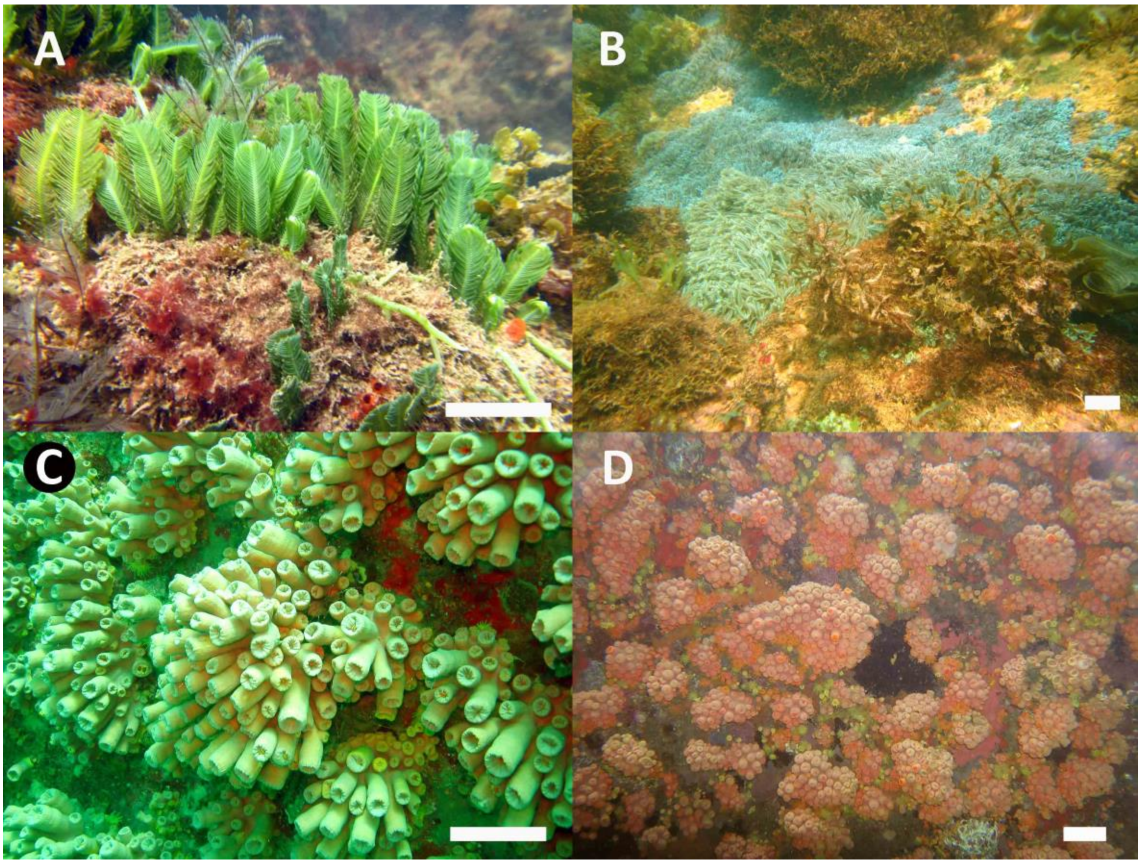
Figura 5 - Mapa dos quatro locais de estudo ao longo da costa do estado do Rio de Janeiro, Brasil e suas respectivas espécies exóticas invasoras.



Legenda: cs = alga verde *Caulerpa scalpelliformis* ▲, s = coral macio *Sansibia* sp. ■, tt = coral azooxantelado *Tubastraea tagusensis* ●, tc = coral azooxantelado *Tubastraea coccinea* ○, PV = Praia Vermelha, PB = Praia da Baleia, IG = Ponta do Bananal, IC = Ilha Comprida e IA = Ilha de Âncora.

Fonte: Adaptado de Pires-Teixeira et al. (2021).

Figura 6 – Espécies exóticas invasoras estudadas.



Legenda: A: alga verde*Caulerpa scalpelliformis*, B: coral mole*Sansibia* sp. C: coral azooxantelado *Tubastraea tagusensis*. D: coral azooxantelado*Tubastraea coccinea*.

Fonte: Pires-Teixeira et al. ,2021.

Estruturação da tese

O presente estudo está estruturado em 5capítulos:

O primeiro capítulo corresponde a uma revisão das informações atualmente disponíveis sobre as EE marinhas no Brasil. Com o objetivo de atualizar, sistematizar e sintetizar as informações atualmente disponíveis, nós realizamosuma pesquisa bibliográfica até maio de 2019 para novos registros e novas pesquisas sobre a situação deEE marinhas no Brasil. Nós também caracterizamos a frequência de eventos de introdução ereavaliamos o status de cada espécie uma década depois da lista INFORME / PROBIO publicada por Lopes et al. (2009). Aqui, está incluído o artigo "A decade on: an updated assessment of the status of marine non-indigenous species in Brazil" publicado no periódico *Aquatic Invasions* (doi: https://doi.org/10.3391/ai.2020.15.1.03). Tal estudo foi importante em possibilitar minha contribuição e coautoria em um estudo maior sobre a temática de tendências na detecção de espécies aquáticas não indígenas em ecossistemas marinhos, estuarinos e de água doce globais: uma perspectiva de 50 anos que, embora não faz parte formal de minha tese, foi um produto científico adicional proveniente dos meus estudos e pesquisas de doutorado publicado no periódico *Diversity and Distributions*:Bailey, S.A., Brown, L., Campbell, M.L., Canning-Clode, J., Carlton, J.T., Castro, N., Chainho, P., Chan, F.T., Creed, J.C., Curd, A., Darling, J., Fofonoff, P., Galil, B.S., Hewitt, C.L., Inglis, G.J., Keith, I., Mandrak, N.E., Marchini, A., McKenzie, C.H., Occhipinti-Ambrogi, A., Ojaveer, H., Pires-Teixeira, L.M., Robinson, T.B., Ruiz, G.M., Seaward, K., Schwindt, E., Son, M.O., Therriault, T.W., Zhan, A., 2020. Trends in the detection of aquatic non-indigenous species across global marine, estuarine and freshwater ecosystems: A 50-year perspective. Diversity and Distributions 26, 1780-1797 (ANEXO B).

No segundo capítulo, que inclui o artigo "*How Do Biological and Functional Diversity Change in Invaded Tropical Marine Rocky Reef Communities*?" publicado no periódico *Diversity* (doi: https://doi.org/10.3390/d13080353) (APÊNDICE 2), nós usamos a abordagem de ajuste e seleção de modelos de distribuição de abundância de espécies, índices de diversidade taxonômica e índices de diversidade funcional baseados em matrizes de agrupamento hierárquico para avaliar os efeitos de quatro espécies marinhas invasoras na diversidade biológica e funcional em quatro costões rochosos invadidos e quatro não invadidos por EEI ao longo do litoral do estado do Rio de Janeiro.

No terceiro capítulocomposto pelo artigo científico que será submetido a revista *Biological Invasions* intitulado "The effect of two invasive azooxanthellate corals *Tubastraea* *coccinea* and *Tubastraea tagusensis* on trophic interactions with native species.”, utilizamos valores de $\delta^{13}C$ e $\delta^{15}N$para investigaras relações tróficas em costões rochosos invadidos pelos corais *Tubastraea tagusensis* e *T. coccinea* ao longo do estado do Rio de Janeiro.Também utilizamos métricas derivadas dos valores isotópicos para analisar o nicho isotópico de *Tubastraea* spp. e outras espécies bentônicas que representam a diversidade trófica nas áreas invadidas e não invadidas, conduzimos uma revisão de conhecimento sobre *Tubastraea* spp. como alimento potencial para outras espécies e investigamos as relações tróficas entre espécies consumidoras e os corais *Tubastraea* spp. usando valores isotópicos de $\delta^{13}C$ e $\delta^{15}N$.

No quarto capítulo intitulado“Análise da diversidade e estrutura trófica em um costão rochoso recentemente invadido por um coral zooxantelado.” é composta por uma *Invasion Note* que será submetida ao periódico *Biological Invasions*: “Diversity analysis and trophic structure of a recently invaded tropical rocky shore.” onde usamosos valores de $\delta^{13}C$ e $\delta^{15}N$paraidentificar o nível trófico dos produtores e consumidores de um costão rochoso invadido pelo coral mole *Sansibia* sp. e investigaras relações tróficas entre a espécie invasora e as espécies nativas. Nós também avaliamos a estrutura da comunidade de locais invadidos e de controle (sem a EEI) e identificamos mudanças desde o último levantamento realizado em 2017 (ano de introdução) por Mantelatto et al. (2018).

O quinto e último capítulo representa um trabalho de extensão universitária desenvolvido em paralelo ao projeto de doutorado e inclui o artigo intitulado “Promovendo a profissão do cientista a partir de um projetode extensão universitária.” publicado no periódico e-Mosaicos Revista Multidisciplinar de Ensino, Pesquisa, Extensão e Cultura do Instituto de Aplicação Fernando Rodrigues da Silveira (CAp-UERJ) (doi: 10.12957/e-mosaicos.2021.47898), no qual relatamos a experiência vivenciada durante as oficinas do Projeto “Pra que Serve?”, um projeto de extensão universitária desenvolvido pelo Laboratório de Ecologia Marinha Bêntica da Universidade do Estado do Rio de Janeiro (LEMB-UERJ) que tem como objetivo trazer a debate a importância da ciência e contribuir para a valorização da pesquisa científica, possibilitando, de forma simples e acessível, vivências de pesquisa e acesso a conteúdo científico. Além disso, analisamos diferentes dimensões de atuação do projeto e a resposta daqueles que participaram das oficinas.

Objetivos

Objetivo Geral: Avaliar o efeito de espécies marinhas exóticas invasoras na diversidade e estrutura trófica em comunidades bentônicas de costão rochoso e divulgar conceitos e resultados para além da academia.

Objetivos específicos:

1) Compilar, atualizar, sistematizar e sintetizar as informações atualmente disponíveis sobre a situação deespécies exóticas(EE) marinhas no Brasil.
2) Caracterizar a frequência de eventos de introdução de EE marinhas no litoral brasileiro.
3) Reavaliar o status de cadaEE uma década depois da lista INFORME / PROBIO publicada por Lopes et al. (2009).
4) Investigar os aspectos biológicos e funcionais da diversidade em comunidades invadidas de costão rochoso.
5) Avaliar a estrutura e função decomunidades invadidas.
6) Avaliar a eficácia do uso de índices de diversidade funcional e taxonômica na avaliação do impacto de EEI nas comunidades de costão rochoso.
7) Investigar mudanças nas relações tróficas em comunidades invadidas.
8) Analisar o nicho isotópico de duas EEI e outras espécies bentônicas que representam a diversidade trófica em comunidades invadidas e não invadidas.
9) Realizar uma revisão de conhecimento sobre *Tubastraea* spp. como alimento potencial para outras espécies.
10) Investigar as relações tróficas entre espécies consumidoras e *Tubastraea* spp. usando valores isotópicos de $\delta^{13}C$ e $\delta^{15}N$.
11) Identificar o nível trófico dos produtores e consumidores de um costão rochoso invadido pelo coral mole *Sansibia* sp.
12) Investigar as relações tróficas entre a EEI e as espécies nativas.
13) Avaliar a estrutura da comunidade de áreas invadidos e não invadidos.
14) Identificar mudanças na diversidade desde o último levantamento da comunidade.
15) Relatar a experiência na elaboração, desenvolvimento e aplicação de oficina de extensão universitária em diferentes contextos.
16) Analisar diferentes dimensões de atuação de um projeto de extensão universitária.

17) Avaliar a resposta dos participantes das oficinas como resultado da efetividade do Projeto.

1 AVALIAÇÃO ATUALIZADA DA SITUAÇÃO DAS ESPÉCIES EXÓTICASMARINHAS NO BRASIL.

1.1 **A decade on: an updated assessment of the status of marine non-indigenous species in Brazil.**

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Abstract

In order to prevent the introduction, control or eradicate non-indigenous species(NIS) whichthreaten native species, habitats or ecosystems, an essential first step isthat countries have and keep up-to-date lists of species non-indigenous to theregion. The last list of marine NIS for Brazil was published a decade ago. Wecompiled an updated list of marine NIS and revised the species' statuses. Onehundred-thirty-eight marine species in 15 classes or functional groups are NIS inBrazil. Brazilian states with greater maritime commerce (greater market share) hadmore marine NIS. From the period between the 1950s to 2010, the number of NIS atleast doubled each decade. We identified a significant mismatch (underestimation) between the previous list and this study, which seemed to be due to improvedscientific knowledge and an often considerable lag between first record (detection),identification and communication of new marine NIS. Currently Brazil has 19 invasive,76 established and 43 detected marine NIS, an increase of 160% in ten yearscompared to the previous national list. We recommend that Brazil implements anational database as a rapid, appropriate, flexible and cost effective method ofmonitoring trends in NIS introductions.

Keywords: class/functional groups; geographical variation; historical change; invasive; national checklist;non native species

1.1.1 Introduction

The Convention on Biological Diversity (to which Brazil is a party, Brasil 1998) states that consenting parties should prevent the introduction, control or eradicate those alien species which threaten ecosystems, habitats or native species. In Brazil this convention was ratified in 1994, with the Ministry of the Environment being the principal entity responsible for planning and decision making with regard to non-indigenous species (NIS) and biological invasion (Lopes et al. 2009). An essential first step is that countries have and keep up-to-date lists of NIS recorded for their region. According to Sliwa et al. (2009) once lists are adopted into themanagement framework, they are often used for long periods without revision. However it is important that these lists are constantly reviewed and updated to incorporate new introductions and changes in species status based on further research (Sliwa et al. 2009). This information may be used to assess management initiatives and targets.

The Brazilian coastline extends for about 8000 km from Cape Orange (4°N) to Chui (34°S) comprising a range of tropical and sub-tropical ecosystems such as sandy beaches, mangrove forests, coral reefs, rocky shores, coastal lagoons, saltmarshes, oceanic islands and sandy to muddy bottoms from the infralittoral realm down to the shelf break (Ferreira et al. 2009). Further offshore the Exclusive Economic Zone of 200 nautical miles and the proposed extension called the Amazônia Azul, or “Blue Amazon” (Wiesebron 2013) form a very large oceanic biome. According to Ferreira et al. (2009) this makes the country a major receptor and donor of tropical and subtropical organisms amongst the world’s oceans.

The INFORME/PROBIO Project, which was conducted in 2005, provided the first comprehensive list of non-indigenous species in coastal areas of Brazil (Ferreira et al. 2009). The I National Report on Invasive Exotic Species affecting the marine environment (fauna, flora and microorganisms) (I Informe Nacional sobre as EspéciesExóticasInvasoras que afetam o ambienteMarinho (fauna, flora e microrganismos)) resulting from the study was published in 2009 by Lopes et al. At the time of that study 58 marine NIS were known from Brazil (Lopes et al. 2009); the species that made the most impact were reviewed by Ferreira et al. (2009). In this paper, we compile, update, systematize and synthesize currently available information on marine NIS in Brazil in order to characterize the frequency of introduction events as well as reassess the status of the species a decade on from the INFORME/PROBIO list published in 2009 by Lopes et al.

1.1.2 Materials and Methods

Based on the INFORME/PROBIO list and data provided therein (Lopes et al. 2009), we conducted a literature search up to May 2019 for new records and new research regarding the status of marine NIS in Brazil. The following databases and literature sources were consulted: Horus Institute (http://i3n.institutohorus.org.br/www/), World Register of Introduced Marine Species (WRIMS) (http://www.marinespecies.org), Google Scholar (https://scholar.google.com/), Researchgate (https://www.researchgate.net/), Scientific Electronic Library Online (http://www.scielo.org/php/index.php), FishBase (http://www.fishbase.org/search.php), and AlgaeBase (http://www. algaebase.org/).

We classified the status of each species by using the same criteria and categories as those described by Lopes and Villac (2009), as these have been adopted by the Brazilian Federal Government. Lopes and Villac (2009) recognized a status hierarchy as the following:

Contained: when the presence of the NIS has only been detected in controlled artificial environments, totally or partially isolated from the natural environment (e.g. commercial aquarium, cultivation for scientific purposes, vessel ballast water tanks, etc.);

Detected: when the presence of the NIS was detected in the natural environment, but with no subsequent increase in its abundance and/or its dispersion (considering the time horizon of research or surveys); or, alternatively, without further information on the population situation of the species (e.g. an isolated record);

Established: when the NIS has been detected on a recurrent basis, with its full life cycle in nature and evidence of population increase over time in a restricted or broad region, but without apparent ecological or socioeconomic impacts;

Invasive: when the NIS has an abundance or geographic dispersion that interfere with the survival capacity of other species in a broad geographic region or even in a specific area (Elliott 2003), or when the established species causes measurable impacts on socioeconomic activities or human health.

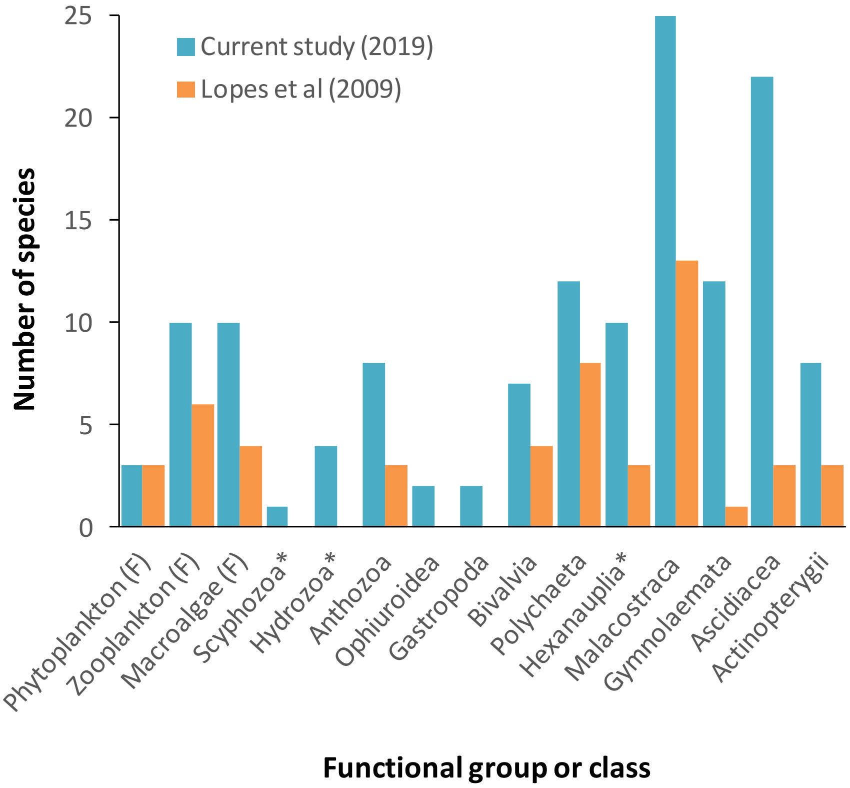
When a species had been assigned different statuses in different studies, we used the classification criteria based on the most recent study available (e.g., compare Farrapeira et al. 2011 and Rocha et al. 2013). Species native to Brazil which demonstrated human-mediated range shift (sensuLonhart 2009) were also included. Furthermore, we noted the occurrence by Brazilian state and the year of first record in the country. This was taken as the year of collection, or record, if reported in the reference(s), or the year of the reference publication when the year of collection or record was not provided. The nomenclature was updated in accordance with the World Register of Marine Species (Worms Editorial Board 2019). Contained or cryptogenic species were not included in the present list of NIS. In order to compare the status of different taxonomic or functional groups, we organized records by functional group, class, order and family. In order to describe temporal changes, we calculated cumulative records and estimated current detection rates. We also compared the status according to Lopes et al. (2009) with the revised status noted here. In order to describe spatial patterns, we also documented species by Brazilian state. As states are of different sizes, we also converted these data to a per km basis using coastline length data obtained from https://pt.wikipedia.org/wiki/Litoral_ do_Brasil accessed on 26/12/2018 (Supplementary material Table S1). To test whether the volume of shipping explained the difference in the abundance of NIS between states, we used a simple linear regression between the number of NIS per state and the “Market share” which is the proportion of the national tonnage of shipping (imports + exports) for which each state is responsible (ANTAQ 2018; Table S1).

1.1.3 Results

We compiled information from more than 120 data sources (Table S2 and S3). Wereviewed all studies and identified and assigned status to 138 marine NISrecorded from

Brazil up to May 2019. Contained or cryptogenic specieswere not included in the list. The updated summary and status list ispresented in Table S3. The NIS comprised 15 classes or functional groups(Figure 7); Malacostraca was the class with most NIS (n = 26), followed byAscidiacea (n = 22), Polychaeta and Gymnolaemata (n = 12 each). Elasmobranchii (n = 1), Ophiuroidea and Gastropoda (n = 2 each) andphytoplankton (n = 3) were the groups with the least NIS. The group withthe largest number of invasive (sensu Methods) NIS was the Anthozoa (n = 7),followed by the phytoplankton and Bivalvia (n = 3 each) (Tables S2, S3, S4 and S5).

Figure 7 - Number of non-indigenous marine species in Brazil by functional group (F) or class in May 2019 and compared to Lopes et al. (2009).



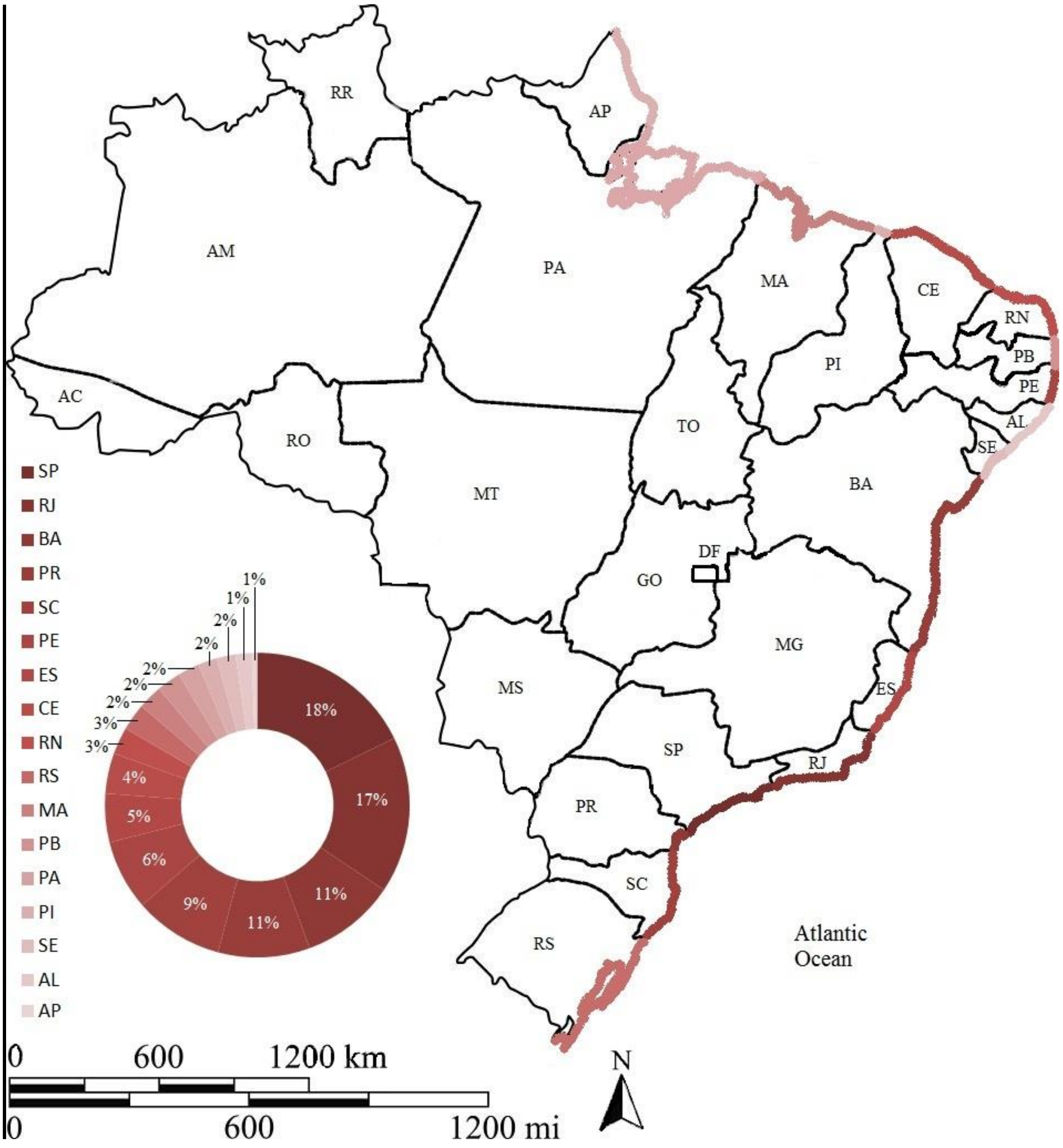
Source: PIRES AND CREED, 2020.

Note: Zooplankton category includes all planktonic Hexanauplia, Scyphozoa and Hydrozoa; * = zoobenthic species of these classes.

1.1.3.1 Distribution in space

Up to May 2019 at least three NIS have been documented in each of the 17Brazilian coastal states, but most were concentrated in southeast Brazil.The state with the greatest absolute number of NIS was São Paulo with 73species (52.9% of total), followed by Rio de Janeiro with 69 (50%), Bahiawith 45 (32.6%) and Paraná with 43 (31.2%); the state with the lowest numberof NIS (three; 2.2%) was Amapá in the far north (Figure 8; Table S2 e S3). However, considering and correcting for the significant variation incoastline extension between states on a per km basis (Table S1), there was atrend of increasing numbers of NIS from north to south to Paraná, whichalthough a small state had the highest number of NIS per 100 km ofcoastline (Figure 9). The states of Piauí and Pernambuco also had a highernumber of NIS than expected by the north-south trend (Figure 9).

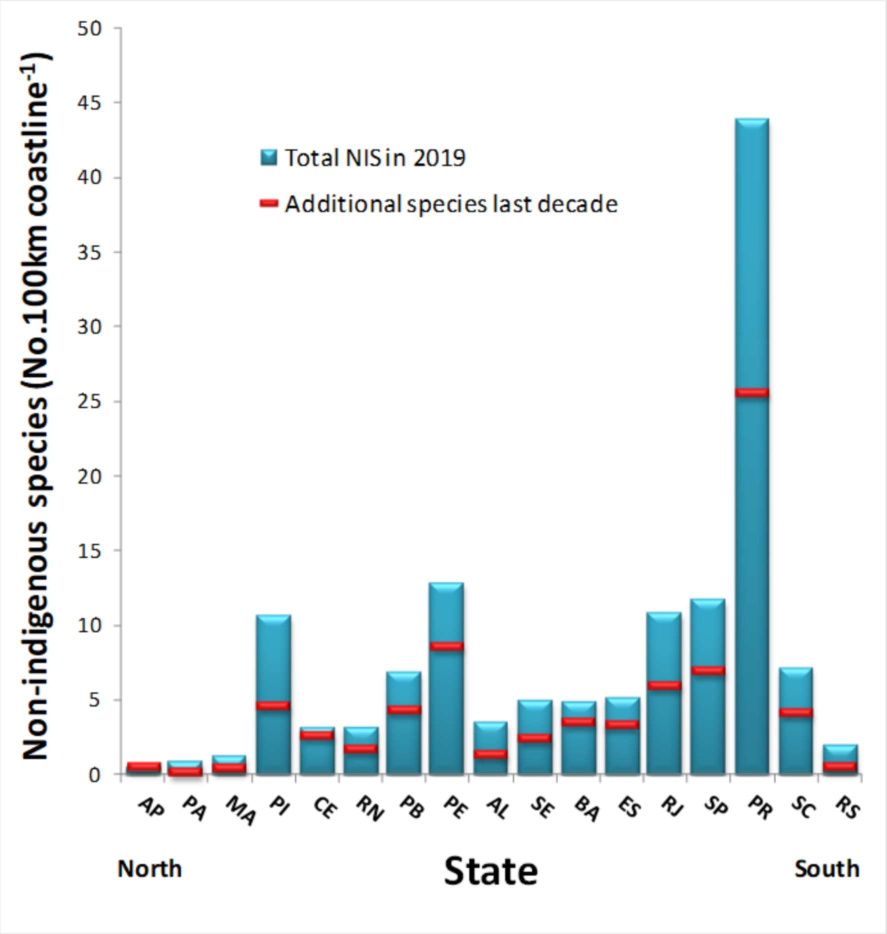
Figure 8 -Map of Brazil highlighting the coastal states in which non-indigenous species (NIS)were detected.



Source: PIRES AND CREED, 2020.

Legend: The color gradation is directly related to the number of NIS, with sites with thehighest number of NIS having darker shades. Abbreviations: Amapá (AP), Pará (PA),Maranhão (MA), Piauí (PI), Ceará (CE), Rio Grande do Norte (RN), Paraíba (PB), Pernambuco(PE), Alagoas (AL), Sergipe (SE), Bahia (BA), Espírito Santo (ES), Rio de Janeiro (RJ), SãoPaulo (SP), Paraná (PR), Santa Catarina (SC), Rio Grande do Sul (RS).

Figure 9 -Standardized comparison of non-indigenous marine species per Brazilian state, per100 km coastline, in May 2019 and those additional species from 2009–2019.

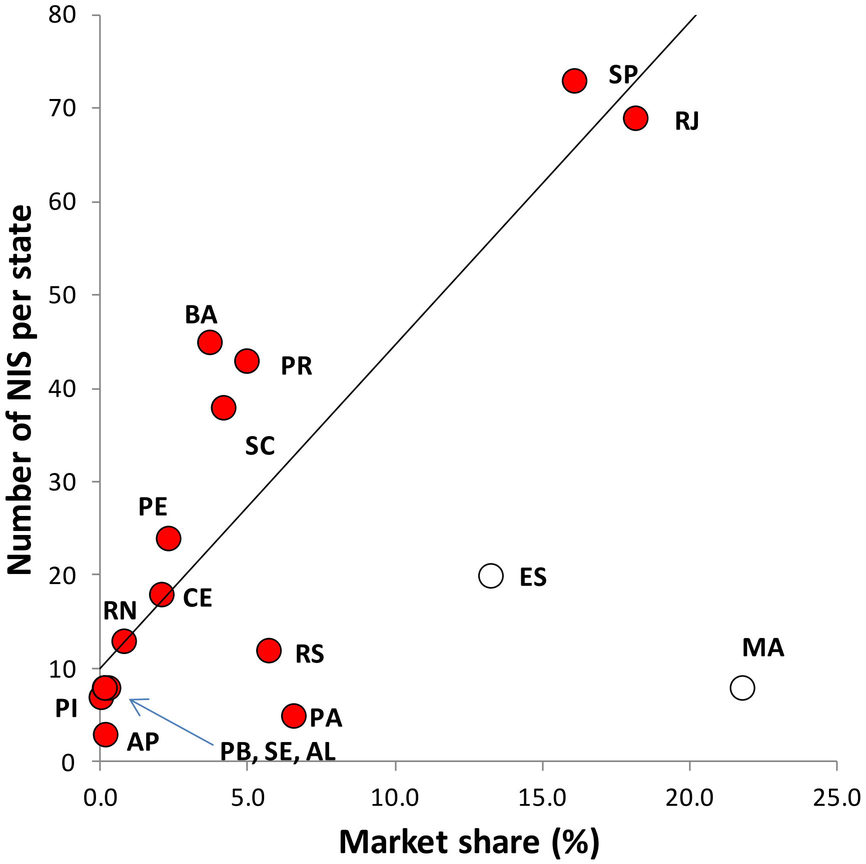


Source: PIRES AND CREED, 2020.
Legend: Names of thestates as in Figure 2.

There were several NIS previously reported in Brazil in 2009 which expanded their ranges into other states over the last 10 years. These species included the mudsleeperButiskoilomatodon (into seven additional states), the orange sun coral *Tubastraea coccinea* (six), yellow sun coral *Tubastraea tagusensis* and the muzzled blenny Omobranchus punctatus (four each) and the boring bivalve Leiosolenusaristatus (three) (Table S2, S3, S4 and S5). The alga *Anotrichiumyagii*, mussel *Mytilopsisleucophaeata*, sabellidpolychaete*Branchiommaluctuosum*, portunid crab *Scylla serrata* and the xanthid crab *Pilumnoidesperlatus*also expanded their ranges (one additional state each). The total number of NIS per 100 km of coastline in each state was dependent on the volume of market share (exports + imports, Table S1); a significant though not a very strong relationship was observed (NIS per 100 km coastline = 1.5748 × Market share + 14.383, Adjusted $R^2 = 0.2494$, $p = 0.01$; Figure 4).

However when two outlier states which have exceptionally large exports of specific commodities were removed (Espírito Santo and Maranhão), a stronger relationship was observed (NIS per 100 km coastline = 3.466 × Market share + 9.918; n = 14, Adjusted R^2 = 0.71, $p \leq 0.001$)(Figure 10).

Figure 10 - Relationship between market share (%) and number of non-indigenous marine species per Brazilian state.

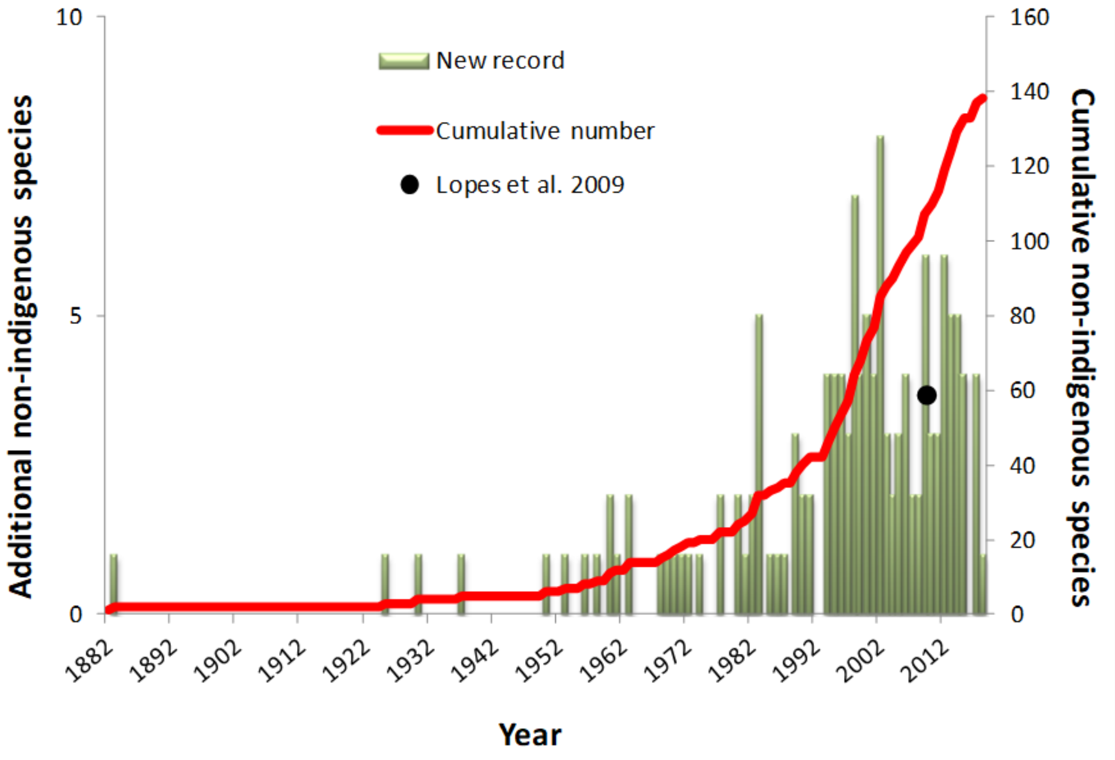


Source: PIRES AND CREED, 2020.
Legend: Market share is proportion of total tonnage of Brazilian maritime imports + exports per state in 2018 (Antaq, 2018). Line fit to filled points (unfilled points were considered outliers).

1.1.3.2 Change over time

The first record of a non-indigenous marine species in Brazil was from 1860 (the bryozoan *Amathiaverticillata*) (Miranda et al. 2018) followed by the ascidian *Styelaplicata* recorded in Rio de Janeiro in 1883 (Lopes et al. 2009) (Figure 11 and Table S2, S3). The third record occurred 40 years later, in 1925 (the ascidian *Clavelina oblonga*) (Rocha et al. 2012). Up through the 1960s additional NIS were sporadically reported, but from 1949 onwards new records of NIS have at least doubled (≥ 100% increase) every decade up to a total of 99 in 2008 (Figure 11). Over the last decade the number of new records of NIS has increased to 138 which represents a 25% decadal increase according to our dataset. The only group which did not increase in NIS abundance over the last decade was the phytoplankton (Figure 1). The state which exhibited the most substantial increase in NIS over the last decade was Paraná (25.5 species/100 km), then Pernambuco (8.6 species/ 100 km) while Rio Grande do Sul, Amapá, Pará and Maranhão only increased by < 1 species/100 km (Figure 9).

Figure 11 - Number of new non-indigenous marine species recorded from Brazil every year from1883 to 2019, together with the cumulative curve reaching a total of 138 species by May 2019;the total by 2008 as reported in Lopez et al. (2009) is also indicated.



Fonte: PIRES AND CREED, 2020.

The current status of marine NIS and the change in status over the last decade as compared to Lopes et al. (2009) is summarized in Table S3. As some species have changed their status and new species have been detected, we considered 19 species to be invasive, 76 established and 43 detected; in the survey by Lopes et al. (2009) there were 9 invasive, 17 established and 27 detected species (Tables S2, S3). According to this comparison, the number of NIS in Brazil has increased by 160% over the last 10 years. There has been no loss of any marine NIS in Brazil over the last 10 years, except for species that previously had been described as non-indigenous but that are currently considered as cryptogenic or native. Compared to the previous list, there was a 347% increase in the number of established species and a 111% increase in invasive species. The lowest increase was in the number of detected species (59%). Five species previously considered established were considered invasive, and eleven species that were previously considered to be detected were considered established (Table S3).

1.1.4 Discussion

Ten years on from the first national effort to compile a list and define thestatus of marine species non-indigenous to Brazil, published by theMinistry of the Environment (Lopes et al. 2009), much has changed. Theeffort by Lopes et al. (2009) was important in providing a first national listas well as focusing on the need for new research on marine NIS, includingresearch on vectors of introduction (Loebmann et al. 2010; Farrapeira et al.2011; Van Ofwegen and Haddad 2011; Skinner et al. 2013; Castro et al.2017; Creed et al. 2017; Mantelatto et al. 2018) and quantification ofimpact and risk (Silva et al. 2010; Carlton et al. 2011; Rocha et al. 2013;Altvater and Coutinho 2015; Bumbeer and Rocha 2016; Miranda et al.2018) (Table S2, S4). In 2013 the National Biodiversity Targets established thatthe National Strategy on Invasive Alien Species should be fully implementedin Brazil by 2020, including the participation and commitment of the statesin the formulation of a National Policy. Central to the national strategy isthe need to identify and list NIS. The present study clearly demonstratesthe need for regularly updating national lists of NIS.

This study is a data compilation, and therefore we compiled previouslypublished information and assigned status according to previouslyestablished classification criteria. This must be done in an accurate andresponsible way but even so the literature contains controversy regardingNIS statuses. Of the 58 NIS listed by Lopes et al. (2009), eight were notincluded in the present study. Five of these are now considered cryptogenicand include the sponge

*Paraleucilla magna*Klautau, Monteiro andBorojevic, 2004 (Rocha et al. 2013; Cavalcanti et al. 2013) and the bryozoanspecies complex *Schizoporella errata* (Waters, 1878) (see Rocha et al. 2013;Miranda et al. 2018), both previously considered established, the bryozoans*Licorniadiadema* (Busk, 1852) and *Virididentula dentata* (Lamouroux,1816) (see Miranda et al. 2018) and the ascidian *Bostrichobranchusdigonas*Abbott, 1951 (Rocha et al. 2013), all previously considered detected. Theisopod *Sphaeromaannandalei*Stebbing, 1911 was described as the newspecies *Sphaeromasilvai*Khalaji-Pirbalouty and Waegele, 2010, and thuslost its NIS status (Khalaji-Pirbalouty and Waegele 2010). The seaweed*Kappaphycusalvarezii* (Doty) Doty ex P.C. Silva, which was introducedintentionally into Brazil for farming, has not been able to establish itselfnaturally outside the culture systems (although broken, unfixed fragmentsare occasionally found on adjacent bottoms), so we considered this tocurrently be a contained species (Castelar et al. 2009; Lima et al. 2018).

With regard to the eighth species, the mussel *Pernaperna* (Linnaeus,1758), that was initially treated by Lopes et al. (2009) as a NIS, much hasbeen discussed about the origin of this bivalve [see contrasting views ofCunha et al. (2014), Pierri et al. (2016) and Oliveira et al. (2017)]. Based onmolecular, ecological and archaeological studies, the species may have beenhistorically transported to Brazil from Africa on slave boats or be native. Itis an edible species which is harvested and farmed and is of significantcommercial importance; maybe for these reasons it has been termed“naturalized” by Oliveira et al. (2017). We did not include it in the presentlist as additional molecular, ecological and archaeological studies of different populations are required to better clarify the origin of the species.As it is of uncertain origin, it should be considered cryptogenic (a conservativecategory of obscure or unknown origin; Carlton 1996). The fact that anumber of previously listed species (n = 6) have had their status redefinedas cryptogenic attests to a more conservative scientific approach as invasionbiology matures in Brazil (Carlton 1996).

Both morphological characteristics and molecular studies can aid indetermining the invasive status of questionable species. Lopes et al. (2009)listed the bivalve *Mytilopsisleucophaeata* as a NIS in Pernambuco state buta subsequent molecular study by Fernandes et al. (2018) identified thatpopulation as *M.*cf*sallei* also a NIS for Brasil; however in the same study theyalso identified a new population in Rio de Janeiro state as *M. leucophaeata,*so the species maintains its status as NIS for Brazil. In addition tomolecular studies, identifying morphological characters is important whendetermining NIS. The ascidian *Ciona intestinalis*, also known as a complexof two species, was later described in 2015 as *C. intestinalis* and *C. robusta*(Brunetti et al. 2015). Here we conservatively maintained the species as*Ciona intestinalis* until future studies establish which species actually occurin Brazil. Five new taxonomic classes not previously listed as NIS in Brazil were added to the list and include the following: two ophiuroids (*Ophiactissavignyi* and *Ophiothela mirabilis*), two gastropods (*Bulbaeolidia alba* and*Eualetestulipa*), two Scyphozoa (*Cassiopea andromeda* and *Phyllorhiza punctata*), five hydrozoans (*Podocorynaloyola*, *Cordylophoracaspia*, *Blackfordia virginica*, *Cnidostomafallax* and *Garveiafranciscana*) and one Elasmobranchii (the whitetip reef shark *Triaenodonobesus*).

The 11 species which were described as detected in 2009 and arecurrently considered established changed their classification because theyhave expanded their ranges and/or have been detected on multiple occasions.The five invasive species that were previously considered established hadtheir status changed because they are now known to cause some type ofdamage, be it environmental, economic and/or to public health (Table S3).For example in 2009 the muzzled blenny *Omobranchus punctatus* wasconsidered to be established and possibly an invasive species. Currently, thisherbivorous fish, which scrapes algae from the bottom, has been describedas competing with the native molly miller *Scartella cristata* (Linnaeus,1758) and thus gained the status of an invasive species (Soares et al. 2011).

The increase in the number of established species and the decrease indetected species demonstrates that we are still ineffective in completelycontrolling the movement of NIS and that we must focus on managementplans to stop NIS increasing their area of coverage and eventuallybecoming invasive (sensu Methods). Rather than focus exclusively onprevention of introduction, the ideal invasive species policy should alsoinvolve a combination of other strategies such as risk assessment, efforts todetect new species and activities to monitor and control existing populationsof newly detected species. If an incipient population of a species is detectedbefore establishment and spread, subsequent control costs may be reducedand eradication may be a viable option (Mehta et al. 2007). It is importantto remember that so far in Brazil no established or invasive marine NIS hasbeen eradicated after its introduction. That having been said, two species,the lionfish *Pterois volitans* and the octocoral *Clavulariaviridis*, were both controlled on detection. They have not since been detected in Brazilian waters (Ferreira et al. 2015; Mantelatto et al. 2018) and may thus beconsidered eradicated.

Those species which have become widespread use multiple mechanismsof expansion. Some have been introduced multiple times for aquaculture(e.g., Pacific White Shrimp *Penaeus vannamei*, Lopes et al. 2009) or onshipping associated with the offshore oil and gas industry (e.g., sun corals*Tubastraea coccinea* and *Tubastraea tagusensis*, and the associated purseoyster *Isognomon bicolor*; Creed et al. 2017). Others, such as the snowflakecoral *Carijoariisei* and the barnacles *Amphibalanus reticulatus* and*Megabalanuscoccopoma*, are commonly found on artificial floatingsubstrates (Ferreira et al. 2006; Carlton et al. 2011). The Indo-Pacificswimming crab *Charybdis* (Charybdis) *hellerii*, the copepod *Temoraturbinata* and mudsleeper*Butiskoilomatodon* were probably spread bycurrents, swimming and/or larval dispersal (Lopes et al. 2009).

In cases where species are introduced into new habitats for economicbenefit or to meet developmental needs, there may be an initial economicgain, but if a species becomes invasive it can cause serious economic andecological damage (Molnar et al. 2008). These risks of invasion are oftennot considered during the decision process of whether to introduce aspecies (Naylor et al. 2001). For example, ten years ago the Pacific oyster*Crassostrea gigas* was considered a contained species because it did notreproduce naturally on the Brazilian coast, and the cultivation of thisspecies depended on the constant imports of seed or reproduction in thelaboratory (Lopes et al. 2009). However*C. gigas* has now been found innatural banks on the south coast of Brazil, at a distance of up to 100 kmsouth of the farms where they are cultivated (Melo et al. 2010). For thisreason, *C. gigas* is now considered an established NIS.

Our study showed that the states with the greatest number of NIS arealso those that have substantial movement of marine commerce. Theseports usually also offer services for the off-shore oil industry, including righarboring, and are important marine navigation hubs. These are three ofthe most important vectors of introduction of marine species (Ruiz andCarlton 2003; Silva and Souza 2004; Ferreira et al. 2006; Yeo et al. 2009). Asoutliers, we excluded two states from the analysis, Maranhão (MA) andEspírito Santo (ES), which both export very high tonnages of mineralsfrom the interior of Brazil. We used market tonnage as a proxy for species dispersal as that data were available but frequency with which ports receive vessels and their origin was also important. Furthermore, some states (suchas ES) are probably understudied while others (Rio de Janeiro – RJ, SãoPaulo – SP and Parana – PR) contribute to the bulk of previously publisheddata (Figure 4). Identifying the spatial distribution and most common pathways for the introduction of harmful marine species can help to focus monitoring efforts, provide information for risk assessment and informand support international policies to prevent such introductions (Molnaret al. 2008). In this respect it would be useful for management if futurestudies attempt to 1) identify the principal pathways and vectors of introduction for these NIS, if this information is available; 2) identify
which states are most critically threatened by NIS (by analyzing firstintroductions at the state level).

When we compared the timeline of reports of marine NIS in Brazil overthe last 10 years to Lopes et al. (2009), we identified apparently incongruentresults. For example we estimated a 160% increase in NIS over the lastdecade compared to Lopes et al.'s (2009) study but only a 25% decadalincrease when comparing our own results. This was because by 2008 there were 99 marine NIS in Brazil compared to only 53 listed by Lopes et al.(2009) (see the point and line indicated in Figure 5). Bearing in mind thatwe used the year of first record (collection date, record date or publicationdate, in that priority order) for each new NIS, the reasons for thismismatch are various and could include the following: 1) while Lopes et al.was published in 2009, the data had been collected some time previously; 2) several NIS species included here, which were known in Brazil pre-2009, were not considered to be NIS at that time; 3) novel NIS may take someyears to be formally identified, or even described, after first being recorded(but the date remains the same); 4) records of novel NIS may take years toget published. For example the brittlestar *Ophiothela mirabilis* was firstdetected in 2000 but the first published record was in 2012 by Hendler etal. Similarly, the octocoral *Stragulum bicolor* was first detected in 2002 inBrazil but only described (and as a new species) by Van Ofwegen andHaddad in 2011.

Given the above, it should be recognized that the apparent reduction inthe rate of new records of marine NIS this last decade may also simply bean artifact of the lag between new NIS being detected and the community becoming aware through communication or publication of those records. Never the less, it may also be the case that the date of first record does notactually reflect the year of introduction, since many species may remainundetected for a while, which generally results in the opposite pattern of anapparent increase in the rate of introductions that is an artifact of increased awareness and sampling effort. These observations further confirm the needfor NIS lists to be constantly reviewed and updated to incorporate newly detected NIS and changes in species status based on further research (Sliwa et al. 2009). Brazil has not yet implemented a national database of marine NIS which we consider may be the most appropriate and cost effectivemethod of moving forward in updating and maintaining current thenational NIS lists as part of the National Strategy on Invasive Alien Species.

1.1.5 Acknowledgements

This work was supported by Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (JCC, FAPERJ-E-26/111.574/2014 and E26/201.286/2014) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (JCC, CNPq- 307117/2014-6). LMPT acknowledges Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) that provided a PhD scholarship. We thank Drs. Evangelina Schwindt, Amy Fowler and the anonymous reviewers for their useful comments.

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1.1.7 Supplementary material

Tabela S1 - Coastal extension and maritime market share of the Brazilian States.

		Coastal extension[1.]		**Market share**[2.]
Abbreviatedstate	**State**	**km**	**%**	**%**
BA	Bahia	932	12.4	3.7
MA	Maranhão	640	8.7	21.8
RJ	Rio de Janeiro	636	8.6	18.2
RS	Rio Grande do Sul	623	8.5	5.7
SP	São Paulo	622	8.5	16.1
AP	Amapá	598	8.1	0.1
CE	Ceará	573	7.8	2.1
PA	Pará	562	7.6	6.5
SC	Santa Catarina	531	7.2	4.2
RN	Rio Grande do Norte	410	5.7	0.8
ES	Espírito Santo	392	5.3	13.2
AL	Alagoas	229	3.1	0.2
PE	Pernambuco	187	2.5	2.3
SE	Sergipe	163	2.2	0.1
PB	Paraíba	117	1.6	0.1
PR	Paraná	98	1.3	4.9
PI	Piauí	66	0.9	0.0
	Total	**7379**	**100**	**100**

Nota: [1]Translated from source https://pt.wikipedia.org/wiki/Litoral_do_Brasil accessed on 26/12/2018. [2]'Market share' is the proportion of the national tonnage of shipping (imports + exports) for which each state is responsible; source: AnuárioEstatísticoAquaviário - 2018, ANTAQ (http://http://web.antaq.gov.br/Anuario/ accessed in 11/07/2019)

Fonte: PIRES E CREED (2020)

Table S2 - Checklist of marine taxa non-indigenous to Brazil (to be continued).

Sp.Code	**FunctionalGroup**	**Class**	**Order**	**Family**	**Taxa**
a	Phytoplankton	Bacillariophyceae	Coscinodiscales	Coscinodiscaceae	*Coscinodiscuswailesii*Gran&Angst, 1931
b	Phytoplankton	Dinophyceae	Gonyaulacales	Gonyaulacaceae	*Alexandriumtamarense* (Lebour, 1925) Balech, 1995
c	Phytoplankton	Dinophyceae	Gymnodiniales	Gymnodiniaceae	*Gymnodiniumcatenatum*H.W.Graham, 1943
d	Zooplankton	Branchiopoda	Onychopoda	Podonidae	*Pleopisschmackeri* (Poppe, 1889)
e	Zooplankton	Hexanauplia	Calanoida	Pseudodiaptomidae	*Pseudodiaptomustrihamatus* Wright S., *1937*
f	Zooplankton	Hexanauplia	Calanoida	Temoridae	*Temoraturbinata* (Dana, 1849)
g	Zooplankton	Hexanauplia	Cyclopoida	Cyclopidae	*Apocyclopsborneoensis* Lindberg, 1954
h	Zooplankton	Hexanauplia	Cyclopoida	Cyclopettidae	*Paracyclopinalongifurca* (Sewell, 1924)
i	Zooplankton	Hexanauplia	Harpacticoida	Tetragonicipitidae	*Phyllopodopsyllussetouchiensis* Kitazima, 1981
j	Zooplankton	Hexanauplia	Harpacticoida	Tetragonicipitidae	*Phyllopodopsyllusaegypticus* Nicholls, 1944
k	Zooplankton	Hexanauplia	Harpacticoida	Tetragonicipitidae	*Laophontellahorrida* (Por, 1964)
l	Zooplankton	Scyphozoa	Rhizostomeae	Mastigiidae	*Phyllorhizapunctata*Lendenfeld, 1884
m	Zooplankton	Hydrozoa	Anthoathecata	Hydractiniidae	*Cnidostomafallax*Vanhöffen, 1911
n	Zoobenthos	Hexanauplia	Sessilia	Archaeobalanidae	*Membranobalanusdeclivis* (Darwin, 1854)
o	Zoobenthos	Hexanauplia	Sessilia	Archaeobalanidae	*Striatobalanusamaryllis* (Darwin, 1854)
p	Zoobenthos	Hexanauplia	Sessilia	Balanidae	*Balanustrigonus* Darwin, 1854
q	Zoobenthos	Hexanauplia	Sessilia	Balanidae	*Amphibalanusreticulatus* (Utinomi, 1967)
r	Zoobenthos	Hexanauplia	Sessilia	Balanidae	*Megabalanuscoccopoma* (Darwin, 1854)
s	Zoobenthos	Hexanauplia	Sessilia	Balanidae	*Amphibalanusamphitrite* (Darwin, 1854)
t	Zoobenthos	Hexanauplia	Sessilia	Balanidae	*Amphibalanussubalbidus* (Henry, 1973)
u	Zoobenthos	Hexanauplia	Sessilia	Tetraclitidae	*Tesseroporaatlantica* Newman & Ross, 1976

Table S2 - Checklist of marine taxa non-indigenous to Brazil (continuation).

v	Zoobenthos	Hexanauplia	Sessilia	Tetraclitidae	*Tetraclitella divisa* (Nilsson-Cantell, 1921)
w	Phytobenthos	Bangiophyceae	Bangiales	Bangiaceae	*Pyropiasuborbiculata* (Kjellman) J.E.Sutherland, H.G.Choi, M.S. Hwang&W.A.Nelson, 2011
x	Phytobenthos	Bangiophyceae	Bangiales	Bangiaceae	*Pyropiaacanthophora* (E.C.Oliveira& Coll) M.C.Oliveira, D.Milstein&E.C.Oliveira, 2011
y	Phytobenthos	Bangiophyceae	Bangiales	Bangiaceae	*Pyropiatanegashimensis* (Shinmura) N.kikuchi& E. Fujiyoshi, 2011
z	Phytobenthos	Bangiophyceae	Bangiales	Bangiaceae	*Pyropiavietnamensis* (Tak. Tanaka &P.H.Ho) J.E.Sutherland&Monotilla, 2011
aa	Phytobenthos	Florideophyceae	Ceramiales	Dasyaceae	*Dasya brasiliensis* E.C.Oliveira Filho &Y.Y.Braga, 1971
ab	Phytobenthos	Florideophyceae	Ceramiales	Rhodomelaceae	*Laurenciacaduciramulosa* Masuda&Kawaguchi, 1997
ac	Phytobenthos	Florideophyceae	Ceramiales	Rhodomelaceae	*Laurencia venusta* Yamada, 1931
ad	Phytobenthos	Florideophyceae	Halymeniales	Halymeniaceae	*Grateloupiaturuturu* Yamada, 1941
ae	Phytobenthos	Rhodophyta	Ceramiales	Wrangeliaceae	*Anotrichiumyagii* (Okamura) Baldock, 1976
af	Phytobenthos	Ulvophyceae	Bryopsidales	Caulerpaceae	*Caulerpa scalpelliformis* (R.Brown ex Turner) C.Agardh, 1817
ag	Zoobenthos	Scyphozoa	Rhizostomeae	Cassiopeidae	*Cassiopeaandromeda* (Forsskål, 1775)
ah	Zoobenthos	Hydrozoa	Anthoathecata	Bougainvilliidae	*Garveia franciscana* (Torrey, 1902)
ai	Zoobenthos	Hydrozoa	Anthoathecata	Cordylophoridae	*Cordylophoracaspia* (Pallas, 1771)
aj	Zoobenthos	Hydrozoa	Anthoathecata	Hydractiniidae	*Podocorynaloyola*Haddad, Bettim&Miglietta, 2014
ak	Zoobenthos	Hydrozoa	Leptothecata	Blackfordiidae	*Blackfordiavirginica* Mayer, 1910
al	Zoobenthos	Anthozoa	Actiniaria	Diadumenidae	*Diadumenelineata* (Verrill, 1869)
am	Zoobenthos	Anthozoa	Alcyonacea	Xeniidae	*Sansibia* sp.
an	Zoobenthos	Anthozoa	Alcyonacea	Clavulariidae	*Clavulariaviridis*(Quoy&Gaimard, 1833) *cf.viridis*
ao	Zoobenthos	Anthozoa	Alcyonacea	Clavulariidae	*Carijoariisei* (Duchassaing&Michelotti, 1860)
ap	Zoobenthos	Anthozoa	Alcyonacea	Clavulariidae	*Stragulum bicolor* Ofwegen& Haddad, 2011

Table S2 - Checklist of marine taxa non-indigenous to Brazil (continuation).

aq	Zoobenthos	Anthozoa	Alcyonacea	Nephtheidae	*Chromonephtheabraziliensis* van Ofwegen, *2005*
ar	Zoobenthos	Anthozoa	Scleractinia	Dendrophylliidae	*Tubastraeacoccinea* Lesson, 1829
as	Zoobenthos	Anthozoa	Scleractinia	Dendrophylliidae	*Tubastraea tagusensis* Wells, 1982
at	Zoobenthos	Ophiuroidea	Amphilepidida	Ophiotrichidae	*Ophiactissavignyi* (Müller &Troschel, 1842)
au	Zoobenthos	Ophiuroidea	Amphilepidida	Ophiotrichidae	*Ophiothelamirabilis* Verrill, 1867
av	Zoobenthos	Gastropoda	Nudibranchia	Aeolidiidae	*Bulbaeolidia alba* (Risbec, 1928)
aw	Zoobenthos	Gastropoda	Littorinimorpha	Vermetidae	*Eualetestulipa* (Rousseau in Chenu, 1843)
ax	Zoobenthos	Bivalvia	Ostreida	Ostreidae	*Crassostrea gigas* (Thunberg, 1793)
ay	Zoobenthos	Bivalvia	Ostreida	Ostreidae	*Talonostreatalonata* Li & Qi, 1994
az	Zoobenthos	Bivalvia	Ostreida	Ostreidae	*Saccostrea* Dollfus&Dautzenberg, 1920
ba	Zoobenthos	Bivalvia	Ostreida	Pteriidae	*Isognomon bicolor* (C. B. Adams, 1845)
bb	Zoobenthos	Bivalvia	Myida	Dreissenidae	*Leiosolenusaristatus* (Dillwyn, 1817)
bc	Zoobenthos	Bivalvia	Myida	Dreissenidae	*Mytilopsisleucophaeata* (Conrad, 1831)
bd	Zoobenthos	Bivalvia	Myida	Dreissenidae	*Mytilopsis*cf*sallei* (Récluz, 1849)
be	Zoobenthos	Polychaeta	Sabellida	Sabellidae	*Branchiommaluctuosum* (Grube, 1870)
bf	Zoobenthos	Polychaeta	Sabellida	Sabellida	*Spirobranchusgiganteus* (Pallas, 1766)
bg	Zoobenthos	Polychaeta	Sabellida	Serpulidae	*Hydroides elegans* (Haswell, 1883) [nomenprotectum]
bh	Zoobenthos	Polychaeta	Sabellida	Serpulidae	*Hydroidesdianthus* (Verrill, 1873)
bi	Zoobenthos	Polychaeta	Spionida	Spionidae	*Boccardiellabihamata* Blake &Kudenov, 1978
bj	Zoobenthos	Polychaeta	Spionida	Spionidae	*Polydoracornuta* Bosc, 1802
bk	Zoobenthos	Polychaeta	Spionida	Spionidae	*Polydoranuchalis* Woodwick, 1953
bl	Zoobenthos	Polychaeta	Spionida	Spionidae	*Pseudopolydoraachaeta* Radashevsky& Hsieh, 2000
bm	Zoobenthos	Polychaeta	Spionida	Spionidae	*Pseudopolydoraantennata* (Claparède, 1869)

Table S2 - Checklist of marine taxa non-indigenous to Brazil (continuation).

bn	Zoobenthos	Polychaeta	Spionida	Spionidae	*Pseudopolydoradiopatra* Hsieh, 1992
bo	Zoobenthos	Polychaeta	Spionida	Spionidae	*Polydorahoplura* Claparède, 1868
bp	Zoobenthos	Polychaeta	Spionida	Spionidae	*Pseudopolydorapaucibranchiata* (Okuda, 1937)
bq	Zoobenthos	Malacostraca	Decapoda	Alpheidae	*Athanasdimorphus* Ortmann, 1894
br	Zoobenthos	Malacostraca	Decapoda	Alpheidae	*Athanasnitescens* (Leach, 1813 [in Leach, 1813-1814])
bs	Zoobenthos	Malacostraca	Decapoda	Belliidae	*Belliapicta* H. Milne Edwards, 1848
bt	Zoobenthos	Malacostraca	Decapoda	Cancridae	*Cancerpagurus* Linnaeus, 1758
bu	Zoobenthos	Malacostraca	Decapoda	Epialtidae	*Taliepusdentatus* (H. Milne Edwards, 1834)
bv	Zoobenthos	Malacostraca	Decapoda	Inachoididae	*Pyromaiatuberculata* (Lockington, 1877)
bw	Zoobenthos	Malacostraca	Decapoda	Lysmatidae	*Lysmatavittata* (Stimpson, 1860)
bx	Zoobenthos	Malacostraca	Decapoda	Portunidae	*Charybdis (Charybdis) hellerii* (A. Milne-Edwards, 1867)
by	Zoobenthos	Malacostraca	Decapoda	Portunidae	*Scyllaserrata* (Forskål, 1775)
bz	Zoobenthos	Malacostraca	Decapoda	Panopeidae	*Rhithropanopeusharrisii* (Gould, 1841)
ca	Zoobenthos	Malacostraca	Decapoda	Panopeidae	*Eurypanopeusdepressus* (Smith, 1869)
cb	Zoobenthos	Malacostraca	Decapoda	Penaeidae	*Penaeusvannamei* Boone, 1931
cc	Zoobenthos	Malacostraca	Decapoda	Penaeidae	*Penaeusmonodon* Fabricius, 1798
cd	Zoobenthos	Malacostraca	Decapoda	Penaeidae	*Metapenaeusmonoceros* (Fabricius, 1798)
ce	Zoobenthos	Malacostraca	Decapoda	Pilumnoididae	*Pilumnoidesperlatus* (Poeppig, 1836)
cf	Zoobenthos	Malacostraca	Decapoda	Polybiidae	*Liocarcinusnavigator* (Herbst, 1794)
cg	Zoobenthos	Malacostraca	Decapoda	Stenopodidae	*Stenopusspinosus* Risso, 1827
ch	Zoobenthos	Malacostraca	Decapoda	Lysmatidae	*Lysmatalipkei* Okuno& Fiedler, 2010
ci	Zoobenthos	Malacostraca	Amphipoda	Ampithoidae	*Cymadusaledoyeri* Peart, 2004
cj	Zoobenthos	Malacostraca	Amphipoda	Photidae	*Photislongicaudata* (Spence Bate & Westwood, 1862)

Table S2 - Checklist of marine taxa non-indigenous to Brazil (continuation).

ck	Zoobenthos	Malacostraca	Amphipoda	Corophiidae	*Laticorophiumbaconi* (Shoemaker, 1934)
cl	Zoobenthos	Malacostraca	Isopoda	Idoteidae	*Synidotealaevidorsalis* (Miers, 1881)
cm	Zoobenthos	Malacostraca	Isopoda	Paracerceis	*Paracerceissculpta* (Holmes, 1904)
cn	Zoobenthos	Malacostraca	Isopoda	Sphaeromatidae	*Sphaeromaterebrans* Bate, 1866
co	Zoobenthos	Malacostraca	Isopoda	Sphaeromatidae	*Sphaeromawalkeri* Stebbing, 1905
cp	Zoobenthos	Malacostraca	Isopoda	Sphaeromatidae	*Sphaeromaserratum* (Fabricius, 1787)
cq	Zoobenthos	Gymnolaemata	Cheilostomatida	Bugulidae	*Bugulaneritina* (Linnaeus, 1758)
cr	Zoobenthos	Gymnolaemata	Cheilostomatida	Bugulidae	*Bugulinastolonifera* (Ryland, 1960)
cs	Zoobenthos	Gymnolaemata	Cheilostomatida	Candidae	*Licorniajolloisii* (Audouin, 1826)
ct	Zoobenthos	Gymnolaemata	Cheilostomatida	Electridae	*Arboperculabengalensis* (Stoliczka, 1869)
cu	Zoobenthos	Gymnolaemata	Cheilostomatida	Hippopodinnidae	*Hippopodinatahitiensis* (Leca& d'Hondt, 1993)
cv	Zoobenthos	Gymnolaemata	Cheilostomatida	Phidoloporidae	*Triphyllozoonarcuatum* (MacGillivray, 1889)
cw	Zoobenthos	Gymnolaemata	Cheilostomatida	Sinoflustridae	*Sinoflustraannae* (Osburn, 1953)
cx	Zoobenthos	Gymnolaemata	Cheilostomatida	Membraniporidae	*Biflustragrandicella* (Canu&Bassler, 1929)
cy	Zoobenthos	Gymnolaemata	Cheilostomatida	Membraniporidae	*Biflustrairregulata* (Liu, 1991)
cz	Zoobenthos	Gymnolaemata	Cheilostomatida	Membraniporidae	*Biflustraokadai* Almeida, Souza & Vieira, 2017
da	Zoobenthos	Gymnolaemata	Cheilostomatida	Bitectiporidae	*Hippoporina indica* MadhavanPillai, 1978
db	Zoobenthos	Gymnolaemata	Ctenostomatida	Vesiculariidae	*Amathiaverticillata* (delleChiaje, 1822)
dc	Zoobenthos	Ascidiacea	Aplousobranchia	Clavelinidae	*Clavelina oblonga* Herdman, 1880
dd	Zoobenthos	Ascidiacea	Aplousobranchia	Didemnidae	*Didemnumcineraceum* (Sluiter, 1898)
de	Zoobenthos	Ascidiacea	Aplousobranchia	Didemnidae	*Didemnumperlucidum* Monniot F., 1983
df	Zoobenthos	Ascidiacea	Aplousobranchia	Holozoidae	*Distapliastylifera* (Kowalevsky, 1874)
dg	Zoobenthos	Ascidiacea	Aplousobranchia	Polyclinidae	*Aplidiopsis* sp.Lahille, 1890

Table S2 - Checklist of marine taxa non-indigenous to Brazil (continuation).

dh	Zoobenthos	Ascidiacea	Aplousobranchia	Polyclinidae	*Polyclinumaurantium* Milne Edwards, 1841
di	Zoobenthos	Ascidiacea	Aplousobranchia	Polyclinidae	*Sidneioidesperegrinus* Kremer et al., 2011
dj	Zoobenthos	Ascidiacea	Aplousobranchia	Polyclinidae	*Aplidiumpentatrema* (Monniot F., 1972)
dk	Zoobenthos	Ascidiacea	Aplousobranchia	Polycitoridae	*Eudistoma carolinense* Van Name, 1945
dl	Zoobenthos	Ascidiacea	Phlebobranchia	Ascidiidae	*Ascidiasydneiensis* Stimpson, 1855
dm	Zoobenthos	Ascidiacea	Phlebobranchia	Ascidiidae	*Ascidiatenue* Monniot C., 1983
dn	Zoobenthos	Ascidiacea	Phlebobranchia	Ascidiidae	*Ascidia interrupta* Heller, 1878
do	Zoobenthos	Ascidiacea	Phlebobranchia	Ascidiidae	*Ascidiacurvata* (Traustedt, 1882)
dp	Zoobenthos	Ascidiacea	Phlebobranchia	Cionidae	*Cionaintestinalis* (Linnaeus, 1767)[3.]
dq	Zoobenthos	Ascidiacea	Phlebobranchia	Corellidae	*Rhodosomaturcicum* (Savigny, 1816)
dr	Zoobenthos	Ascidiacea	Stolidobranchia	Pyuridae	*Pyuragangelion*(Savigny, 1816)
ds	Zoobenthos	Ascidiacea	Stolidobranchia	Pyuridae	*Pyura beta* Skinner, Rocha & Counts, 2019
dt	Zoobenthos	Ascidiacea	Stolidobranchia	Styelidae	*Botryllusschlosseri* (Pallas, 1766)
du	Zoobenthos	Ascidiacea	Stolidobranchia	Styelidae	*Cnemidocarpa irene* (Hartmeyer, 1906)
dv	Zoobenthos	Ascidiacea	Stolidobranchia	Styelidae	*Eusynstyela* sp. Michaelsen, 1904
dw	Zoobenthos	Ascidiacea	Stolidobranchia	Styelidae	*Styelaplicata*(Lesueur, 1823)
dx	Zoobenthos	Ascidiacea	Stolidobranchia	Styelidae	*Styelacanopus* (Savigny, 1816)
dy	Necton	Actinopterygii	Batrachoidiformes	Batrachoididae	*Opsanus beta* (Goode&Bean, 1880)
dz	Necton	Actinopterygii	Perciformes	Acanthuridae	*Acanthurusmonroviae* Steindachner, 1876
ea	Necton	Actinopterygii	Perciformes	Blenniidae	*Omobranchuspunctatus* (Valenciennes, 1836)
eb	Necton	Actinopterygii	Perciformes	Chaetodontidae	*Heniochusacuminatus* (Linnaeus, 1758)
ec	Necton	Actinopterygii	Perciformes	Eleotridae	*Butiskoilomatodon* (Bleeker, 1849)
ed	Necton	Actinopterygii	Perciformes	Pomacentridae	*Chromislimbata* (Valenciennes, 1833)

Table S2 - Checklist of marine taxa non-indigenous to Brazil (conclusion).

ee	Necton	Actinopterygii	Perciformes	Pomacanthidae	*Pomacanthusmaculosus* (Forsskål, 1775)
ef	Necton	Actinopterygii	Perciformes	Scorpaenidae	*Pteroisvolitans* (Linnaeus, 1758)
eg	Necton	Elasmobranchii	Carcharhiniformes	Carcharhinidae	*Triaenodonobesus* (Rüppell, 1837)

Table S3 - Marine taxa non-indigenous to Brazil andthe date first registered, states of occurrence, status assigned in 2019 (to be continued).

		Status			**Presence in state**[3.]																	**References**[4]
Code[1]	**Year offirst record**[2].	**D**	**E**	**I**	AP	PA	MA	PI	CE	RN	PB	PE	AL	SE	BA	ES	RJ	SP	PR	SC	RS	
a	*1983*			x											x		x	x	x	x	x	Lopes et al. (2009); Castro et al. (2017)
b	*1996*			x															x		x	Lopes et al. (2009)
c	*1998*			x														x	x	x	x	Lopes et al. (2009); Hallegraeff et al. (2012); Vieira (2017)
d	1983		x														x	x		x		Lopes et al. (2009)
e	1977		x						x	x	x	x			x							Lopes et al.(2009); Almeida et al. (2012)
f	1980		x			x	x					x		x	x	x	x	x	x	x	x	Lopes et al. (2009)
g	*1983*		x															x				Lopes et al. (2009); Mohammed (2014)
h	*2000*		x																x			Lopes et al. (2009)
i	*2002*		x															x				Lopes et al. (2009)

Table S3 - Marine taxa non-indigenous to Brazil andthe date first registered, states of occurrence, status assigned in 2019 (continuation).

j	*2013*	X												x				BjörnbergandKihara (2013)
k	*2013*	X												x				BjörnbergandKihara (2013)
l	1950		x			x					x			x	x	x		Haddad and Nogueira Júnior (2006); Morandini et al. (2006)
m	2012		x											x		x	x	Nascimento et al. (2019)
n	1991		x						x		x							Farrapeira (2010)
o	*1982*		x		x				x		x				x			Lopes et al. (2009); Rainbown (2000); Marques et al. (2013); Bumbeer and Rocha (2016)
p	*1994*		x								x					x		Marques et al. (2013); Kremer and Rocha (2016)
q	*1990*		x	x					x	x	x		x	x	x			Lopes et al. (2009)
r	*1974*		x				x					x	x	x	x	x	x	Lopes et al. (2009)
s	*1994*		x												x			Bumbeerand Rocha (2016)
t	*2010*		x				x	x	x									Farrapeira (2010); Carlton et al. (2011); Rodríguez-Almarazand García-Madrigal (2014)
u	*1983*	X							x									Farrapeira (2010); Rocha et al. (2013)
v	*1986*		x		x	x			x		x							Farrapeira (2010); Rocha et al. (2013)

Table S3 - Marine taxa non-indigenous to Brazil andthe date first registered, states of occurrence, status assigned in 2019 (continuation).

w	*1985*		x								x	x				Lopes et al. (2009)
x	1968		x				x		x	x	x	x	x	x	x	Oliveira Filho and Coll (1975); Milstein et al. (2015)
y	2008	X										x				Milstein et al. (2015)
z	2002	X				x										Milstein et al. (2015)
aa	*1963*		x								x	x				Lopes et al. (2009)
ab	*2006*		x								x					Cassano et al. (2006); Cassano (2008); Klein et al. (2005)
ac	2003	X								x						Silva et al. (2010)
ad	*2015*	X												x		Azevedo et al. (2015)
ae	1997		x							x	x	x		x		Pacheco (2011); Batista (2012)
af	*2001*			x							x					Lopes et al. (2009)
ag	2012		x								x					Morandini et al. (2017)
ah	*1998*		x					x								Calder and Maÿal (1998); Neves et al. (2007); Rocha et al. (2013); Neves and Rocha (2008)
ai	*1996*		x		x						x	x	x			Rocha et al. (2013)
aj	2007		x										x	x		Haddad et al. (2014); Bettim and Haddad (2017)

Table S3 - Marine taxa non-indigenous to Brazil andthe date first registered, states of occurrence, status assigned in 2019 (continuation).

ak	1963	x						x					x	x	x	Nogueira andOliveira(2006); Bardi and Marques (2009); Júnior (2012)
al	1977		x									x				Benet et al. (2015); Rocha et al. (2013)
am	2017		x									x				Mantellato et al. (2018)
na	2017		x									x				Mantellato et al. (2018)
ao	1981	x		x	x		x	x		x	x	x	x			Concepcion et al. (2010); Kahng and Grigg (2005); Marques et al. (2013)
ap	2002		x			x						x	x	x	x	Altvater and Coutinho(2015); Van Ofwegen and Haddad (2011)
aq	*2003*		x									x				Lopes et al. 2009
ar	*2001*		x			x			x	x	x	x	x		x	Lopes et al. 2009; Miranda et al. (2012); Bianco et al. (2016); Creed et al. (2017)
as	*2001*		x			x			x	x	x	x	x		x	Lopes et al. 2009; Miranda et al. (2012); Bianco et al. (2016); Creed et al. (2017)

Table S3 - Marine taxa non-indigenous to Brazil andthe date first registered, states of occurrence, status assigned in 2019 (continuation).

at	1970		x		x		x			x	x			x			x			Rocha et al. (2013); Lima et al. (2011)
au	2000		x											x	x	x	x	x		Hendler et al. (2012); Mantelatto et al. (2016)
aw	2005	X														x				Padulaand Santos (2005); Rocha et al. (2013)
ax	2005		x					x	x							x				Spotorno-Oliveira et al. (2018)
ay	2006		x																x	Melo et al. (2010); Gamain et al. (2016)
az	2008	X																	x	Cavaleiro et al. (2019)
ba	2014	X															x			Galvão et al. (2018)
bb	*1994*			x		x			x		x	x	x	x	x	x	x	x	x	Lopes et al. (2009); Breves-Ramos (2010)
bc	*2005*			x				x						x		x	x	x	x	Lopes et al. (2009); Vinagre et al. (2018)
bd	*2014*			x												x				Lopes et al. (2009); Rizzo et al. (2014); Fernandes et al. (2018)
be	2004		x								x									Fernandes et al. (2018)
bf	2002			x						x						x	x			Lopes et al. (2009); De Assis et al. (2012)
bg	1865		x						x		x			x		x				Skinner et al. (2012)
bh	*1991*			x												x				Schwan et al. (2015)

Table S3 - Marine taxa non-indigenous to Brazil andthe date first registered, states of occurrence, status assigned in 2019 (continuation).

bi	2012		x											x					Sun et al (2017)
bj	*1998*	X														x	x		Lopes et al. (2009)
bk	1998	X											x	x	x	x			Lopes et al. (2009); Cangussu (2010)
bl	1995	X							x			x		x	x	x			Lopes et al. (2009)
bm	2004	X													x				Lopes et al. (2009)
bn	1994	X										x		x	x				Lopes et al. (2009)
bo	2002	X														x			Lopes et al. (2009)
bp	2015	X													x				RadashevskyandMigotto (2016)
bq	1999	X												x					Lopes et al. (2009)
br	2007		x				x		x						x				Pachelle et al. (2011); Almeida et al. (2015); Almeida et al. (2012)
bs	2009		x												x				Pachelle et al. (2011); Almeida et al. (2015); Almeida et al. (2012)
bt	1972	X																x	Lopes et al. (2009)
bu	*1930*	X													x				Lopes et al. (2009)
bv	1996	X												x					Lopes et al. (2009)
bw	1989		x			x								x	x	x	x	x	Lopes et al. (2009)
bx	2009		x								x	x		x	x				Soledade et al. (2013)
by	1995			x	x	x	x	x	x	x	x	x	x	x	x		x		Lopes et al. (2009)

Table S3 - Marine taxa non-indigenous to Brazil andthe date first registered, states of occurrence, status assigned in 2019 (continuation).

bz	1983		x												x	x				Lopes et al. (2009); Tavares andMendonça(2011)
ca	*1998*		x																x	Lopes et al. (2009)
cb	1985		x																x	Horn and Tolley (2009); Rodrigues et al. (2014); O'Shaughnessy et al. (2014)
cc	1971		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		Lopes et al. (2009); Krummenauer et al. (2011); Furtado et al. (2011); Rebouças et al. (2011); Schveitzer et al. (2013)
cd	1987		x		x				x		x					x				Lopes et al. (2009)
ce	*1995*	X																	x	Lopes et al. (2009)
cf	2000		x												x	x				Lopes et al. (2009); Silva and Barros (2011)
cg	1966	X													x					Lopes et al. (2009)
ch	2014		x															x		Giraldesand Freire (2015)
ci	2012		x				x	x				x			x					Pachelle et al. (2016)
cj	1953		x					x					x	x	x	x				Stofel et al. (2008); Rocha et al. (2013); Tavares et al. (2013); Santos and Soares (1999); Dubiaski-Silva andMasunari (1995)

Table S3 - Marine taxa non-indigenous to Brazil andthe date first registered, states of occurrence, status assigned in 2019 (continuation).

ck	1989		x				x			x	x			Rocha et al. (2013); Ribeiro et al. (2003); Santos and Pires-Vani (2004)
cl	2001	X								x	x			Valério-Berardo and S (2009); Serejoand Siqueira (2
cm	1969		x							x	x			Rocha et al. (2013); Chapman and Carlton
cn	1980		x	x						x	x		x	Rocha et al. (2013); Oliveira (2008)
co	1960		x		x	x		x		x	x		x	Oliveira (2008); Rocha et al. (2013)
cp	1960		x	x			x	x		x	x	x		Oliveira (2008); Rocha et al. (2013)
cq	1989		x							x				Lopes et al. (2009)
cr	*1937*		x							x	x	x		Miranda et al. (2018); Vieira et al. (2008)
cs	*2015*	X							x			x		Almeida et al. (2015); Bumeer (2017); Miranda et al. (2018)
ct	2013	X							x					Miranda et al. (2018); Kremerand Rocha (20
cu	2018	X							x					Miranda et al. (2018)

Table S3 - Marine taxa non-indigenous to Brazil andthe date first registered, states of occurrence, status assigned in 2019 (continuation).

cw	*2003*	X							x				Lopes et al. (2009)
cx	2007	X				x	x						Almeida et al. (2015)
cy	2017		x								x		Miranda et al. (2018)
cz	2014		x				x			x			Miranda et al. (2018); Siqueira et al. (2017)
da	1997	X					x						Miranda et al. (2018); Almeida et al. (2017)
db	1997	X					x						Miranda et al. (2018); Almeida et al. (2017)
dc	1990		x							x	x	x	Miranda et al. (2018); Vieira andMigotto (2008)
dd	1860		x		x		x		x	x		x	Santos et al. (2017); Miranda et al (2018)
de	*1925*		x						x	x	x	x	Rocha et al. (2012); Skinner et al. (2016)
df	*2009*		x	x			x	x	x	x			Rocha et al. (2009); Kremer and Rocha (2016)
dg	1995		x				x			x			Kremerand Rocha (2016)
dh	2009	X								x			Marques et al. (2013)
di	2009	X								x			Marques et al. (2013)
dj	*2010*	X							x				Marins et al. (2010); Svane (1984)
dk	2010	X									x		Bumbeerand Rocha (2016)

Table S3 - Marine taxa non-indigenous to Brazil andthe date first registered, states of occurrence, status assigned in 2019 (continuation).

dl	2002	X									x		Bumbeer et al. (2016)
dm	1996	X									x	x	Moreno and Rocha (2001); Bumbeer et al. (2016)
dn	*1956*		x					x	x	x	x	x	Lopes et al. (2009)
do	2011	X					x			x	x	x	Bumbeerand Rocha (2016)
dp	1999		x				x		x	x			Rocha et al. (2013); Nassar and Silva (1999)
dq	*1998*		x						x		x		Rocha and Nasser (1998); Granthom-Costa et al. (2016)
dr	*1958*		x						x	x	x		Lopes et al. (2009); Brunetti et al. (2015)
ds	1999		x				x		x				Lotufo (2002); Skinner et al. (2013); Granthom-Costa et al. (2016)
dt	2012		x					x					Skinner et al. (2019)
du	1961		x					x	x	x			Skinner et al. (2019)
dv	*2002*		x		x	x	x						Lotufo (2002); Rocha et al. (2013)
dx	2011		x				x			x			Rocha et al. (2012)
dw	1998	X								x			Marques et al. (2013)
dy	*1883*			x			x		x	x	x	x	Lopes (2009); Marins et al. (2010); Thiyagarajan and Qian(2003)

Table S3 - Marine taxa non-indigenous to Brazil andthe date first registered, states of occurrence, status assigned in 2019 (conclusion).

dz	1969		x					x		x		x		x	x	x	x	Granthom-Costa et al. (2016)
ea	2006		x												x	x		Caires et al. (2007)
eb	*1999*		x											x	x			Lopes et al. (2009)
ec	*2002*			x	x		x					x		x	x		x	Lopes et al. (2009); Soares et al. (2011); Loebmann et al. (2010)
ed	*2000*	X												x	x			Lopes et al. (2009)
ee	*2000*		x		x	x			x		x	x	x	x	x			Lopes et al. (2009); Vinagre et al. (2018); Macieira et al. (2012)
ef	2009		x														x	Domingues et al. (2006); Leite et al. (2009); Anderson et al. (2017)
eg	2017	X														x		Soeth et al. (2018)
eh	2014	X												x				Ferreira et al. (2015); AlbinsandHixon (2008)
ei	2013	X														x		Bornatowski et al. (2018)

Legenda: Detected (D); Established (E); Invasive (I).

Nota: [1]To check the species name see Table S2; [2]The year of collection, or record, if reported in the reference(s), or the year of the reference publication (denoted in italic)when the year of collection or record were not provided; [3]For the full name of the states see table S1.

Fonte: adapted from PIRES AND CREED (2020)

Table S4 - Marine taxa non-indigenous to Brazil andthe date first registered, states of occurrence, status assigned in 2009 (to be continued).

	Status					**Presence in state[2.]**																
Code[1]	**D**	**E**	**I**	**C**	**NL**	AP	PA	MA	PI	CE	RN	PB	PE	AL	SE	BA	ES	RJ	SP	PR	SC	RS
a			x													x		x	x	x	x	x
b			x																	x		x
c		x																	x	x	x	x
d		x																x	x		x	
e		x								x	x	x	x			x						
f		x					x	x					x		x	x	x	x	x	x	x	x
g	x																		x			
h	x																			x		
i	x																		x			
j					x																	
k					x																	
l					x																	
m					x																	
n					x																	
o					x																	
p					x																	
q		x						x					x	x		x		x	x	x		
r		x									x						x	x	x	x	x	x
s					x																	
t					x																	
u					x																	
v					x																	

Table S4 - Marine taxa non-indigenous to Brazil andthe date first registered, states of occurrence, status assigned in 2009 (continuation).

w		x			x	x	
x				x			
y				x			
z				x			
aa	x				x	x	
ab				x			
ac				x			
ad				x			
ae		x			x	x	x
af			x		x		
ag				x			
ah				x			
ai				x			
aj				x			
ak				x			
al				x			
am				x			
na				x			
ao				x			
ap				x			
aq		x			x		
ar			x		x		
as			x		x	x	x
at				x			

Table S4 - Marine taxa non-indigenous to Brazil andthe date first registered, states of occurrence, status assigned in 2009 (continuation).

au					x											
aw					x											
ax					x											
ay				x												
az					x											
ba					x											
bb			x			x	x	x	x	x	x	x	x	x	x	x
bc			x										x	x		x
bd		x						(x)								
be					x											
bf		x											x	x		
bg					x											
bh					x											
bi					x											
bj	x														x	x
bk	x											x	x	x	x	
bl	x							x			x		x	x	x	
bm	x													x		
bn	x										x		x	x		
bo	x														x	
bp					x											
bq	x												x			
br					x											
bs					x											

Table S4 - Marine taxa non-indigenous to Brazil andthe date first registered, states of occurrence, status assigned in 2009 (continuation).

bt	x																			x
bu	x																x			
bv	x															x				
bw		x					x									x	x	x	x	x
bx				x																
by			x			x	x	x	x		x	x	x	x	x	x	x		x	
bz	x																x			
ca		x																		x
cb				x																
cc	x				x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
cd	x					x				x		x					x			
ce	x																			x
cf	x																x			
cg	x															x				
ch				x																
ci				x																
cj				x																
ck				x																
cl				x																
cm				x																
cn				x																
co				x																
cp				x																

Table S4 - Marine taxa non-indigenous to Brazil andthe date first registered, states of occurrence, status assigned in 2009 (continuation).

cq		x			x			
cr			x					
cs			x					
ct			x					
cu			x					
cw	x				x			
cx			x					
cy			x					
cz			x					
da			x					
db			x					
dc			x					
dd			x					
de			x					
df			x					
dg			x					
dh			x					
di			x					
dj			x					
dk			x					
dl			x					
dm			x					
dn		x		x	x	x	x	x
do			x					

Table S4 - Marine taxa non-indigenous to Brazil andthe date first registered, states of occurrence, status assigned in 2009 (conclusion).

dp				x						
dq				x						
dr	x						x	x	x	
ds				x						
dt				x						
du				x						
dv				x						
dx				x						
dw				x						
dy			x			x	x	x	x	x
dz				x						
ea				x						
eb	x						x	x		x
ec		x				x				x
ed	x						x	x		
ee	x				x					
ef				x						
eg				x						
eh				x						
ei				x						

Legenda: Detected (D); Established (E); Invasive (I); Contained (C); Not listed until 2009 (NL)

Nota: [1]To check the species name see Table S2; [2]For the full name of the states see table S1; To check the year of first record see Table S2; To check the references see Table S2

Fonte: adapted from PIRES AND CREED (2020)

Table S6 - Summary checklist and current status of marine non-indigenous species in Brazil(to be continued).

Taxon[1,2]	**Current status**[3,4.]
Acanthurusmonroviae Steindachner, 1876	Established
Alexandriumtamarense (Lebour, 1925) Balech, 1995	Invasive
Amathiaverticillata (delleChiaje, 1822)	Established
Amphibalanusamphitrite (Darwin, 1854)	Established
Amphibalanusreticulatus (Utinomi, 1967)	Established
Amphibalanussubalbidus (Henry, 1973)	Established
Anotrichiumyagii (Okamura) Baldock, 1976	Established
Aplidiopsis sp.Lahille, 1890	Detected
Aplidiumpentatrema (Monniot F., 1972)	Detected
Apocyclopsborneoensis Lindberg, 1954	Established
Arboperculabengalensis (Stoliczka, 1869)	Detected
Ascidiacurvata (Traustedt, 1882)	Established
Ascidia interrupta Heller, 1878	Established
Ascidiasydneiensis Stimpson, 1855	Established
Ascidiatenue Monniot C., 1983	Detected
Athanasdimorphus Ortmann, 1894	Established
Athanasnitescens (Leach, 1813 [in Leach, 1813-1814])	Established
Balanustrigonus Darwin, 1854	Established
Belliapicta H. Milne Edwards, 1848	Detected
Biflustragrandicella (Canu&Bassler, 1929)	Established
Biflustrairregulata (Liu, 1991)	Detected
Biflustraokadai Almeida, Souza & Vieira, 2017	Detected
Blackfordiavirginica Mayer, 1910	Established
Boccardiellabihamata Blake &Kudenov, 1978	Detected
Bostrichobranchusdigonas Abbott, 1951	(NowCryptogenic)
Botryllusschlosseri (Pallas, 1766)	Established
Branchiommaluctuosum (Grube, 1870)	Invasive
Bugulaneritina (Linnaeus, 1758)	Established
Bugulinastolonifera (Ryland, 1960)	Detected
Bulbaeolidia alba (Risbec, 1928)	Detected
Butiskoilomatodon (Bleeker, 1849)	Established
Cancerpagurus Linnaeus, 1758	Detected
Carijoariisei (Duchassaing&Michelotti, 1860)	Established
Cassiopeaandromeda (Forsskål, 1775)	Established

Table S6 - Summary checklist and current status of marine non-indigenous species in Brazil (continuation).

Caulerpa scalpelliformis (R.Brown ex Turner) C.Agardh, 1817	Invasive
Charybdis (Charybdis) hellerii (A. Milne-Edwards, 1867)	Invasive
Chromislimbata (Valenciennes, 1833)	Established
Chromonephtheabraziliensis van Ofwegen, *2005*	Invasive
Cionaintestinalis (Linnaeus, 1767)[2.]	Established
Clavelina oblonga Herdman, 1880	Established
Clavulariaviridis(Quoy&Gaimard, 1833) *cf.viridis*	Invasive
Cnemidocarpa irene (Hartmeyer, 1906)	Established
*Cnidostomafallax*Vanhöffen, 1911	Established
Cordylophoracaspia (Pallas, 1771)	Established
*Coscinodiscuswailesii*Gran&Angst, 1931	Invasive
Crassostrea gigas (Thunberg, 1793)	Established
Cymadusaledoyeri Peart, 2004	Established
Dasya brasiliensis E.C.Oliveira Filho &Y.Y.Braga, 1971	Established
Diadumenelineata (Verrill, 1869)	Invasive
Didemnumcineraceum (Sluiter, 1898)	Established
Didemnumperlucidum Monniot F., 1983	Established
Distapliastylifera (Kowalevsky, 1874)	Detected
Eualetestulipa (Rousseau in Chenu, 1843)	Established
Eudistoma carolinense Van Name, 1945	Detected
Eurypanopeusdepressus (Smith, 1869)	Established
Eusynstyela sp. Michaelsen, 1904	Detected
Garveia franciscana (Torrey, 1902)	Established
Grateloupiaturuturu Yamada, 1941	Detected
*Gymnodiniumcatenatum*H.W.Graham, 1943	Invasive
Heniochusacuminatus (Linnaeus, 1758)	Detected
Hippopodinatahitiensis (Leca& d'Hondt, 1993)	Detected
Hippoporina indica MadhavanPillai, 1978	Established
Hydroidesdianthus (Verrill, 1873)	Established
Hydroides elegans (Haswell, 1883) [nomenprotectum]	Invasive
Isognomon bicolor (C. B. Adams, 1845)	Invasive
Kappaphycusalvarezii (Doty) DotyexP.C.Silva	(NowContained)
Laophontellahorrida (Por, 1964)	Detected
Laticorophiumbaconi (Shoemaker, 1934)	Detected
Laurenciacaduciramulosa Masuda&Kawaguchi, 1997	Established
Laurencia venusta Yamada, 1931	Detected

Table S6 - Summary checklist and current status of marine non-indigenous species in Brazil (continuation).

Leiosolenusaristatus (Dillwyn, 1817)	Invasive
Licornia diadema (Busk, 1852)	(NowCryptogenic)
Licorniajolloisii (Audouin, 1826)	Detected
Liocarcinusnavigator (Herbst, 1794)	Detected
Lysmatalipkei Okuno& Fiedler, 2010	Established
Lysmatavittata (Stimpson, 1860)	Established
Megabalanuscoccopoma (Darwin, 1854)	Established
Membranobalanusdeclivis (Darwin, 1854)	Established
Metapenaeusmonoceros (Fabricius, 1798)	Detected
Mytilopsiscfsallei (Récluz, 1849)	Established
Mytilopsisleucophaeata (Conrad, 1831)	Invasive
Omobranchuspunctatus (Valenciennes, 1836)	Invasive
Ophiactissavignyi (Müller &Troschel, 1842)	Established
Ophiothelamirabilis Verrill, 1867	Established
Opsanus beta (Goode&Bean, 1880)	Established
Paracerceissculpta (Holmes, 1904)	Established
Paracyclopinalongifurca (Sewell, 1924)	Established
*Paraleucilla magna*Klautau, Monteiro &Borojevic, 2004	(NowCryptogenic)
Penaeusmonodon Fabricius, 1798	Established
Penaeusvannamei Boone, 1931	Established
Perna perna (Linnaeus, 1758)	(NowCryptogenic)
Photislongicaudata (Spence Bate & Westwood, 1862)	Established
Phyllopodopsyllusaegypticus Nicholls, 1944	Detected
Phyllopodopsyllussetouchiensis Kitazima, 1981	Established
*Phyllorhizapunctata*Lendenfeld, 1884	Established
Pilumnoidesperlatus (Poeppig, 1836)	Established
Pleopisschmackeri (Poppe, 1889)	Established
*Podocorynaloyola*Haddad, Bettim&Miglietta, 2014	Established
Polyclinumaurantium Milne Edwards, 1841	Detected
Polydoracornuta Bosc, 1802	Detected
Polydorahoplura Claparède, 1868	Detected
Polydoranuchalis Woodwick, 1953	Detected
Pomacanthusmaculosus (Forsskål, 1775)	Detected
Pseudodiaptomustrihamatus Wright S., *1937*	Established
Pseudopolydoraachaeta Radashevsky& Hsieh, 2000	Detected
Pseudopolydoraantennata (Claparède, 1869)	Detected
Pseudopolydoradiopatra Hsieh, 1992	Detected

Table S6 - Summary checklist and current status of marine non-indigenous species in Brazil (continuation).

Pseudopolydorapaucibranchiata (Okuda, 1937)	Detected
Pteroisvolitans (Linnaeus, 1758)	Detected
Pyromaiatuberculata (Lockington, 1877)	Established
Pyropiaacanthophora (E.C.Oliveira& Coll) M.C.Oliveira, D.Milstein&E.C.Oliveira, 2011	Established
Pyropiasuborbiculata (Kjellman) J.E.Sutherland, H.G.Choi, M.S. Hwang&W.A.Nelson, 2011	Established
Pyropiatanegashimensis (Shinmura) N.kikuchi& E. Fujiyoshi, 2011	Detected
Pyropiavietnamensis (Tak. Tanaka &P.H.Ho) J.E.Sutherland&Monotilla, 2011	Detected
Pyura beta Skinner, Rocha & Counts, 2019	Established
Pyuragangelion(Savigny, 1816)	Established
Rhithropanopeusharrisii (Gould, 1841)	Established
Rhodosomaturcicum (Savigny, 1816)	Established
Saccostrea Dollfus&Dautzenberg, 1920	Detected
Sansibia sp.	Invasive
Schizoporella errata (Waters, 1878)	(NowCryptogenic)
Scyllaserrata (Forskål, 1775)	Established
Sidneioidesperegrinus Kremer et al., 2011	Detected
Sinoflustraannae (Osburn, 1953)	Established
*Sphaeromaannandalei*Stebbing, 1911	(Redescribed as a new species)
Sphaeromaserratum (Fabricius, 1787)	Established
Sphaeromaterebrans Bate, 1866	Established
Sphaeromawalkeri Stebbing, 1905	Established
Spirobranchusgiganteus (Pallas, 1766)	Established
Stenopusspinosus Risso, 1827	Established
Stragulum bicolor Ofwegen& Haddad, 2011	Invasive
Striatobalanusamaryllis (Darwin, 1854)	Established
Styelacanopus (Savigny, 1816)	Established
Styelaplicata(Lesueur, 1823)	Invasive
Synidotealaevidorsalis (Miers, 1881)	Established
Taliepusdentatus (H. Milne Edwards, 1834)	Detected
Talonostreatalonata Li & Qi, 1994	Detected
Temoraturbinata (Dana, 1849)	Established
Tesseroporaatlantica Newman & Ross, 1976	Detected
Tetraclitella divisa (Nilsson-Cantell, 1921)	Established

Table S6 - Summary checklist and current status of marine non-indigenous species in Brazil (conclusion).

Triaenodonobesus (Rüppell, 1837)	Detected
Triphyllozoonarcuatum (MacGillivray, 1889)	Detected
Tubastraeacoccinea Lesson, 1829	Invasive
Tubastraea tagusensis Wells, 1982	Invasive
Virididentuladentata (Lamouroux, 1816)	(NowCryptogenic)

Nota: [1]Highlighted taxons are additional to those described as NIS by Lopes et al. (2009); [2]Green text indicates listed by Lopes et al. (2009) but not now considered NIS in Brazil.; [3]Status is based on the categories detected, established or invasive as defined by Lopes et al., 2009; [4]Red text indicates status change compared to the last survey by Lopes et al. (2009).
Fonte: adapted from PIRES AND CREED (2020)

1.1.9 Supplementary material references

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2 DIVERSIDADE BIOLÓGICA E FUNCIONAL EM COMUNIDADES COSTÃO ROCHOSO INVADIDAS.

2.1 How Do Biological and Functional Diversity Change in Invaded Tropical Marine Rocky Reef Communities?

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Abstract

Evidence so far shows that most alien species (AS) have negative impacts on native biodiversityand are changing biodiversity in almost all environments. Here, we study eight rocky shoresat four sites containing reefs with invaded communities and other not-invaded (control) communities,to evaluate the effects of four marine invasive species on biological and functional diversity.We used the adjustment and selection approach of species abundance distribution models (SAD),taxonomic diversity indices and functional diversity indices based on hierarchical grouping matrices(FD—Functional Diversity). In addition to comparing invaded and not-invaded communities, wealso performed the same analysis, but removed the invaders (AS removed) from the matrices. Thegeometric-series model was best adjusted to the majority of communities. The diversity indicessuggest that the taxonomic diversity is lower in invaded communities, while the functional diversityindices suggest a change in the functional space of invaded and not-invaded communities, witha greater amount of functional space filled by species in the not-invaded communities. Taxonomicand functional diversity indices were successful in identifying processes that determine the biologicaldiversity of invaded communities, as they seem to obey a pattern that reflects the reduced diversityof invaded communities.

Keywords: diversity indices; functional diversity; invasive; alien species; rank abundance plots;species abundance distribution models.

2.1.1 Introduction

The introduction of new species into a new habitat represents a change and adjustment in the pre-existing state of the receiving community. These changes can occur atdifferent intensities and affect one or more species that already make up part of the receptorcommunity (Carlton 2002). Alien species (AS) can transform marine environments, displacing nativespecies, changing community structure and food webs, as well as impacting the dynamicsof nutrients and sedimentation rates (Ruiz et al. 997). In the marine environment the number of documentedbiological invasions is increasing in the tropical southwest Atlantic Ocean (Teixeira and Creed 2020),which reflects a worldwide trend in marine ecosystems (Bailey et al. 2020), and the evidence shows thatmost AS have negative impacts on native biodiversity and human well-being, and arechanging the biodiversity of almost all environments (Occhipinti-Ambrogi et al. 2003; Gallardo et al. 2015; Giakoumi et al. 2016).

Native and AS often have different biological characteristics and interactions with thecommunity, for example chemical defenses or the high reproductive output of the AS or escape from predators within the new community. Such factors can favor their dominancein the community invaded by AS, as they become more abundant than the other species (Hansen et al. 2013).The abundance of a species, at least to some extent, reflects its success in competing for limited resources (Maurran 2003), so the effects of an AS will increase with its abundance and vary with its functional attributes. The arrival of a new species may bring with it traits whichare novel to the ecosystem as well as increase species richness (always by one, at leastinitially), so the establishment of AS in the community can change species and functionaldiversity (Bremner 2003, 2006; Gallardo et al. 2015; Thomsen et al. 2011).

A new AS can establish itself in the receptor community by occupying a differentempty niche, using different resources [the Empty Niche Hypotheses (MacArthur 1970)], with minimalcompetition (Emery 2007; Strayer et al. 2006, 2017; Catford et al. 2009; Hejda et al. 2013). In contrast, if an AS is functionally similar to the species alreadyexisting in the invaded community, they may compete with the resident species of thecommunity [Biotic Resistance/Diversity–Invasibility Hypotheses (Elton 1958; Riva et al. 2019)]. Both processes result in changes in the functional diversity of a community after the invasion (Shuai et al. 2018; Toussaint et al. 2019; Milardi et al. 2019; Matsuzaki et al. 2013).

Here, we used wave-protected shallow subtidal tropical rocky shore benthic communities as models. Typically, such communities are highly diverse, highly productive(including symbiotic autotrophic organisms such as corals) and space may be limiting, resulting in competition between sessile autotrophic and heterotrophic species. Underthis scenario we would predict that for a species to have successfully established andinvaded it will dominate and displace native species. Assuming that the abundance ofa species is most often a reflection of its success in competing for limited resources (Magurran 2003; Rosindell et al. 2013),we tested the hypothesis that invaded communities reflect a pattern of species abundancedescribed by models that fit communities with less equitability (e.g., Geometric SeriesModel). Considering that functional diversity indices have the potential to reveal the processes of assembling the community (Mason et al. 2013), we also tested the hypothesis that invadedcommunities present a smaller proportion of functional space traits (functional richness,FRic), overuse of resources, and thus a less even distribution of abundance in functional space traits (functional evenness, FEve) and species loss associated with a decrease in therange of characteristic values (Villéger et al. 2008; Fried et al. 2019).

In order to test these hypotheses,we investigated (1) the biological and functional diversity of invaded rocky shore communities using the adjustment and selection approach of species abundance distribution (SAD) models and (2) the structure and function of communities using functional diversity indexes based on hierarchical grouping matrices (FD—Functional Diversity). We also (3) assess the effectiveness of using these parameters in evaluating the impact of AS on rocky shore communities.

2.1.2 Materials and Methods

We conducted the present study at four different shallow subtidal tropical rocky shorelocations along about 280 km of the coast of the state of Rio de Janeiro, Brazil (SouthwestAtlantic; Figure 5, f.35), a region which has received multiple invasions (Teixeira and Creed 2020). We comparedcommunity composition and structure of invaded and not-invaded communities at eachsite (hereby termed invasion state).

2.1.2.1 Study Sites and Species

2.1.2.1.1 *Caulerpa scalpelliformis* at Praia da Baleia (PB)

Located in the Baía da Ilha Grande (BIG), Angra dos Reis (23º01’63” S, 44º14’18”),this wave-protected site has shallow (<5 m) waters where rocky reefs intermingle withsandy patches. Introduced in 2001, the green alga *Caulerpa scalpelliformis* is considered anAS at this site (Falcão andSzéchy 2005; Lopes et al. 2009). The species is widely distributed in tropical and sub-tropical watersin the Red Sea, Indian and Pacific Oceans, Caribbean Sea and Atlantic Ocean (AtlanticIslands, Western Atlantic and South America from Venezuela south to Espírito SantoState, Brazil) (Vasconcelos et al. 2011). It is considered non-native in the Mediterranean Sea and in Brazil atthe studied location due to its disjoint distribution in a very well-studied region (Rio deJaneiro) (Vasconcelos et al. 2011) (Figure 6A, f.36). At this site it is able to grow both in the sand and on isolatedboulders. Although access to PB is restricted by a private condominium and a steep path,the beach often receives pleasure craft and commercial fishing boats due to its protectedlocation. Among the possible vectors of introduction and dispersal of this species areshipping (fouling anchors and fishing gear on boats which use the site for fishing andrecreational boating) and the aquarium trade (irregular disposal of aquarium species bycomercial traders or aquarists)(Vasconcelos et al. 2011).

2.1.2.1.2 *Sansibia* sp. at Praia Vermelha (PV)

Located in Angra dos Reis, in the inner part of the BIG (23º01’34”S, 44º30’05”W),this site has calm and shallow waters, with maximum depths of rocky reefs from 4–7 mwhere a sand plain starts. The main local activities are nautical tourism and fishing. In2017, two species of soft coral were detected on the rocky coast, *Clavularia* cf. *viridis* and*Sansibia* sp. Both species are of Indo-Pacific origin and have never been recorded in theAtlantic although Sansibia sp. is still little-known and has been described recently (Alderslade et al. 2000).

After being removed, *C. viridis* was eradicated at PV, however the control of *Sansibia* sp.,which has since expanded its range (Mantelatto et al. 2018; Carpinelli et al. 2020), is ongoing. As all the detected species areused by aquarium hobbyists, it is highly probably that the introduction was by disposal ofa domestic aquarium (Mantelatto et al. 2018) or an in situ coral farming strategy (Carpinelli et al. 2020) (Figure 6B, f.36).

2.1.2.1.3 *Tubastraeatagusensis*at Ilha Comprida (IC)

Located about 5 km off Rio de Janeiro (23º02’15”S,43º12’17”W), it is one of the five islands and two islets that make up the Cagarras Archipelago, a Marine Protect Area. TheIC study site is positioned in the interior of the archipelago sheltered from wave action. Themaximum reef depth is 40 m and it is impacted by eutrophication from Rio de Janeiro cityas well as receiving high levels of tourism (diving and boat trips) (Creed et al. 2020). The azooxantellatedcoral *Tubastraeatagusensis* is endemic and native to the Galapagos Archipelago where itis reported as abundant and forms an important component of the coral fauna. It wasintroduced into Brazil on oil platforms in the 1980s along with its congener *T. coccinea* [36].*Tubastraea tagusensis* has also been reported in India, Palau and the Persian Gulf, though thevalidity of those reports has been questioned (Creed et al. 2017). In the Cagarras Archipelago *T. tagusensis*was detected and manually removed in 2004 but in 2011 the species was again reported atthe site (Creed et al. 2017) (Figure 6C, f.36).

2.1.2.1.4 *Tubastraeacoccinea*and *T. tagusensis*at Ilha de Âncora (IA)

IA is an island located 8kmoffshore farther northwest at Armação dos Búzios (22º46’16”S,41º47’08”W). It is also a popular dive site in the region, with transparent, calm and shallowwaters (depth < 22 m). IA is subject to a seasonal upwelling of Central South AtlanticWater, characterized by higher nutrient supply (nitrate up to 18 µM) and low temperatures(down to 14ºC) (Coelho-Souza et al. 2012). In addition to *T. tagusensis*, IA has also been invaded by an AS ofthe same genus *T. coccinea*, which was first recorded there in 2011 (Santos et al. 2019). *Tubastraea coccinea*has a native range throughout the tropical and sub-tropical Indo-Pacific and has invadedsome Atlantic Islands, the Caribbean Sea, the Gulf of Mexico and the southwest Atlantic(Brazil) (Figure 6D, f.36)(Creed et al. 2017).

2.1.2.2 Sampling

We carried out quantitative surveys of the benthic communities in continuous extensionsof the benthos along 50 m of each rocky shore in 2017 (at PB and IA in July; at ICin September) and 2018 (at PV after the invasion was detected, in December). At eachsite, sampling was carried out in communities under the two different invasion states.Using SCUBA and the photo-quadrat method (digital photography at 300 dpi resolutionusing a NIKON COOLPIX AW130 and a fixed frame), twelve 0.25 m2 sample quadratswere obtained randomly in invaded and non-invaded areas. Since at PB the hard substrateconsisted of boulders within a sand matrix (discontinuous), we randomly chose fourboulders with the macroalgae C. scalpelliformis and four without sampling. Fieldwork wasconducted under research licenses INEA 005/2009 and 044/2018 and IBAMA No 02/2016(Proc. 02001.003231/2014-02).

2.1.2.3 Data Analysis

2.1.2.3.1 Species Abundance Analysis

Using photo-quadrats and additional digital photography, macroscopic species weresubsequently identified to the lowest possible taxonomic level. Species nomenclaturewas standardized to the World Register of Marine Species (WoRMS) database (http://www.marinespecies.org/, accessed on 2 April 2020). The photo-quadrats wereused to estimate the percentage of cover of each taxon of the sessile macrobenthos. Weused 100 random points generated by the CPCe software (Coral Point Count with Excelextension) (Kohler and Gill 2006) for each photo quadrat, thus generating a matrix of average relativeabundances of each taxon by location and invasion state. In order to investigate the differencesin species diversity caused by invasion state we plotted ranking-species abundances (= dominance and diversity curves), where the x-axis corresponds to the species ranked indecreasing abundance and the y-axis corresponds to the relative abundances of species ona logarithmic scale.

In order to better characterize and compare communities under different invasion states, five SAD models were applied: Broken Stick, Geometric Series, Lognormal, Zipfand Mandelbrot. For the adjustment and selection of the SAD models, we used the methodof maximum likelihood estimation selected through the Akaike Information Criterion(AIC) and ΔAIC≤2. AIC is a relative measure derived from the likelihood function thatcompares models and can be used in addition to visual inspection of the plotted data. TheAIC selects the model that best fits the data by measuring the distance from the real modelto the model analyzed, and the one with the lowest AIC value is considered the mostappropriate, and ΔAIC≤2 values establish that the model is plausible to be used (Burnham and Anderson 2004).

We tested the differences in communities between invasion states using the Permutational MANOVA (PERMANOVA) based on Bray–Curtis similarity measures of the squareroot of the percentage of cover of each taxon of the sessile macrobenthos + 1. Simpson’sdiversity index (1-λ), Margalef’s diversity index (d), Shannon’s (H’), Fisher and Equality of Pielou (J’) of each community were calculated. We also carried out this analysis on the data set from which the AS had been removed and other species standardized in the abundance matrix (the cover of AS was reassigned to the native species proportionally totheir abundance) termed “AS removed”. The SAD analyzes were performed in the programR v3.6.0 (R Core Team 2020), and we use the ‘vegan’ R-package (Oksanen et al. 2013). For PERMANOVAwe used the statistical program PERMANOVA+ add-on for Primer v6 (Clarke and Gorley 2006; Anderson et al. 2008).

2.1.2.3.2 Functional Diversity Analysis

A set of 14 relevant species traits (Zaiko et al. 2021) (Table S7) were identified and modalities for eachtrait category were defined through bibliographic survey and expert consultation (TableS7). The information for each trait was ordered as binary or continuous characteristics andcompiled for all species in the analyzed data sets. For mixed trait data, we used the "Cailliez"correction, which consists of adding the smallest possible constant to the distances to eliminate all negative eigenvalues (Cailliez1983; Lalibertéet al. 2014; Laliberté and Legendre 2010). To evaluate the impact of AS on functionalcharacteristics of the rocky shore communities, we estimated five multidimensional indices of functional diversity (FRic: Functional richness, FEve: Functional evenness, FDiv: Functional divergence, FDis: Functional dispersion and RaoQ: Rao's quadratic entropy).

To assess patterns in the communities under different invasion states, we estimatedthe effect sizes in each diversity index as the response ratios (RR) to control rocky shorecommunity differences:

$$RR = (I_{with}/I_{without}) \qquad (1)$$

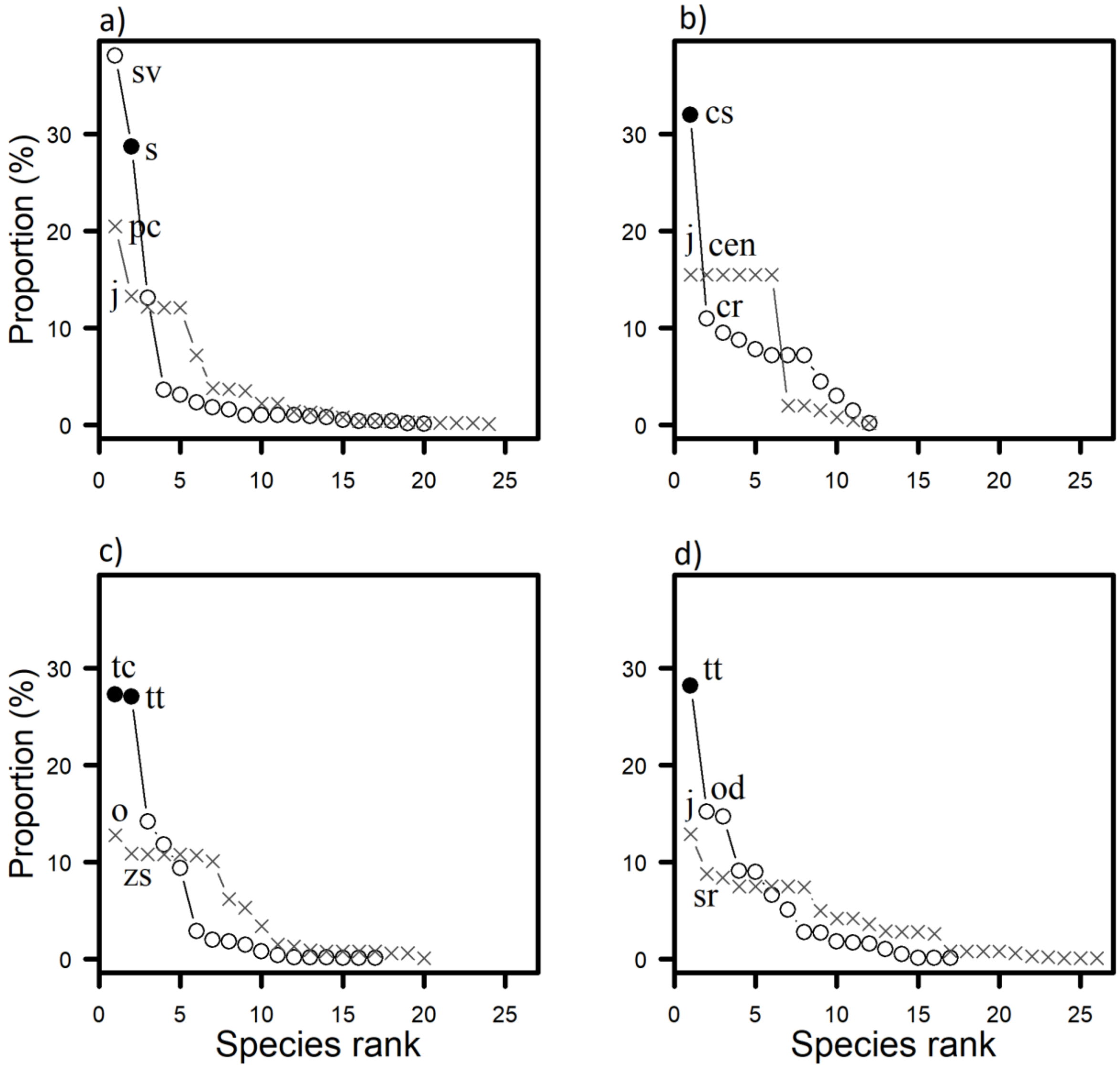
where "I" represents the taxonomic or functional diversity indices of rocky reef-invaded (numerator) or not-invaded (denominator) by the AS. The RR has a >1 or <1 value accordingto the relative increase or decrease, respectively, in the diversity index of the rocky shore invaded compared to the rocky shore-not-invaded. The RR is 1 when there is no difference.

In addition to comparing communities under different invasion states, we also performed the same analysis, but removed the invaders ("AS removed"), thus clarifying whether there are possible sources of variation caused only by the contribution of the AS.All functional diversity metrics were computed in the FD package (Lalibertéet al. 2014; Laliberté and Legendre 2010) of the R v 3.6.0program (R Core Team 2013).

2.1.3 Results

Over the four sites we found a total of 66 taxa of sessile macrobenthic species,23 of which were algae, 13 sponges, four bryozoans, 18 cnidarians, three ascidians,two echinoderms, two molluscs and one crustacean (Table S8). The taxon richness waslower in invaded communities, except for PB site (Figure 12). In three of the invaded communities,the AS was/were the most abundant taxon(s), with the exception of PV where theinvading soft coral *Sansibia* sp. was the second most abundant species in the communityafter the (native) alga *Sargassum vulgare* (Figure 12). Sessile macrobenthos assemblage coverwas significantly different between invasion states in each rocky shore sites (PERMANOVA:PV, df = 23; Pseudo-F = 13.016; p = 0.001; IA, df = 23; Pseudo-F = 12.626; p = 0.001; CI, df = 23; Pseudo-F = 11.271; p = 0.001; PB, df = 7; Pseudo-F = 2.932; p = 0.026).

Figure 12 – Species rank abundance plots for benthic taxons in four invaded communities represented by the symbol ○ andfour not-invaded communities represented by the symbol × on marine tropical rocky shores along the coast of the State ofRio de Janeiro, Brazil at (a) Praia Vermelha (PV), (b) Praia da Baleia (PB), (c) Ilha de Âncora (IA) and (d) Ilha Comprida(IC).

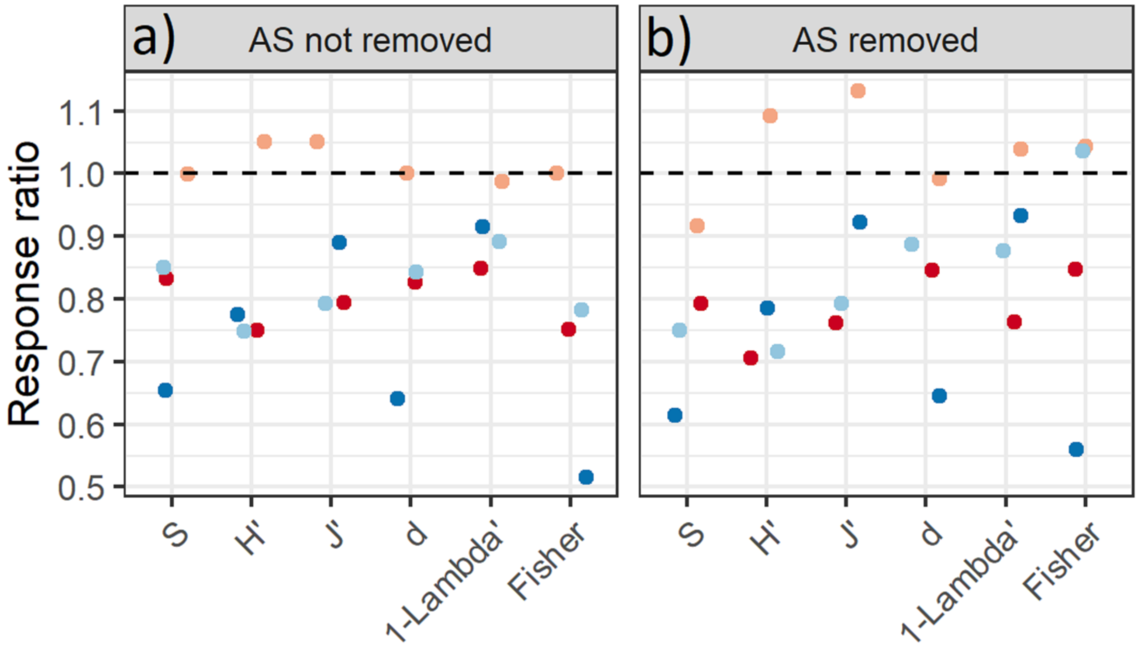


Legenda: AS are represented by the symbol ●. sv = *Sargassum vulgare*, s = *Sansibia* sp., pc = *Palythoacaribaeorum*, j = *Janiaadhaerens*, o = *Echinometralucunter*, cs = *Caulerpa scalpelliformis*, cen = *Centroceras* sp., c = *Caulerpa racemosa*, tt = *Tubastraeatagusensis*, tc = *Tubastraea coccinea*, zs = *Zoanthus sociatus*, od = *Obelia dichotoma*, sr = *Scopalinaruetzleri*. According to the diversity indices, not-invaded communities

Fonte: PIRES-TEIXEIRA ET AL. 2021.

According to the diversity indices, not-invaded communities had greater diversitythan invaded ones, except for the PB site that had similar values in both communities.Under the AS removed scenario, there was no change in the general pattern of the results ofthe taxonomic diversity over sites. PB once again stood out in this respect as the Simpson,Fisher and Shannon indices, which were not different between invasion states but werereduced under the AS removed scenario. According to these indices, the diversity wasgreater in the not-invaded communities and under the AS removed scenario it increasedfor the three other sites (Figure 13) (Table S9).

Figure13 – Response ratio between the taxonomy diversity indices (S, H ', J', d, 1-Lambda' and Fisher) of the invadedcommunities (numerator) and not-invaded communities (denominator) under two scenarios: (a)Alien species (AS) notremoved and (b) AS removed on marine tropical rocky shores along the coast of the State of Rio de Janeiro, Brazil at PraiaVermelha (red), Praia da Baleia (orange); Ilha de Âncora (light blue) and Ilha Comprida (dark blue).



Fonte: PIRES-TEIXEIRA et al., 2021.

Considering the smallest AIC and depending on the invasive state or NS removedscenario all five models were retained, although the Zipf model least so (Table 4). Thegeometric-series model was the most ubiquitously retained, best adjusting to allcommunities, regardless of the invasion state or NS removal scenario, with the exceptionof the invaded community at PB and under the NS removal scenario from the PVcommunity. The broken-stick model showed the best fit to invaded communities, evenunder the removal scenario, the exception being PV where the broken stick model wasnot retained for the invaded and NS removed communities (Table 4).

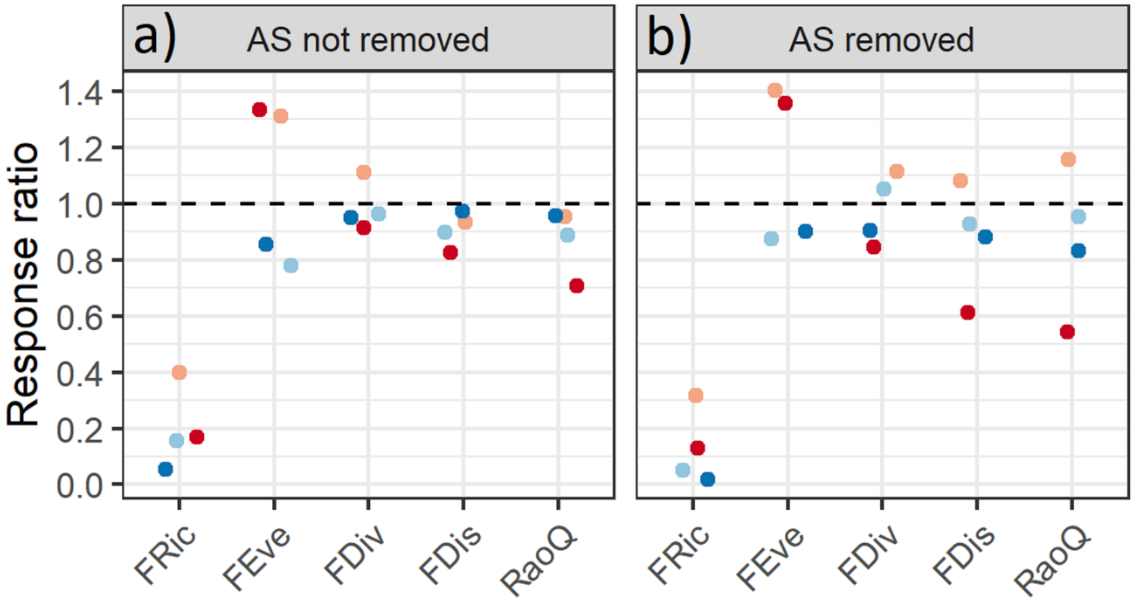
Table 4 - Models of rank abundance by site and situation with and without nonnative species (NIS) retained with better adjustments based on the lowest AIC criteria and ΔAIC ≤ 2.

Site	Not-Invaded	Invaded	AS Removed
PV	bs, gs	gs, m	z, m
PB	gs, ln, m	bs, ln, z	gs, ln
IA	gs, ln, m	bs, gs	bs, gs
IC	gs, ln	bs, gs	bs, gs

Legenda: Bs = Broken-stick; gs = Geometric Series; ln = Log-normal; z = Zipf e m = —Madelbrot.
Fonte: Pires-Teixeira et al. 2021

Regarding the traits, the scores used for each trait modality in this study are presented in Table S4. The values of the functional dispersion (FDis), functional divergence (FDiv)and Rao quadratic entropy (RaoQ) index were lower in the invaded communities. Therange of FDis and RaoQ was between > 0.7 and <1.0, which represented a reduction of3% to 29% in these indices in the invaded communities compared to the not-invadedcommunities. However, when considering AS removed, the results of these indices werenot as consistent and indicated an increase of up to 20% in FDis and RaoQ in the invadedcommunity compared to the not-invaded community of the PB site. Functional richness(FRic) was ≤ 0.4 in invaded communities and AS removed, which means a ≥ 60% reductionin FRic in the invaded community compared to not-invaded communities. In AS removedat PB, the indices that quantify the functional dispersion (FDis and RaoQ) increased andshowed higher values than in not-invaded communities. The FRic index was lower ininvaded communities and it was also the functional diversity index that best reflectedthe difference in the functional attributes in the invasion state. FDiv results also variedbetween sites, showing an increase or decrease of approximately 10%. The not-invadedcommunity at PB had higher FDiv, FDis and FEve indexes than the invaded community,and the NS removed scenario resulted in an increase in the RaoQ index. The same variationin FEve index was observed in PV, higher even than in the invaded community, showingan increase of approximately 30% when AS were removed. In IA and IC sites, FEve indexshowed a reduction of up to 20% in the invaded community compared to the non-invadedone (Figure 14).

Figure 14 – Response ratio between the functional diversity indices (FRic, FEve, FDiv, FDis and RaoQ) of the invadedcommunities (numerator) and not-invaded communities (denominator) in two scenarios: (a) Alien species (AS) not removedand (b) AS removed on marine tropical rocky shores along the coast of the State of Rio de Janeiro, Brazil at Praia Vermelha(red), Praia da Baleia (orange); Ilha de Âncora (light blue) and Ilha Comprida (dark blue).



Fonte: Pires-Teixeira et al. 2021

2.1.4 Discussion

Our study provides evidence of the impact of different alien species (AS), not onlyin structure but also in function, in different invaded tropical rocky shore communitiesin the southwest Atlantic. Although more is known about effects on community speciesabundance and diversity, functional diversity analysis is not commonly applied.

We tested different parameters to measure the effect of an AS on invaded communities,and although the rank-abundance plots make it possible to observe the greater abundanceof AS in relation to the other species in the invaded communities and the greater equitabilityin not-invaded communities, we consider that point-paired species abundance distribution(SAD) models are not the most sensitive tool for detecting the effects of AS. The geometricseries model had the best fit for most communities regardless of the presence or absenceof a AS or in AS removed treatments. Geometric series reflect a relationship between theabundance of a species and its constant predecessor, therefore, its plot representation in therank-abundance is a steep line, which implies an assembly with high dominance (Magurran 1988, 2007).The broken-stick model was better adjusted to invaded communities. The exception wasPV, recently invaded (2017) by the soft coral *Sansibia* sp. The uniform abundance predictedby the broken-stick model does not seem to match the values of the diversity indexes withinvaded communities. Still, the curves fitted to the broken-stick and log-normal modelsare less steep and represent relatively high uniformity in the community (Fattorini 2005; McGill et al. 2007).

In three of the invaded communities studied here, AS were the most abundant species.Different studies have demonstrated that an increase in the abundance of NS after invasionevents in aquatic environments is usual and that there is consequent dominance in theinvaded areas (Meineszet al. 2001; Piazzi et al. 2001; Branch andSteffani2004; Zabin and Altieri 2007). Invasive corals *T. coccinea* and *T. tagusensis* have been known toincrease their distribution in Brazilian waters since their introduction in the late 1980s (Creed et al. 2020).The abundance of *Tubastraea* spp. increased by up to 76% in just one year in the Baía da IlhaGrande (BIG) (Lages et al. 2011). Similarly, there was a change in the rocky and sandy substrates at Praiada Baleia (PB) after the introduction of *C. scalpelliformis*, which became dominant over thealga *S. vulgare*(Falcão and Széchy2005). Our results show that after 17 years the invasive algae *C. scalpelliformis*remains the most abundant species in the invaded area.

At Praia Vermelha (PV), the invasive soft coral *Sansibia* sp. was the second-mostabundant species, second only to the alga *S. vulgare*. Among all the invaded communitiesanalyzed in the present study, PV represents the most recent invasion (2017) and theinvasive soft coral still seems to be increasing in abundance over the years. *Sansibia* sp.was the third-most abundant species in PV in 2017 (Mantelatto et al. 2018), but was second in our study; thischange in local diversity suggests that the invading soft coral Sansibia sp. may also becomethe most abundant species at PV in the future.

As expected, the diversity indexes used in the present study showed that diversity washigher in not-invaded communities than in invaded communities, and the same patternwas repeated in AS removed treatments. Our results suggest that the impact of AS variesin proportion to the species that already exist in the community and that AS effects theinvaded community not only by representing one more species in the community, but byconsiderably impacting evenness (the relative abundance of the other species). However,at PB, Shannon's diversity index (H’) and Pielou’s Equability indice (J’) were higher in theinvaded community while the other indices showed similar values in invaded and notinvadedcommunities. Under AS removed, Fisher, H ’and J’ indices had the highest valuescompared to other situations. As well as the fact that invasive algae *C. scalpelliformis* is byfar the most abundant species in the community, this is thought to be because there werefewest native species at this site, so the richness aspect of diversity was more important(increased due to the presence of the invader). This was the exception to the rule as atPV, Ilha de Âncora (IA) and Ilha Comprida (IC), H’ was between 20% and 30% lower ininvaded communities. Fisher’s diversity was between 20% and 50% lower in invadedcommunities.

1-Lambda and H’ provide complementary information on community diversity, whilethe first emphasizes the uniformity component, the second is influenced by functionalrichness (FRic) (Nagendra 2002; Magurran 2003). According to the hypothesis of biotic resistance, the higher biodiversityof an ecosystem can make it more resistant to invasion (Elton, 1958; Kennedy et al. 2002; Stachowiczet al. 2002; Fridley et al. 2007;Kimbro et al. 2013). The reduceddiversity found at three of the four (native species richer) sites is not inconsistent with thehypothesis of biotic resistance, in that successful invasions would explicitly imply strongercompetitive interactions between AS and natives. The Empty Niche Hypotheses wouldbe consistent with the invasion of the algae *C. scalpelliformis* at PB, especially seeing asthis alga was sufficiently plastic with regard to substratum use such that it was observedto grow in nearby (unvegetated) sediment as well as on the rocky substrate we studied,so clearly it could occupy an empty niche space. The rocky shore nearby the rock–sandinterface typically has higher sediment cover, which may be a niche little exploited by thenative benthos.

Functional diversity analysis is a tool that considers that all species are not equivalent,and perform different functions in the ecosystem (Villéger et al. 2008; Guilhaumonet al. 2015). This type of analysis has notcommonlybeen applied to invaded marine environments and the amount of effort dedicatedto studies to understand and predict marine invasions is not consistent when compared tostudies carried out on terrestrial systems (Arenas et al. 2006; Chan and Briski2017). Functional wealth (FRic) was lower ininvaded communities and in NS removed communities. It is possible that the NS in thepresent study have redundant functional attributes, since FRic measures the portion of thefunctional space filled by the species with the most extreme characteristic values (Toussaint et al. 2018). Thefunctional evenness index (FEve) was higher in the invaded communities at PV and PB,and this shows how regularly the abundances of species are distributed in the functionalspace, suggesting a more regular distribution of the attributes in the invaded communities(Mouchetet al. 2010). This is consistent with the observations above regarding degrees of competitionin more recently invaded (PV) and lower richness/empty niche (PB) communities. Theintroduction of the green algae *C. salpeliformis* incorporates attributes similar to those of themost abundant species in the community, since in the NS removed treatment, the values ofthe functional dispersion index increased, suggesting that before removal, the species werecloser to the centroid defined by all traces of species in the community, with lower valuesof FDis and RaoQ compared to not-invaded communities.

Our results provide evidence that species identity is more important than speciesrichness in determining the number and biomass of NS, similar to the results found inother studies for terrestrial plants (Crawley et al. 1999). Invasions by non-native macroalgae are likely tocause biotic homogenization and have an overall negative effect on their competitors, spatiallymonopolizing the habitat and resulting in the reduction of abundance and biomassof native macroalgae (Olden et al. 2006; Schaffelke and Hewitt 2007; Thomsen et al. 2011). The few studies that explore the relationship betweenfunctional diversity and invasion in seaweed communities have focused on the availabilityof resources and the success of invasion (Crawley et al. 1999; Britton-Simmons 2006; Vaz-Pinto et al. 2012). Functional traits in macroalgae communitiescan also influence the availability of resources (i.e., light and substrate) and haveinhibitory effects on new colonizers (Crawley et al. 1999). The availability of resources can vary accordingto functional diversity, as when functional diversity is high the availability of resources(i.e., photosynthetically active radiation) is low (Vaz-Pinto et al. 2012). However, functional diversity indicesbetween communities invaded and not-invaded by *Carpobrotus* spp. showed similar resultsto the present study (Castro-Díezet al. 2016), suggesting that the low functional diversity in the invadedcommunities reveals a functional homogenization within the community.

We consider the taxonomic diversity and functional diversity indices to be usefultools for identifying processes that determine the biological diversity of invaded communities,as they seem to obey a pattern that reflects the greatest diversity in communitiesnot-invaded by IS. Additional information on the impacts of IS on ecosystems is crucialfor formulating conservation goals for specific species or habitats, and a thorough understandingof their role in the functioning of the ecosystem and the consequent provision ofecosystem services is needed in order to better define strategies for control and eradicationof an invaded area (Giakoumi et al. 2016; Macic et al. 2018). We studied consolidated or consolidating invasions, but anotheraspect of using these methods that would be enlightening and informative would be toinvestigate the temporal element of changes that occur in communities during a boom–bust invasion cycle typical of some species (Strayer et al. 2017). Thus, we recommend further studiesthat consider not only taxonomic diversity, but also the differences in the roles played byspecies and their contributions to the relationships of diversity and functioning of invadedmarine ecosystems.

2.1.5 Acknowledgments

This work was supported by Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (JCC, FAPERJ E-26/010.003031/2014 and E26/203.002/2017)and Conselho Nacional de Desenvolvimento Científico e Tecnológico (JCC, CNPq- 305924/2018-4) and received support for fieldwork logistics and equipment from the Brazilian Institute for Biodiversity (BrBio) as part of the Coral-sol Project funded through the Commitment to Conduct Adjustment Agreement signed by Chevron Brazil with the Brazilian Federal Prosecution Service (MinistérioPúblico Federal), with implementation by the Brazilian Biodiversity Fund (FUNBIO).LMPT acknowledges Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) that provided a PhD scholarship. VNL acknowledges a Teaching Support Scholarship (PAPD-UERJ/2019).We thank Amanda Guilherme, Augusto Machado, Bruno Masi, Herick Simas, Edson Faria, Katia Capel, Marcello Mantellato, Vanessa Bettcher and Vinícius Kerr for their support in the field. Thanks to Anastasija Zaiko and the Global Hotspots for Marine Bioinvasions group members for providingand allowing us to use the traits list. This article is no. 48 from the Projeto Coral-Sol.

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2.1.7 Supplementary Materials

Table S7 -Trait categories of species and their modalities considered in this study (to be continued).

Traits	Score code	Modalities
Size*	1	11-100 mm
	2	>100 mm
Life form**	1	zoobenthos - animals living on or in the seabed.
	2	phytobenthos - algae and higher plants living on or in the seabed.
Sociability	1	solitary - living alone, not gregarious
	2	gregarious - Living in groups or communities, growing in clusters in close association with conspecifics (i.e. more likely to occur in dense aggregations than as scattered individuals)
	3	colonial - Organisms produced asexually which remain associated with each other; in many animals, retaining tissue contact with other polyps or zooids as a result of incomplete budding
Trophic position	1	autotroph - an organism obtains metabolic energy from light by a photochemical process such as photosynthesis.
	2	mixotroph - an organism both autotrophic and heterotrophic.
	3	suspension feeder - an organism feeds on particulate organic matter from the water column.

Table S7 - Trait categories of species and their modalities considered in this study (to be conclusion).

	4	deposit feeder - an organism feeds on fragmented particulate organic matter from the substratum.
	5	omnivore - an organism feeds on a mixed diet including plant and animal material.
	6	herbivore - an organism feeds types of plant material.
	7	predator - a predator that feeds a type of animal prey.
Mobility (adult stage)	1	sessile encrusting - attached to substrate, cover with a crust or thin coating.
	2	sessile turfing - low growing erect or filiform organisms.
	3	sessile bed/reef-builder - forms consolidated biogenic habitat on the seabed or shore.
	4	sessile erect - upright in position or posture.
	5	crawler - an organism that moves slowly along the substrate.
Habitat forming	1	canopy - providing floating substrate by their living and dead tissues
	2	matrix-forming - provide seafloor substrate by their living and dead tissues
	3	substrate-modifying - modify physical/chemical properties of the habitat
Exterior surface/Fragility	1	hard/robust
	2	fragile/brittle
	3	rigid
	4	soft
Longevity	1	2 month - <year
	2	1-2 years
	3	>2 years
Tolerancetoeutrophication	1	low
	2	medium
	3	high
	4	unknown
Tolerancetochemicalpollution	1	low
	2	medium
	3	high
Salinitytolerance	1	marine - >5 PSU
	2	eurihaline - tolerates wide range of salinities
Temperature tolerance	1	euthermic
	2	eurithermic
Light (irradiation) requirement	1	low
	2	high
Hypoxiatolerance	1	low
	2	medium
	3	high

Note: * For colonial animals we consider the size of the colony.**Adult stage.
Source: PIRES-TEIXEIRA ET AL. 2020, adapted from ZAIKO ET AL. 2021.

Table S8 - Major space-occupying taxa/functional groups, their percentage cover (%) in invaded and not invaded communities in marine rocky shores along the coast of the state of Rio de Janeiro, Brazil (to be continued).

Taxon/ functionalgroup	code	Local (%)							
		Invaded				Notinvaded			
		PV	PB	IC	IA	PV	PB	IC	IA
ALGAE									
Articulatedcalcareousalgae	aca	0.417	0.000	9.083	0.000	2.167	0.000	7.500	3.417
Crustosecorallinealgae	aci	0.250	0.000	0.083	2.917	3.500	0.500	8.417	10.083
Janiaadhaerens J.V.Lamouroux	j	2.333	7.250	0.000	0.000	13.333	15.500	12.917	0.000
Hypnea J.V.Lamouroux	hy	1.000	7.250	0.000	11.833	12.083	0.000	0.000	10.750
Polysiphonia Greville	pol	0.000	0.000	0.000	0.000	0.000	0.000	7.417	0.000
Centroceras Kützing	cen	0.417	0.000	2.750	0.000	7.250	15.500	2.917	0.000
Melanothamnusferulaceus (SuhrexJ.Agardh) Díaz-Tapia&Maggs	nf	1.750	0.000	0.000	0.000	3.667	0.000	0.000	0.000
Dichotomariamarginata (J.Ellis&Solander) Lamarck	dm	13.083	0.000	0.000	0.000	1.333	0.000	0.000	0.000
Pterocladiellacapillacea (S.G.Gmelin) Santelices&Hommersand	ptc	0.000	0.000	9.000	0.000	0.000	0.000	7.500	0.000
Gelidium J.V. Lamouroux	a1f	1.000	0.000	0.000	0.000	12.083	0.000	0.000	0.000
Caulerpa scalpelliformis (R.Brown ex Turner) C.Agardh	cs	0.000	32.000	0.000	0.000	0.000	0.000	0.000	0.000
Caulerpa racemosa (Forsskål) J.Agardh	cr	0.000	11.000	0.000	0.000	0.000	0.000	0.000	0.000
Bryopsis J.V.Lamouroux	bry	0.000	0.000	0.000	0.000	0.000	0.000	7.500	0.000
Acetabularia J.V.Lamouroux	ace	1.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Chlorophyta NI	avd	1.000	0.000	0.000	0.000	0.000	15.500	0.000	0.000
Sargassum (Sargassum)*vulgare* C. Agardh	sv	38.083	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Colpomenia sinuosa (Mertensex Roth) Derbès&Solier	cos	0.000	0.000	0.000	0.000	0.000	0.000	0.083	6.167
Padinagymnospora (Kützing) Sonder	pg	0.417	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Dictyota J.V.Lamouroux	d	3.083	7.750	0.000	0.000	12.250	2.000	0.000	0.000
Dictyopterisdelicatula J.V.Lamouroux	dp	0.000	8.750	0.000	0.000	0.000	0.000	0.000	0.000
Dictyotamenstrualis (Hoyt) Schnetter, Hörning& Weber-Peukert	dg	0.000	0.000	0.000	0.000	0.000	0.000	0.000	10.750

Table S8 - Major space-occupying taxa/functional groups, their percentage cover (%) in invaded and not invaded communities in marine rocky shores along the coast of the state of Rio de Janeiro, Brazil (to be continued).

Dictyotafriabilis Setchell	dfluo	0.000	0.000	0.000	0.000	0.000	15.500	0.000	0.000
Ochrophyta NI	apf	0.000	0.000	0.000	14.167	0.000	0.000	0.000	10.750
SPONGIAE									
Iotrochotabirotulata (Higgin, 1877)	iob	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Iotrochota arenosa Rützler, Maldonado, Piantoni&Riesgo, 2007	ia	0.000	0.000	0.000	0.000	0.750	0.000	0.833	0.000
Desmapsammaanchorata (Carter, 1882)	da	0.917	9.500	0.000	0.000	3.833	2.000	0.000	0.000
Tedania(Tedania) *ignis* (Duchassaing&Michelotti, 1864)	ti	0.000	0.000	0.000	0.000	0.333	0.000	0.000	0.000
Mycale(Aegogropila) *americana* van Soest, 1984	ma	0.500	0.000	0.000	0.000	1.417	0.000	0.000	0.000
Mycale (Arenochalina)*laxissima* (Duchassaing&Michelotti, 1864)	man	0.000	1.500	0.000	0.000	0.000	0.750	0.000	0.000
Scopalinaruetzleri(Wiedenmayer, 1977)	sr	0.000	0.250	5.083	0.417	0.417	0.000	8.750	1.333
*Dysideaetheria*Laubenfels, 1936	de	0.000	0.000	0.083	1.500	0.000	0.000	0.167	0.833
Arenosclera brasiliensis Muricy & Ribeiro, 1999	eb	0.000	0.000	0.000	0.167	0.000	0.000	0.000	0.000
Amphimedonviridis Duchassaing&Michelotti, 1864	av	3.583	0.000	0.000	0.000	0.250	0.000	0.000	0.000
Aplysina fulva (Pallas, 1766)	af	0.000	0.000	0.000	0.000	0.167	0.000	0.000	1.500
Chondrillanucula Schmidt, 1862	cn	0.000	0.000	1.583	0.000	0.000	0.000	2.750	0.833
Paraleucilla magna Klautau, Monteiro &Borojevic, 2004	pm	0.000	0.000	1.000	0.000	0.000	0.000	2.583	0.000
BRYOZOA									
Schizoporella errata (Waters, 1878)	se	0.000	0.000	1.833	0.000	1.250	0.000	5.000	0.000
Bugulaneritina (Linnaeus, 1758)	bun	0.750	0.000	0.000	0.000	0.417	15.500	0.083	0.000
Caberea glabra MacGillivray, 1886	cg	0.000	0.000	0.000	0.000	0.000	0.000	7.500	0.000
Amathiaverticillata (delleChiaje, 1822)	zv	0.000	7.250	0.000	0.000	0.000	0.000	0.000	0.000
CNIDARIA									
Macrorhynchiaphilippina Kirchenpauer, 1872	mp	0.000	3.000	0.000	0.250	0.000	0.250	0.000	0.000
Obeliadichotoma (Linnaeus, 1758)	od	0.000	0.000	15.167	9.417	0.000	0.000	3.583	0.000
Pennariadisticha Goldfuss, 1820	hp	0.000	0.000	0.000	0.000	0.000	15.500	0.000	10.667
Milleporaalcicornis Linnaeus, 1758	mia	0.000	0.000	0.000	0.833	0.000	0.000	0.000	5.333

Table S8 - Major space-occupying taxa/functional groups, their percentage cover (%) in invaded and not invaded communities in marine rocky shores along the coast of the state of Rio de Janeiro, Brazil (conclusion).

Palythoacaribaeorum Duchassaing&Michelotti, 1860	pc	1.583	4.500	1.667	0.000	20.500	0.000	0.000	0.000
Parazoanthusswiftii (Duchassaing de Fonbressin&Michelotti, 1860)	pz	0.000	0.000	0.000	0.000	0.000	0.000	0.750	0.000
Zoanthussociatus (Ellis, 1768)	zs	0.000	0.000	0.000	0.000	2.167	0.000	0.000	10.917
Carijoariisei (Duchassaing&Michelotti, 1860)	cari	0.000	0.000	0.000	0.000	0.000	0.000	0.583	0.000
Leptogorgiapunicea (Milne Edwards &Haime, 1857)	lp	0.000	0.000	0.000	1.750	0.000	0.000	0.000	0.583
Sansibia Alderslade, 2000	s	28.750	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Siderastreastellata Verrill, 1868	ss	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.917
*Poritesbranneri*Rathbun, 1888	pb	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.583
Madracisdecactis (Lyman, 1859)	md	0.000	0.000	0.000	0.083	0.000	0.000	0.000	0.833
Mussismilia hispida (Verrill, 1902)	mh	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.833
Tubastraea tagusensis Wells, 1982	tc	0.000	0.000	28.167	27.333	0.000	0.000	0.000	0.000
Tubastraeacoccinea Lesson, 1829	tt	0.000	0.000	0.000	27.083	0.000	0.000	0.000	0.000
Bunodosomacaissarum Corrêa in Belém, 1987	bc	0.000	0.000	0.500	0.000	0.000	0.000	0.750	0.000
*Anthopleura Duchassaing*de Fonbressin&Michelotti, 1860	an	0.000	0.000	0.000	0.000	0.000	0.000	0.083	0.000
CHORDATA									
Didemnumperlucidum Monniot F., 1983	dp	0.000	0.000	14.667	0.167	0.167	0.000	4.250	0.000
Diplosomalisterianum (Milne Edwards, 1841)	dl	0.000	0.000	6.583	0.000	0.000	0.000	2.750	0.000
Botrylloidesniger Herdman, 1886	bn	0.000	0.000	0.083	0.000	0.000	0.000	0.333	0.000
ECHINODERMATA									
Echinaster(Othilia) *brasiliensis* Müller &Troschel, 1842	e	0.000	0.000	0.000	0.000	0.417	0.000	0.000	0.000
Echinometralucunter (Linnaeus, 1758)	o	0.000	0.000	0.000	2.000	0.000	0.000	4.167	12.833
MOLLUSCA									
Mollusk	m	0.083	0.000	0.000	0.000	0.167	1.500	0.000	0.000
bivalve mollusk	mb	0.000	0.000	0.000	0.000	0.083	0.000	0.000	0.000
ARTHROPODA									
Barnacle	c	0.000	0.000	2.667	0.083	0.000	0.000	0.833	0.083

Fonte: PIRES-TEIXEIRA et al, 2020.

Table S9 - Values of the taxonomic diversity index and functional diversity index (to be continued).

Site	NS removed	index type	index	notinvaded	invaded	resp.ratio
PV	no	FDis	Funcional	0.314	0.259	0.826
PB	no	FDis	Funcional	0.303	0.284	0.934
IA	no	FDis	Funcional	0.374	0.336	0.898
IC	no	FDis	Funcional	0.363	0.353	0.972
PV	no	FDiv	Funcional	0.940	0.860	0.915
PB	no	FDiv	Funcional	0.856	0.952	1.112
IA	no	FDiv	Funcional	0.932	0.897	0.962
IC	no	FDiv	Funcional	0.943	0.897	0.951
PV	no	FEve	Funcional	0.494	0.659	1.333
PB	no	FEve	Funcional	0.452	0.592	1.310
IA	no	FEve	Funcional	0.596	0.464	0.779
IC	no	FEve	Funcional	0.570	0.487	0.854
PV	no	FRic	Funcional	0.013	0.002	0.169
PB	no	FRic	Funcional	0.000	0.000	0.398
IA	no	FRic	Funcional	0.011	0.002	0.157
IC	no	FRic	Funcional	0.028	0.002	0.055
PV	no	RaoQ	Funcional	0.108	0.076	0.708
PB	no	RaoQ	Funcional	0.098	0.093	0.952
IA	no	RaoQ	Funcional	0.143	0.127	0.887
IC	no	RaoQ	Funcional	0.135	0.129	0.957
PV	no	1-Lambda'	Taxon	0.894	0.759	0.849
PB	no	1-Lambda'	Taxon	0.863	0.852	0.987
IA	no	1-Lambda'	Taxon	0.916	0.816	0.891
IC	no	1-Lambda'	Taxon	0.939	0.859	0.915
PV	no	d	Taxon	4.994	4.126	0.826
PB	no	d	Taxon	2.389	2.389	1.000
IA	no	d	Taxon	4.126	3.474	0.842
IC	no	d	Taxon	5.429	3.474	0.640
PV	no	Fisher	Taxon	10.014	7.518	0.751
PB	no	Fisher	Taxon	3.561	3.561	1.000
IA	no	Fisher	Taxon	7.518	5.881	0.782
IC	no	Fisher	Taxon	11.410	5.881	0.515
PV	no	H'	Taxon	2.431	1.823	0.750
PB	no	H'	Taxon	2.031	2.136	1.051
IA	no	H'	Taxon	2.527	1.892	0.749
IC	no	H'	Taxon	2.817	2.183	0.775
PV	no	J'	Taxon	0.765	0.608	0.795
PB	no	J'	Taxon	0.818	0.860	1.051
IA	no	J'	Taxon	0.844	0.668	0.792
IC	no	J'	Taxon	0.865	0.770	0.891
PV	no	S	Taxon	24.000	20.000	0.833
PB	no	S	Taxon	12.000	12.000	1.000

Table S9 - Values of the taxonomic diversity index and functional diversity index (continuation).

IA	no	S	Taxon	20.000	17.000	0.850
IC	no	S	Taxon	26.000	17.000	0.654
PV	yes	FDis	Funcional	0.314	0.192	0.612
PB	yes	FDis	Funcional	0.303	0.328	1.081
IA	yes	FDis	Funcional	0.374	0.346	0.927
IC	yes	FDis	Funcional	0.363	0.320	0.881
PV	yes	FDiv	Funcional	0.949	0.803	0.846
PB	yes	FDiv	Funcional	0.842	0.938	1.113
IA	yes	FDiv	Funcional	0.938	0.986	1.052
IC	yes	FDiv	Funcional	0.939	0.849	0.904
PV	yes	FEve	Funcional	0.494	0.670	1.356
PB	yes	FEve	Funcional	0.452	0.634	1.403
IA	yes	FEve	Funcional	0.597	0.523	0.876
IC	yes	FEve	Funcional	0.570	0.513	0.900
PV	yes	FRic	Funcional	0.019	0.002	0.129
PB	yes	FRic	Funcional	0.000	0.000	0.316
IA	yes	FRic	Funcional	0.013	0.001	0.052
IC	yes	FRic	Funcional	0.030	0.000	0.017
PV	yes	RaoQ	Funcional	0.108	0.058	0.542
PB	yes	RaoQ	Funcional	0.098	0.114	1.158
IA	yes	RaoQ	Funcional	0.143	0.136	0.952
IC	yes	RaoQ	Funcional	0.135	0.112	0.833
PV	yes	S	Taxon	24.000	19.000	0.792
PB	yes	S	Taxon	12.000	11.000	0.917
IA	yes	S	Taxon	20.000	15.000	0.750
IC	yes	S	Taxon	26.000	16.000	0.615
PV	yes	d	Taxon	4.994	4.219	0.845
PB	yes	d	Taxon	2.389	2.370	0.992
IA	yes	d	Taxon	4.126	3.664	0.888
IC	yes	d	Taxon	5.429	3.509	0.646
PV	yes	J'	Taxon	0.765	0.583	0.762
PB	yes	J'	Taxon	0.818	0.925	1.132
IA	yes	J'	Taxon	0.844	0.668	0.792
IC	yes	J'	Taxon	0.865	0.797	0.922
PV	yes	Fisher	Taxon	10.014	8.478	0.847
PB	yes	Fisher	Taxon	3.561	3.716	1.044
IA	yes	Fisher	Taxon	7.518	7.786	1.036
IC	yes	Fisher	Taxon	11.410	6.386	0.560
PV	yes	H'	Taxon	2.431	1.716	0.706
PB	yes	H'	Taxon	2.031	2.219	1.092
IA	yes	H'	Taxon	2.527	1.808	0.716
IC	yes	H'	Taxon	2.817	2.211	0.785
PV	yes	1-Lambda'	Taxon	0.894	0.682	0.763
PB	yes	1-Lambda'	Taxon	0.863	0.897	1.039

Table S9 - Values of the taxonomic diversity index and functional diversity index (conclusion).

IA	yes	1-Lambda'	Taxon	0.916	0.803	0.876
IC	yes	1-Lambda'	Taxon	0.939	0.876	0.933

Table S10 - Scores adopted for each trait modality in this study (to be continued).

Taxon/ functionalgroupcode	Traitsmodalities										
	Size	Life form	Sociability	Trophic position	Mobility (adultstage)	Habitat forming	Exterior surface/ Fragility	Longevity	Tolerancetoeutrophication	Tolerancetochemicalpollution	Salinitytolerance	T
aca	1	2	2	1	4	1	1	2	2	1	1	1
aci	2	2	2	1	3	3	1	3	2	1	1	2
pol	1	2	2	1	2	3	4	1	3	3	2	2
hy	1	2	2	1	2	3	4	1	3	3	2	1
j	1	2	2	1	4	1	1	1	2	3	1	1
cen	1	2	2	1	2	1	4	1	3	3	1	1
dm	2	2	1	1	4	3	1	2	3	1	1	1
nf	1	2	2	1	2	1	4	1	3	1	1	1
ptc	1	2	2	1	2	1	4	1	1	1	1	1
a1f	1	2	2	1	2	1	4	2	3	2	1	1
cs	2	2	1	1	3	3	4	2	3	3	1	1
ace	1	2	1	1	3	1	2	1	3	3	1	1
cr	2	2	1	1	3	3	4	2	3	3	1	1
bry	1	2	2	1	3	3	4	1	3	2	1	2
avd	1	2	2	1	2	1	4	1	3	2	2	1
sv	2	2	2	1	4	3	1	2	2	3	1	1
cos	1	2	1	1	4	1	1	1	3	3	1	2
pg	2	2	1	1	4	3	1	1	2	3	1	1
d	1	2	2	1	2	3	1	1	3	3	1	2
dp	1	2	2	1	2	3	4	1	2	2	1	1
dg	1	2	2	1	2	3	1	1	2	3	1	2

Table S10 - Scores adopted for each trait modality in this study (continuation).

dfluo	1	2	2	1	2	3	1	1	2	2	1	2	2	1
apf	1	2	2	1	2	3	4	1	4	2	1	1	2	2
iob	2	1	1	3	4	1	4	2	2	2	2	1	1	1
ia	2	1	1	3	1	1	4	2	3	3	2	1	1	1
sr	2	1	1	3	1	1	4	2	2	3	2	1	1	2
da	2	1	1	3	4	1	4	2	3	3	2	1	1	1
ti	2	1	1	3	4	1	4	2	1	3	2	1	1	1
de	2	1	1	3	1	1	4	2	3	3	2	1	1	1
ma	2	1	1	3	1	1	4	2	4	2	2	1	1	1
man	2	1	1	3	1	1	4	2	3	2	2	1	1	1
av	2	1	1	3	1	1	4	2	1	3	2	1	1	1
af	2	1	1	3	4	1	4	2	1	3	2	1	1	1
pm	2	1	1	3	1	1	4	2	3	3	2	2	1	1
cn	2	1	1	3	1	1	4	2	1	3	2	2	1	1
eb	2	1	1	3	1	1	4	2	4	3	1	1	1	1
se	2	1	3	3	1	1	1	2	2	3	2	2	1	2
bun	1	1	3	3	4	1	2	1	3	3	2	2	1	2
cg	1	1	3	3	4	1	3	1	4	3	1	2	1	2
zv	1	1	3	3	2	1	4	1	3	3	2	2	1	2
mp	1	1	3	3	4	1	3	1	4	2	2	1	1	1
hp	1	1	3	3	4	1	3	1	2	2	2	2	1	1
od	1	1	3	3	4	1	3	1	3	3	2	2	1	1
mia	2	1	3	3	4	3	1	3	1	1	1	1	2	1
pc	2	1	3	3	3	3	1	3	2	2	1	1	2	1
pz	2	1	3	3	4	1	4	2	1	2	1	1	2	1
zs	2	1	3	3	6	1	4	2	1	2	1	1	2	1
cari	2	1	3	3	6	1	3	3	2	2	1	1	1	1
ss	2	1	3	3	6	3	1	3	2	2	1	1	2	1

Table S10 - Scores adopted for each trait modality in this study (conclusion).

pb	2	1	3	3	6	3	1	3	1	1	1	1	2	1
md	2	1	3	3	6	3	1	3	1	1	1	1	2	1
mh	2	1	3	3	6	3	1	3	2	1	1	1	2	1
tc	2	1	3	3	6	3	1	3	2	1	1	1	1	2
tt	2	1	3	3	6	3	1	3	2	1	1	1	1	2
s	2	1	3	3	1	3	4	2	2	1	1	1	2	1
lp	2	1	3	3	4	3	3	3	1	1	1	1	1	1
bc	1	1	1	3	4	1	4	2	2	3	1	1	1	2
an	2	1	1	3	4	1	4	3	3	2	1	2	1	1
dp	1	1	3	3	1	1	4	2	3	3	2	2	1	2
bn	1	1	3	3	1	1	4	2	3	3	2	2	1	1
dl	1	1	3	3	1	1	4	2	3	3	2	2	1	1
e	2	1	1	3	5	2	1	3	2	1	2	1	1	1
o	2	1	2	2	5	2	1	3	2	2	1	1	1	2
m	1	1	1	3	5	2	1	3	2	2	1	1	1	2
mb	1	1	1	2	5	2	1	3	2	2	1	1	1	2
c	1	1	2	3	6	1	1	1	3	3	1	2	1	3

3 O EFEITO DE DOIS CORAIS AZOOXANTELADOS INVASORES NAS INTERAÇÕES TRÓFICAS COM ESPÉCIES NATIVAS.

3.1 **The effect of two invasive azooxanthellate corals *Tubastraea coccinea* and *Tubastraea tagusensis* on trophic interactions with native species.**

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Abstract

When a species is introduced in a new location, it is common for it to establish itself when it finds favorable conditions in the receiving community that involve interspecific interactions with native species. The azooxanthellate corals *Tubastraea coccinea* and *Tubastraea tagusensis* are invasive species introduced in the Caribbean Sea, in the Gulf of Mexico and in the Brazilian Southwest Atlantic. They are successful competitors for space, excellent in sexual reproduction, larval dispersion and recruitment, however, studies on food and trophic relationships of species of the genus *Tubastraea* are still scarce. In the present study, we used isotopic values of δ^{13}C and δ^{15}N to investigate trophic relationships in rocky shores with different oceanography and anthropogenic context invaded by *T. tagusensis* and *T. coccinea* corals. The metrics derived from the isotopic values, we show that invaded communities have a lower degree of trophic diversity with species characterized by similar trophic ecologies and abiotic factors seem to contribute to the biotic resistance of communities exposed to invasion events. *Tubastraea* spp. occupies a niche space similar to that occupied by the native community of suspension filters, sharing resources already consumed by the receiving community, which makes invading corals successful species also in food competition.

Keywords: Nonnative species; isotopic niche metrics; suspension feeder's; empty niche theory; biotic resistance hypotheses; trophic relationships.

3.1.1 Introduction

Marine and coastal ecosystems around the world are being invaded at extraordinary rates as a result of human activities but the amount of effort dedicated to the study of invasive species in these ecosystems is still inconsistent (Chan and Briski 2017; Bailey et al. 2020; Teixeira and Creed 2020). The introduction of a nonnative species (NS) can change the diversity in the invaded community, modify interactions between species, leading to the decrease and extinction of native species, interruption of ecosystem functions and substantial damage to natural resources and ecosystem services (Simberloff et al. 2013; Pires-Teixeira et al. 2021).

For a NS to establish itself where it was introduced it needs to be able to extract enough resources from the environment to support the continuous mass and energy demands associated with growth, survival and reproduction so understanding NS diets helps to identify physiological characteristics that contribute to or limit the success of the invasion (McCue et al. 2019). The introduction of species into aquatic ecosystems can profoundly disrupt the strong trophic links existing in those communities, making these environments ideal ecosystem models to test hypotheses about the direct and indirect ecological impacts of NS (Gallardo et al. 2015). Inn invaded area the effects on the trophic web may depend on the invader's trophic position, feeding strategy and the ability to modify the habitat (Thomsen et al. 2014; Maggi et al. 2015; Gallardo et al. 2015). Omnivorous consumers, such as suspension or filter-feeding organisms, can prey (and compete) at more than one trophic level, controlling, for example, the abundance of phytoplankton and zooplankton or larval supply. Predators with rapid growth capacity can reduce the abundance and biomass of important food resources and consumers. NS that are considered ecosystem engineers can alter primary production and nutrient cycles, creating novel habitat and modifying the abundance of organisms in the invaded area, as well as alter other essential ecosystem processes (Grosholz and Ruiz 2009; Gallardo et al. 2015).

In coastal marine ecosystems biological invasions can considerably increase the number of suspension feeders, detritivores, depositivores and other primary consumers (Byrnes et al. 2007). In addition NS are often generalists that may access unexploited resources thus occupying a vacant trophic niche or reducing niche overlap with populations from the native community (Shea and Chesson 2002; Rilov 2009). A knowledge of the trophic interactions in an invaded community can help to understand, assess the impacts on the trophic structure and composition of the community and even better manage invasion events (Rilov 2009; Jackson et al. 2012; Howard et al. 2017;McKnight et al. 2017; Miranda et al. 2018).

Stable isotope analysis is a tool used to characterize the trophic structure of an ecosystem. Isotopic values, especially carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), are effective natural tracers for monitoring energy and nutrient flows, estimating trophic levels, resource use and the composition of consumers' diets (Michener and Kaufman 2007; Bouillon et al. 2008; Albrecht et al. 2021). These two stable isotopes are the most often used to assess trophic interactions as they make it possible to identify different sources of basal food resources and to estimate the trophic position of consumers, respectively (Zanden and Rasmussen 2001; Neres-Lima et al. 2017; Ferrier-Pagès and Leal 2018). The use of $\delta^{13}C \times \delta^{15}N$ biplots makes it possible to infer aspects of the studied species' trophic niche in food web from its relative position in the isotopic space. Although this is a well-established proceedure for studying the trophic structure and dynamics of a community there are alternative analytical approaches that allow the calculation the measurements of the trophic structure of a community using stable isotope ratios (Brito et al. 2006; Hoffman et al. 2008; Syväranta et al. 2013; Middelburg 2014; Rigolet et al. 2015; Linnebjerg et al. 2016). One example is the population and community isotopic niche structure metrics that reflect specific aspects of trophic structure such as width and niche overlap (Layman et al. 2007). In studies of invaded communities, metrics derived from stable isotope data can be applied to quantify the interactions between populations of native species and NS, interactions between two NS, assess the trophic niche in invaded and non-invaded communities and quantify niche overlap. Stable isotope analyses are therefore a promising tool for predicting the impacts of invaders on native communities and identifying potential management options (Jackson et al. 2012; Guzzo et al. 2013; Karlson et al. 2015; Alomar et al. 2016; McCue et al. 2019).

The azooxanthellate corals *Tubastraea coccinea* Lesson, 1830 and *Tubastraea tagusensis* Wells, 1982 are invasive species introduced in the Caribbean Sea by shipping or floating platforms and into the Gulf of Mexico and the Brazilian Southwest Atlantic on oil platforms (Creed et al. 2017). In Brazil, *Tubastraea* spp. have already been found on rocky shores and oil platforms along more than 3,000 km of the coast at depths ranging between 1 and 22 m (with record of a single colony of *T. coccinea* trawled from 100 m depth in the state of São Paulo) (Creed et al. 2017; Soares et al. 2016). The species of the genus *Tubastraea* are heterotrophic and obtain food exclusively through particle feeding mechanisms (i.e. have no association with symbiotic photosynthetic zooxanthellae) . Due to the highly invasive nature and multiple impacts the corals have caused a large number of studies have now been carried out regarding the expansion, distribution and increased abundance of *Tubastraea* spp. (Silva et al. 2014; Soares et al. 2016; Creed et al. 2017; Figueroa et al. 2019; López et al. 2019; Derouen et al. 2020; Soares et al. 2020; Braga et al. 2021) as well as investigations of competition with native species, chemical defenses, reproduction and facilitation of other species (Lages et al. 2010; Moreira and Creed 2012; Santos et al. 2013; Hoeksema and Harry 2017; Luz et al. 2019; Guilhem et al. 2020). However, studies on feeding and trophic relationships of species of the genus *Tubastraea* are still scarce (Sampaio et al. 2012; Vinagre et al. 2018).

When a species is introduced in a new location it is common for it to establish itself when it finds favorable conditions in the receptor community (i.e., niche requirements, Shea and Chesson 2002) bringing about novel interspecific interactions with native species (i.e., competition and predation, Gallardo et al. 2015). If the NS is a predator it may cause direct "top-down effects" on its prey with cascading consequences for lower trophic levels; or if as well as being a predator it is also a resource for predators at higher trophic levels it can cause "bottom-up effects" in the food chain by acting as a new food source. A predatory NS may also compete with native species for resources (McCue et al. 2019).

These corals are known to produce bioactive chemicals that deter predators and there are few natural predators amongst the native species (Lages et al. 2010; Moreira and Creed 2012). This trait may be explain the overall dearth of evidence of significant predation of *T. tagusensis* e *T. coccinea* in Braziland this escape may in part explain their highly invasive nature. Studies of the diet of *Tubastraea* spp. in the wild suggest the consumption of heterotrophic prey as well as the consumption of microalgae when offered in aquaria (Muscatine et al. 1989; Leal et al. 2014; Rezek et al. 2018; Chang et al. 2018).

Where native *Tubastraea* spp. are found in heterogeneous benthic communities both in more pristine and locations as well as those suffering from anthropogenic stressors such as sedimentation (Witman and Smith 2003; Ponti et al. 2016; Safuan et al. 2016; Sutthacheep et al. 2019). In the invaded range in Brazil native species, such as the zoanthid

Palythoacaribaeorum, the corals *Siderastrea stellata* and *Mussismiliahispida*, and the sponges *Desmapsammaanchorata* and *Iotrochotaarenosaparecem* provide some biotic resistance and compete with the invasive corals (Santos et al. 2013; Miranda et al. 2016; Silva et al. 2017; Guilhem et al. 2020). However there is an information gap regarding competition for food resources between *Tubastraea* spp. and other native species in the invaded range. The only evidence from isotopic analysis of $\delta^{13}C$ and $\delta^{15}N$ shows that *Tubastraea* spp. can share the same food source or a similar mixture of food as the probably comensal boring bivalve *Leiosolenusaristatus* (Vinagre et al. 2018).

In the present study we investigated how trophic relationships vary along three rocky shores invaded by *T. tagusensis* and *T. coccinea*. On each rocky shore the benthic marine communities were sampled in invaded and not-invaded communities. We used isotopic values of $\delta^{13}C$ and $\delta^{15}N$ to compare the isotopic niche of the invasive corals and the native benthic species in invaded and not invaded communities. We also conducted a review of knowledge of *Tubastraea* spp. as a potential food source (prey) for other species and we investigated the trophic relationships between potential consumer species and invading corals using isotopic values of $\delta^{13}C$ and $\delta^{15}N$.

Based on the fact that biotic acceptance or biotic resistance are both a function of the richness or diversity of native communities (biotic resistance hypothesis; empty niche hypothesis; the invasion paradox, Fridley et al. 2007). we tested two hypothesis regarding trophic relationships that developed during the invasion of Tubastraea spp.: 1) the invaded communities present a lower degree of trophic diversity, with species characterized by similar trophic ecologies; 2) *Tubastraea* spp. occupies a different niche from other benthic suspension feeding species, even though they belong to the same functional feeding group.

3.1.2 Materials and Methods

3.1.2.1 Study area

Our study was carried out on tropical rocky shores at three distinct locations along the state of Rio de Janeiro, Brazil (Figure 5, f.35):

a) Ilha Comprida (IC) - located about 5 km from Rio de Janeiro (23º02'15"S, 43°12'17"W), it is one of the five islands and two islets that make up the Cagarras Archipelago. site is on the inside the archipelago where it is relatively wave protected and has a maximum depth is 40m. The Cagarras Archipelago is impacted by eutrophic waters from Guanabara Bay (Rio de Janeiro city)(Creed et al. 2021; Fistarol et al. 2015). *T. tagusensis* was first detected (and removed) from the Cagarras Archipelago in 2004, but in 2011 the species was again present and has expanded at the site (Creed et al. 2017).

b) Ilha de Âncora (IA) – an island located 8km off the northwest coast of the state of Rio de Janeiro, at Armação dos Búzios, Cabo Frio region (22º46'16"S, 41°47'08"W). It is a popular diving spot, with clear, calm shallow waters (depth <22 m). AI is subject to a seasonal upwelling of nutrient rich, cold, high salinity South-Central Atlantic Water. It was first invaded by Both *Tubastraea* spp. have invaded the site since first detected in 2011 (Creed et al. 2017).

c) Ponta do Bananal (IG) – located in Ilha Grande Bay (IGB), Angra dos Reis, south of the Rio de Janeiro state (23°05'55"S 44°15'34"W), it is a region of intense maritime traffic, including shipping and oil platforms in transit. Oil platforms stop for repairs or maintenance or while waiting for berthing at the BrasFels shipyard (Silva et al. 2014) at the nearby Bananal Anchorage. The IG site is located inside the BIG, is characterized by shallow, clear water, and is probably the first point of introduction of *Tubastraea* spp. in natural ecosystems in Brazil (Creed et al. 2017).

3.1.2.2 Field sampling and abiotic data measurement

Fieldwork was carried out in July/2017 (IG), September/2017 (IC), June/2018 (IA). Between one and five replicate individuals / colonies of each of the most abundant species were sampled for analysis of C and N stable isotopes. At sites IA and IC the samples were taken over invaded and not invaded 30m extensions of the reef. At the IG site it was not possible to find areas without *Tubastraea* spp. so there we only sampled invaded areas. Due to their size (<1cm) planktonic organisms and the ophiuroid *O. mirabilis*, were collected in greater quantity.

The encrusting benthic species were removed with a hammer and chisel (corals and bryozoans), scissors (sponges and algae) and spatulas (ascidians and anemones). The species turf forming algae (a mixture of small entangled filamentous species) were separated after collection for individaul analysis. Planktonic organisms were collected with 68µm nylon plankton nets. All samples were frozen immediately after collection and taken for screening and preparation in the laboratory.

To characterize the conditions on collection we measured temperature, pH, salinity and dissolved oxygen with a waterproof multi-parameter probe (HI 9828, Hanna Instruments, Woonsocket, Rhode Island, USA). Water transparency (water visibility) was estimated as the Secchi depth using a Secchi disk.

3.1.2.3 Sample processing

After defrost the samples the muscle tissue of the macroconsumers (sea urchins, crustaceans, gastropods and fish) was removed. Corals and bryozoans had their tissues scraped, while very small animals, such as ophiuroids, were kept whole and grouped together to compose a sample. Sponges, ascidians and anemones had their soft tissues selected. All samples were washed with distilled water, so that any contaminants that could influence the isotopic compositions were removed. We removed any epiphyte or epizoa from the animals and macroalgae sampled. The samples were dried in an oven for 48 hours at 60° C and macerated to a fine powder. Organisms with calcium carbonate structures that could not be removed, such as calcareous macroalgae, phytoplankton, zooplankton, bryozoans, hydrozoans, corals, polychaetes and small crustaceans were acidified (only for δ^{13}C, Pires-Teixeira et al. 2020). The samples were then placed in tin capsules, weighed and analyzed for the isotopic composition of carbon and nitrogen at the Divisão de Funcionamento de EcossistemasTropicais in the Centro de Energia Nuclear na Agricultura da Escola Superior de Agricultura Luiz de Queiroz, São Paulo University (CENA-USP).

Stable isotope analyses were performed using a Delta Plus Continuous Flow Isotope Ratio Mass Spectrometer (CF-IRMS, Finnigan MAT, Bremen, Germany) coupled to an elemental analyzer (CE Instruments, Wigan, UK). The isotopic composition is expressed in terms of a delta value (δ) in parts per thousand (‰), obtained by dividing the sample's isotopic ratio by the isotopic ratio of an internationally accepted standard multiplied by one thousand, according to the formula: $\delta X = [(R_{sample}/ R_{standard}) -1] .10^3$, where δX is $\delta^{13}C$ or $\delta^{15}N$ and R the ratio ^{13}C: ^{12}C or ^{15}N: ^{14}N. The standard material for carbon was Pee Dee Belamite limestone (PDB) and the standard material for nitrogen was atmospheric air (Fry 1988). The standard deviation of isotopic measurements was estimated at 0.09 for $\delta^{13}C$ and 0.21 for $\delta^{15}N$ through repeated measures of the internal standard (sugar cane).

3.1.2.4 Data analysis

We conducted a literature search during April 2021 for research on the predation of corals of the genus *Tubastraea* and the results were organized in a table. The following databases were consulted: Google Scholar (https: //scholar.google.com/), Researchgate (https://www.researchgate.net/) and Scientific Electronic Library Online (http: //www.scielo. org / php / index.php). We used a biplot of the values of $\delta^{13}C$ and $\delta^{15}N$ of the basal resources and consumers of the sites invaded by the corals *Tubastraea* spp. with the presence of potential predators to provide an overview of the trophic structure and identify possible trophic relationships between food sources and consumers.

We used the SIBER (Bayesian Ellipses to Stable Isotope Data) package (Jackson et al. 2011) in Program R (R Core Team 2017) to analyze stable isotope data at the trophic group and species level. To test hypothesis 1, we calculated the isotopic niche metrics in invaded and non-invaded communities in the three studied locations (IC, IA and IG) using a Bayesian approach to fit multivariate normal distributions to stable isotope data (Layman et al. 2007). These distributions can then be used to calculate probability distributions of standard ellipse areas to compare sets of data or to calculate Layman's metrics (Layman et al. 2007) to compare entire communities (Jackson et al. 2011). Layman's metrics relate the characteristics of the isotopic space filled by each species and reflect important aspects of the trophic structure and trophic diversity of the entire community:1)N_range (Distance between the two species with the maximum and minimum values of $\delta^{15}N$, larger intervals suggesting more trophic levels and a greater trophic length); 2) C_range (distance between the two species with the maximum and minimum values of $\delta^{13}C$, longer intervals are expected in communities with a greater diversity of basal resources):3) TA (Total isotopic niche area, represents a measure of the total amount of niche space occupied and, therefore, a proxy for niche width); 4) CD (Average distance from the centroid, greater distances suggest a higher average degree of trophic diversity within the food chain); 5) MNND (Average distance from the nearest neighbor, low values suggesting trophic webs with species characterized by similar trophic ecologies and high trophic redundancy); 6) SDNND (Standard deviation of the distance from the nearest neighbor, low values suggesting a more uniform distribution of the trophic niche).

In order to test hypothesis 2 we performed a more specific analysis among consumers within the same functional food characteristic as that of *Tubastraea* spp., that is, suspension feeder consumers. We used the SEA metric (value of the Standard Ellipse Area that covers 65% data and indicates the central average of the community's isotopic niche) (Jackson et al. 2011). Due to the lack of natural predators we did not carry out the same analyzes for the guild of potential predators of *Tubastraea* spp. (Lages et al. 2010; Sampaio et al. 2012). To estimate and compare the width of the isotopic niche of *Tubastraea* spp. in the three studied locations (IC, IA and IG) we used the isotopic niche width analysis measured as the ellipse area (SEAc), a corrected SEA value proposed by Jackson et al. (2011) used to circumvent the bias that arises when sample sizes are small. To determine what fraction of the isotopic niche of suspensionfeeders was occupied by *Tubastraea* spp. we calculated the overlap of the SEAc of *Tubastrea* spp. and the SEAc of the suspension feeder guild and divided the overlapped area by the SEAc of the invaded community:

$$(A \cap B)/B \qquad (2)$$

3.1.3 Results

Measurements of the abiotic parameters of seawater showed that the IA site had greater clarity, followed by IG and IC. The lowest pH was found at IG, followed by similar values at IA and IC. The highest temperature was at IA, followed by IG and IC, as well as the values of dissolved oxygen, IA with (mean ± SD) 12.97 mg/l ± 3.79, IG with 11.71 mg/l and IC with (mean ± SD) 5.98 mg/l ±1.44. The highest salinity was in IG, followed by IC and IA (Table 5). The values were conducive with the general oceanographic situations of the sites as described above.

Table5 - Visibility (m), pH, Temperature (°C), Dissolved oxygen [DO (mg/l)] Salinity (PSU), measured by sensors in situ at Ponta do Bananal (IG), IlhaComprida (IC) and Ilha de Âncora (IA).

Data	Local	Visibility (m)	pH	Temperature (°C)	DO (mg/l)	Salinity (PSU)
July 2017	IG	12	7.63	21.89	11.71	37.89
Sept 2017	IC	7	8.42	20.28	5.00	36.62
Sept 2017	IC	7	8.56	18.39	7.63	36.57
Sept 2017	IC	2	8.40	19.90	5.31	34.94
June 2018	IA	20	8.13	22.14	8.6	32.13
June 2018	IA	18	8.08	22.16	14.9	32.38
June 2018	IA	20	8.09	22.91	15.4	32.55

A total of 61 species / taxa were sampled, 16 taxa in invaded and 18 in not invaded communities at IC, 24 in invaded and 22 in not invaded at IA and 26 in the (totally invaded) community at IG were analyzed for δ^{13}C and δ^{15}N. The consumers with the highest mean value of δ^{15}N were the carnivorous fish *Haemulonauroline*, *H. steindachneri*, the omnivorous fish *Stephanolepishispidus* and the omnivorous fireworm (polychaete) *Hermodicecarunculata*, all sampled at the IG site invaded by the invasive corals *Tubastraea* spp. The hydroids *Macrorhynchiaphilippina*, *Milleporaalcicornis* and the ascidian *Diplosomalisterianum*were the consumers with the lowest values of δ^{15}N, both suspension feeders and sampled at site IA in invaded (*M. philippina* and *D. listerianum*) and not invaded (*M. alcicornis*) by *Tubastraea* spp. The mean values of δ^{15}N of the basal food resources varied between 5.58‰ for the articulated coralline algae (Rhodophyta) *Janiaadhaerens* and 8.23‰ for the unidentified crustose coralline algae (Rhodophyta), both at IG in the invaded communities. The macroalgae showed average values of δ^{13}C ranging from -6.17‰ in *J. adhaerens* (invaded community - IA) to -20.35‰ and -20.31‰ in *Hypnea* sp. and *J. adhaerens*, respectively (both at IA in not invaded communities).

There was little intrageneric variation and the δ^{13}C values of *T. coccinea* (IG: -21.37‰; -21.65‰; -21.15‰; IA: -20.53‰; -19.52‰; -19.71‰) and *T. tagusensis* (IG: -20.94‰; -21.12‰; -20.80‰; IA: -19.76‰; -19.10‰; -19.74‰; IC: -17.66‰; -18.42‰; -19.22‰) were grouped, as were the δ^{15}N values (IG: *T. coccinea*: 9.79‰; 10.18‰; 9.56‰; *T. tagusensis*: 9.71‰; 9.79‰; 10.14‰; IA: *T. coccinea*: 8.35‰; 8.17‰; 8.45‰; *T. tagusensis*: 8.82‰; 9.06‰; 9.66‰; IC: *T. tagusensis*: 9.45‰; 9.50‰; 9.55‰). IG was the only site where it was possible to sample a potential predator, the omnivorous fireworm*Hermodicecarunculata* (which the literature search revealed had been previously observed to feed on *Tubastraea* spp. in Brazil); it had isotopic values consistent with the consumption of the invasive corals, (δ^{13}C: -17.15‰; -16.82‰; -15.89‰; δ^{15}N: 12.54‰; 12.01‰; 12.03‰) (Figure 2E). At IA no omnivorous or carnivorous consumer had isotopic values of δ^{13}C and δ^{15}N that consistent with predation of *Tubastraea* spp. (Figure 14B). At IC a single omnivorous predator the red swimming crab *Croniusruber* presented values consistent with it being a potential consumer of the invading corals (δ^{13}C: -20.09‰; -19.42‰; δ^{15}N: 9.55‰; 10.64‰) (Figure 14D).

We found eight studies reporting the consumption of *Tubastraea* spp. by generalist and specialist predators, and one personal observation. Among them, only two reports are from places where *Tubastraea* spp. is invasive (Table 6).

Table 6 - Species of predators that consume *Tubastraea* spp., natural distribution of predators, where the predation event was observed and type of feeding.

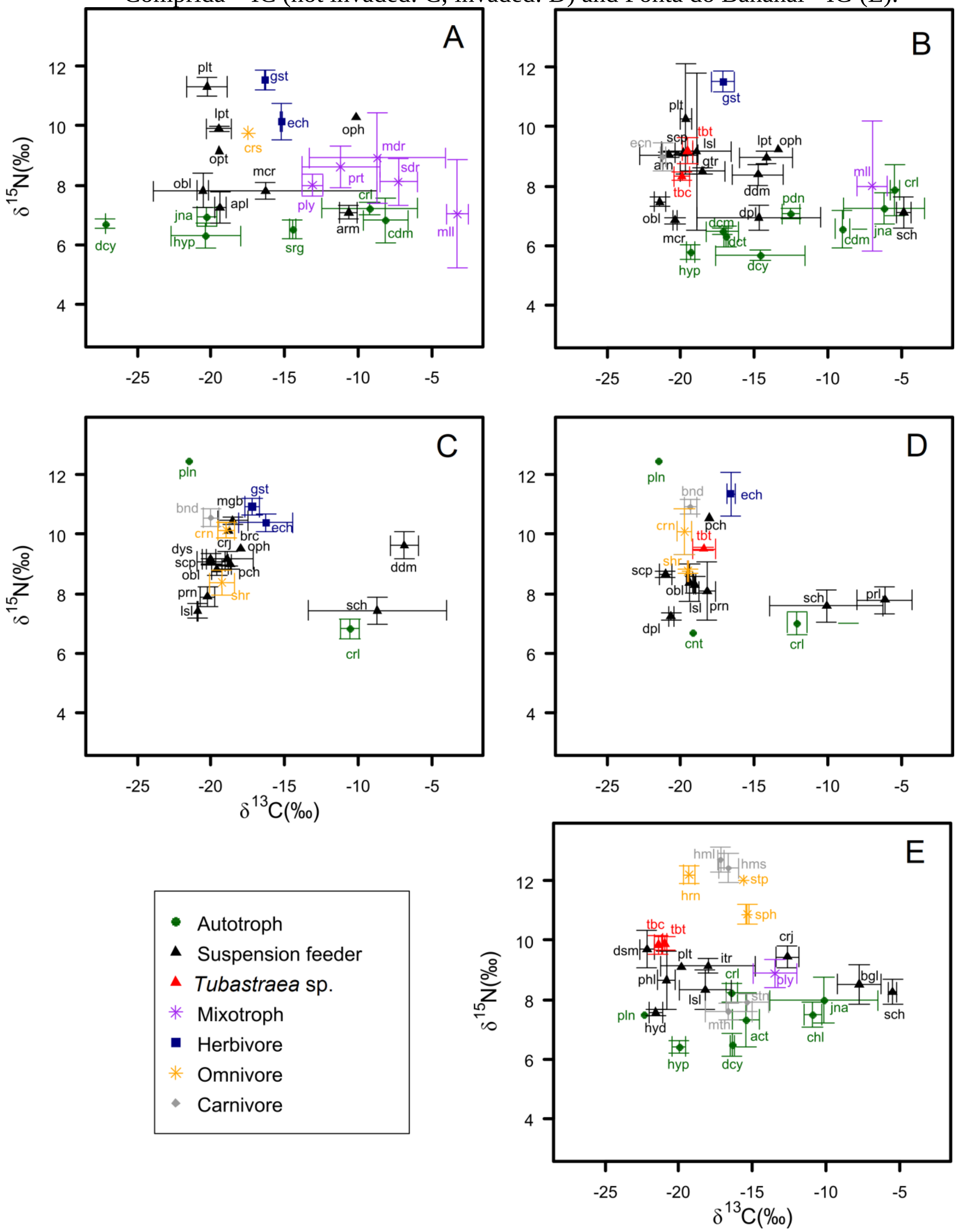
predatorspecies	consumedspecies	natural distribution	observation site	feedingtype		Bibliografia
				generalist	specialist	
Epidendriumbilleeanum (DuShane&Bratcher, 1965)	*Tubastraea* spp.	Galápagos	Galapagos; Hawaii; Hawaiian Gulf of California; Maldives; Singapore; Philippines		x	Witmanand Smith (2003); Robertson (1970)
Epidendriumbilleeanum (DuShane&Bratcher, 1965)	*T. coccinea*	Galápagos	SudaneseRed Sea; Nicaragua (Pacific)		x	Oliverio et al. (1997); Rodríguez-Villalobos et al. (2016)
Hermodicecarunculata (Pallas, 1766)	*T. tagusensis*	Mediterranean	Brazil	x		Sampaio et al. (2012)
Hermodicecarunculata (Pallas, 1766)	*T. aurea*	western Pacific	Venezuela	x		Martín andLosada (1991)
Hexaplex princeps (Broderip, 1833)	*Tubastraea* spp.	Gulf of California to Peru	Galapagos		x	Witmanand Smith (2003)
Oreasterreticulatus (Linnaeus, 1758)	*Tubastraea* spp.	Caribbean	Brazil	x		Author'spersonalobservation (JCC)
*Phestillamelanobrachia*Bergh, 1874	*T. coccinea*	western Pacific	Hawaii; Guam		x	Faucci et al. (2007)
*Phestillamelanobrachia*Bergh, 1874	*T. micranthus*	western Pacific	Palau		x	Faucci et al. (2007)
*Phestillamelanobrachia*Bergh, 1874	*T. aurea*	western Pacific	Hawaii (in laboratory)		x	Harris (1975)

Source: PIRES-TEIXEIRA ET AL. (manuscript in preparation)

Suspension feeding consumers showed isotopic values similar to those of *Tubastraea* spp.: the sponge *Desmapsammaanchorata* at IG (δ^{13}C: -22.73‰; -21.93‰; -21.85‰; δ^{15}N: 10.31‰; 9.69‰; 9.06‰) (Figure14E); the sponges *Guitarra sepia* (δ^{13}C: -19.86‰; -18.83‰; -16.88‰; δ^{15}N: 8.38‰; 8.59‰; 8.51‰), *Arenosclerabrasiliensis*(δ^{13}C: -18.55‰; -21.95‰; -21.94‰; δ^{15}N: 8.98‰; 9.15‰; 9.02‰) and *Scopalinaruetzleri* (-18.55‰; -21.95‰; -21.94‰) at IA; an unidentified tubicolous polychaete worm (δ^{13}C: -19.30‰; -20.09‰; -19.57‰; δ^{15}N: 12.38‰; 9.27‰; 9.12‰) at IA (Fig 14B). At the IC site no consumers had δ^{13}C and δ^{15}N values overlapping those of *T. tagusensis* and the consumers with the closest values were the brown mussel *Pernaperna* (δ^{13}C: -18.86‰; -17.87‰; -17.91‰; δ^{15}N: 7.48‰; 9.20‰; 7.56‰) with is also a suspension (filter) feeder(Fig 14D).

The isotopic values of plankton at IG (δ^{13}C: -22.40‰; δ^{15}N: 7.50‰) and the macroalga *Hypnea* sp. at IG(δ^{13}C: -20.54‰; -19.68‰; -19.74‰; δ^{15}N: 6.18‰; 6.53‰; 6.54‰) and IA (δ^{13}C: -19.14‰; -19.55‰; δ^{15}N: 5.61‰; 5.96‰) are consistent with their consumption by invading corals *Tubastraea* spp. and the above mentioned suspension feeding (Figure14B, E). The red macroalga *Centroceras* sp. (δ13C: -19.21‰; δ15N: 6.68‰) was another resource with values a consistent with its consumption by *T. tagusensis* at IC, although only one sample was analyzed (Figure14D).

Figure 14 -Stable isotope biplot of species in invaded and non-invaded communities in the three studied locations: Ilha de Âncora – IA (not invaded: A; invaded: B), Ilha Comprida – IC (not invaded: C; invaded: D) and Ponta do Bananal - IG (E).



Legend: Symbols indicate the average (± SD) of resources and consumers separated by guilds. Code by guild: Autotroph: act – *Acetabularia schenckii*, cdm – *Codium intertextum*, chl – Chlorophyta, cnt – *Centroceras* sp., crl – Crustose coralline algae, dcm – *Dictyotamenstrualis*, dct – *Dictyopteris* sp., dcy – *Dictyota* sp., hyp – *Hypnea* sp., jna – *Janiaadhaerens*, pdn – *Padina gymnospora*, pln – plankton, srg – *Sargassum vulgare*. Suspension feeders: apl – *Aplysina fulva*, arn – *Arenosclerabrasiliensis*, bgl–

Bugula sp., brc – *Brachidontessolisianus*, crj – *Carijoariisei*, ddm – *Didemnumperlucidum*, dpl – *Diplosomalisterianum*, dsm – *Desmapsammaanchorata*, dys – *Dysideaetheria*, gtr – *Guitarra sepia*, hyd – hydrozoan, itr – *Iotrochotabirotulata*, lpt – *Leptogorgiapunicea*, lsl – *Leiosolemusaristatus*, mcr – *Macrorhynchiaphilippina*, mgb – *Megabalanuscoccopoma*, obl – *Obelia dichotoma*, oph – Ofiuroidea, opt – *Ophiothela mirabilis*, pch – *Pachychelesmonilifer*, phl – *Phalusia nigra*, plt – Tubular polychaete, prl – *Paraleucilla magna*, prn – *Pernaperna*, sch – *Schizoporellaunicornis*, scp – *Scopalinaruetzleri*, tbc – *Tubastraea coccinea*, tbt – *Tubastraea tagusensis*. Mixtroph: mdr – *Madracisdecatis*, mll – *Milleporaalcicornis*, ply – *Paliythoacaribaeorum*, prt – *Porites branneri*, sdr– *Siderastrea stellate*. Herbivore: ech – *Echinometralacunter*,gst – Gastrophoda. Omnivore: crs – Crustacea, hrm – *Hermodicecarunculata*, shr – Shrimp, sph – *Sphoeroidesspengleri*, stp – *Stephanolepishispidus*. Carnivore: crn – *Croniusruber*, hml – *Haemulonauroline*, hms – *Haemulonsteindachneri*, bnd – *Bunodosomacaissarum*, ecn – *Echinasterbrasiliensis*, mth – *Mithraculus forceps*, stn – *Stenorhynchusseticornis*.

Source: PIRES-TEIXEIRA et al. (submited)

The total niche area (TA) was greater in the community not invaded at IA and was very similar between invaded and not invaded communities in IC. The C_range in IA was higher in the not invaded community. Also at IA the SDNND in the not invaded community was more than double that of the invaded community. The other metrics showed similar values, regardless of location or status invaded or not invaded (Table 7).

Table 7 - Isotope niche metrics calculated for the entire community in invaded and not invaded communities at the three study sites: IC: Ilha Comprida, IA: Ilha de Âncora, IG: Ponta do Bananal.

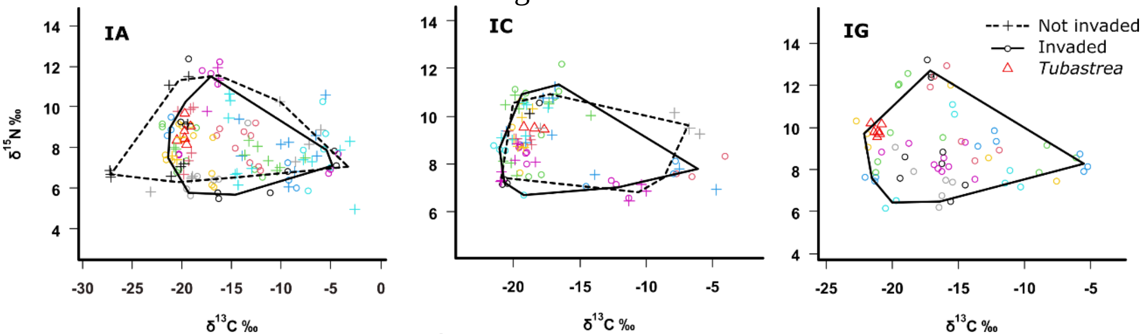
Site	metricvalues*	invaded	notinvaded
Ilha de Âncora	N_range	5.84	5.24
	C_range	16.56	23.94
	TA	58.64	76.32
	CD	4.72	5.22
	MNND	1.10	1.80
	SDNND	0.64	1.34
Ilha Comprida	N_range	4.67	4.11
	C_range	14.91	14.05
	TA	41.32	41.85
	CD	3.80	3.28
	MNND	1.39	0.84
	SDNND	0.94	0.76
Ponta do Bananal	N_range	6.28	
	C_range	16.71	
	TA	58.79	
	CD	3.91	
	MNND	1.14	
	SDNND	0.52	

Legend: N_range = distance between the two species with the maximum and minimum values of $\delta^{15}N$; C_range = distance between the two species with the maximum and minimum values of $\delta^{13}C$; TA = total area of the isotopic niche; CD = mean centroid distance; MNND = average distance from the nearest neighbor; SDNND = standard deviation of the distance from the nearest neighbor.

Source: PIRES-TEIXEIRA et al. (submited)

The consumers’ niche in the invaded communities presented very similar patterns of distribution in the isotopic space at the three invaded locations, with equal total areas and overlapping niches of invaded and not invaded communities. The largest isotopic niche was the not invaded community at IA. The smallest isotopic niche was in the IC invaded community (Figure 15).

Figure 15 - Isotopic niche (convex polygon) of invaded and non-invaded communities in three different locations along the coast of the state of Rio de Janeiro in Brazil.

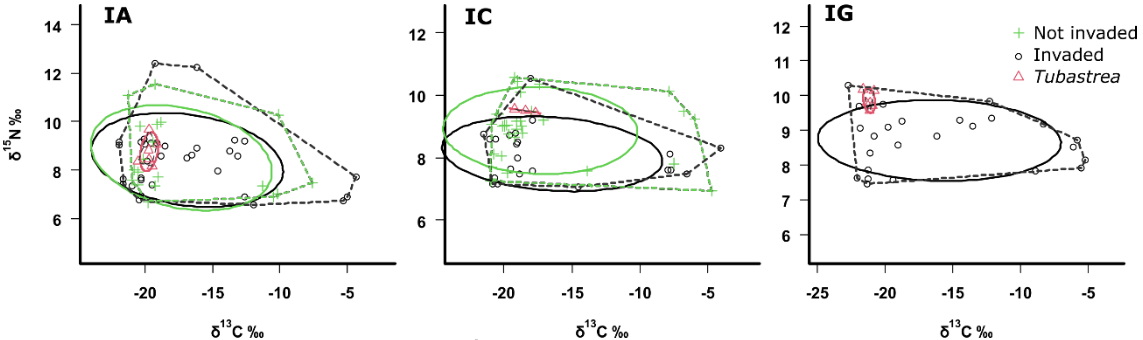


Legend: IC: Ilha Comprida, IA: Ilha de Âncora, IG: Ponta do Bananal. Convex hulls of the total isotopic niche areas of the community are plotted in the isotopic space. Different colors represent different trophic groups.

Source: PIRES-TEIXEIRA et al. (submited)

The guild of suspension feeders occupies a wide area of isotopic niche in both invaded and not invaded communities, (in invaded area: at IA, SEA = 20.10; at IC, SEA= 14.28; at IG, SEA= 15.62; in not invaded area: at IA, SEA = 21.5; at IC, SEA= 14.87) (Fig 4). In invaded communities the average values of δ^{13}C of suspension feeders range from -22.73‰ (*D. anchorata* at IG) to -5.16‰ (*Schizoporellaunicornis* at IG) and δ^{15}N ranging from 5.87‰ (*Milleporaalcicornis* at IA) to 12.38‰ (unidentified tubicolous polychaete worm at IA). In not invaded communities the average values of δ^{13}C of suspension feeders range from -20.91‰ (*Leiosolemusaristatus* at IC) to -3.25‰ (*M. alcicornis* at IA) and δ^{15}N range from 7.04‰ (*M. alcicornis* at IA) to 11.54‰ (gastrophoda at IA). The niche area, represented by SEAc, of *Tubastraea* spp. occupies a specific and limited area of the standard ellipse of suspension feeders in the three locations (at IA: 4.63%; at IC: 0.02%; at IG: 1.76%) (Figure16).

Figure 16 - Isotopic niche of suspension filter consumers between not invaded (green) and invaded (black) areas in three different locations along the coast of the state of Rio de Janeiro in Brazil.



Legend: IC: Ilha Comprida, IA: Ilha de Âncora, IG: Ponta do Bananal. Dashed line - convex hulls area; continuous line - ellipse areas with a 65% confidence interval.

Source: PIRES-TEIXEIRA et al. (submited)

3.1.4 Discussion

This study gives us new insights into trophic relationships in shallow tropical rocky reef communities in the southwest Atlantic which have been invaded by corals *T. tagusensis* and *T. coccinea* . These insights include an assessment of interactions between the two invasive species and native counterparts and the first study of trophic relationships involving predation and competition for food resources by species of the genus *Tubastraea* within their invasive range. In addition, we successfully tested the applicability of the empty niche and biotic resistance hypotheses in the context of this marine biological invasion. To do so we used the isotopic values of δ^{13}C and δ^{15}N in three discrete invaded and not invaded communities with different oceanography and anthropogenic settings along the coast of the state of Rio de Janeiro.

Since the nitrogen isotopic values reflect the trophic position of the species (Couch 1989; Lepoint et al. 2004; Hanson et al. 2010) basal food resources, represented by macroalgae from three different phyla, showed the lowest values of δ^{15}N when compared to consumer values. In addition to the macroalgae the mixotrophic hydrocoral *Milleporaalcicornis*which has symbiotic zooxanthellae algae which represents an additional source of resource and reflects the assimilation of N also showed lower values of δ^{15}N despite being a consumer. The δ^{13}C values of the basal food resources were notably wide, especially in the Rodophyta. The wide variation in δ^{13}C values of marine algae which can vary from –3‰ to –35‰ has previously been documented in an extensive review carried out by Raven et al. (2002).

Macroalgae are exposed to a range of water movement that varies according to depth, tidal stage, wave action and currents and such variation coupled to the polyphyletic nature or algae and their consequent diverse metabolic pathways has effects on inorganic carbon and other nutrients available for assimilation (Smith e Walker 1980; Raven 1984; Wheeler 1988). However, while other have attributed variability in values to taxonomy and the ecology of the macroalgae studied we found considerable variation in $\delta^{13}C$ the same species at the same collection site within invades and not invaded areas (e.g., *Janiaadhaerens* at IA: -20.31‰ in not invaded area and -6.17‰ in invaded area). Also different from Raven (2002) whereRodophyta algae with $\delta^{13}C$ values below –30‰ were from submarine, shaded intertidal environments or from the upper coast, in our study not only Rodophytas, but Phaeophytas like *Dictyota* sp. (in AI not invaded: -27.18‰) and *Padina gymnospora* (in AI invaded: -12.51‰) showed variation and our collections were carried out between 5 and 10m in depth. Finally, most of the red algae (from the North-East Atlantic) that had very low $\delta^{13}C$ values were collected under low light and temperatures (Raven 2002), but in the locations of our study the lowest temperature recorded was at IC (18.39°C). We suggest that future studies assess the variation in $\delta^{13}C$ of benthic marine algae over a wider latitudinal range.

The sponges *D. anchorata*; *G. sepia*; *A. brasiliensis* and *S. ruetzleri* presented values of $\delta^{13}C$ and $\delta^{15}N$ close to the values of *Tubastraea* spp. Other studies have shown that in the invaded range in Brazil the encrusting sponge *S. ruetzleri* is among the porifera species that most frequently compete for space by contact with *Tubastraea* spp. and *D. anchorata* is one of the few benthic species capable of overgrowing and occasionally killing the invasive corals (Meurer et al. 2010; Silva et al. 2017). Our results that indicate an overlapping of the niches of these species is thus supported by these field observations that suggest that competition for resources can occur in situations where the food resource is limiting.

No previous studies have indicated the feeding preferences for corals of the genus *Tubastraea*. The macroalgae *Hypnea*sp. was collected along with other species as part of the turf community and at two sites (IG and IA) this algae had values of $\delta^{13}C$ and $\delta^{15}N$ consistent with it being consumed as a food source by the two species of *Tubastraea* spp., probably captured as fragments of suspended debris after breakage by waves or herbivores..The $\delta^{13}C$ and $\delta^{15}N$ values of another turf forming red algae *Centroceras* sp. at IC suggested the same. *Hypnea*sp. it is a fast-growing macroalgae that develops as an epiphyte or as a primary substrate, contains a considerable amount of protein and has no chemical protection against predation (Stachowicz and Hay 1999; Craft et al. 2013). Studies show that *Hypnea* sp. is an important food resource consumed by fish, sea turtles, crustaceans and gastropods in shallow marine habitats (Schenkman 1989; Cruz-Rivera and Villareal 2006; Angell et al. 2012). Similarly*Centroceras* sp. is a filamentous turf that grows on primary or epiphyte substrate and is consumed by fish, gastropods and sea urchins (Cruz-Rivera and Villareal 2006; Queiroz 2020). Algal turfs are very important for primary productivity in tropical reef environments and amongst the most abundant taxons/functional groups at our study sites (Creed et al, 2021); they have also been found to be the group most excluded by *Tubastraea* spp. (Paula et al. 2017; Creed et al, 2021) so again field observations support the trophic relationships determined from δ^{13}C and δ^{15}N values. These data also suggest that the mechanism of capture and consumption of suspended food is selective and not simply a function of the composition of particles of food that are presented to to the sessile consumer, in this case the invasive corals *Tubastraea*spp by the currents.. We will discuss later the food preference of suspension feeding consumers for specific resources which was also corroborated by our isotopic niche results.

Another trophic relationship that our results also confirmed another trophic interaction by providing evidence consistent with *Tubastraea* spp. being preyed upon by the fireworm*H. carunculata* (Sampaio et al. 2012). However it appears that this predation pressure is not strong enough to have a significant impact on invasive *Tubastraea* spp. as they have rapidly expanded throughout the tropical and subtropical southwest Atlantic and significant damage to polyps that would be conducive with feeding is not observed. These fireworms are not very abundant so probably predate (damage) infrequently and *Tubastraea* spp. have substantial ability to recover from partial polyp or colony damage (Luz et al. 2018; Creed et al. 2019). One proviso is the number of individuals sampled: even in three equidistant locations along the coast of Rio de Janeiro only three individuals of *H. carunculata* were found and sampled.

Biotic resistance may result from abundant native predators or strong competitors which limit establishment or expansion (population size) or habitat use by NS, and predation can also mediate competitive interactions and, in turn, affect species abundance and structure in the community (DeRivera et al. 2005; Ruesink 2007; Leclerc et al. 2020). However, strong biotic resistance may occur only when native predators possess characteristics such as high abundance, strong predation pressure on NS prey and high feeding rates (Skein et al. 2020). These characteristics seem far from the only observed and documented predation of *Tubastraea* spp.in Brazil - three *T. tagusensis* polyps eaten by a fireworm*Hermodicecarunculata* reported by Sampaio et al. (2012 - and corroborated by our results). In 20 years of field studies the starfish *Oreaster reticulatus* has been observed only once preying on *Tubastraea* spp. [author's (JCC) personal observation]. We did not find individuals of the starfish *O. reticulatus* to be sampled. The carnivorous crustacean *C. ruber* was yet another predator with values of $\delta^{13}C$ and $\delta^{15}N$ that were consistent with a possible consumption of *Tubastraea* spp. but it was only possible to sample one individual. In the Indo-Pacific, the native range of *T. coccinea* and *T. micranthus*, these species are preyed upon by highly specialist predators which are not very voracious consumers but can resist the secondary metabolites used as chemical defense, , and, in some cases, actually sequester it for their own defense (Witman and Smith 2003; Rodríguez-Villalobos et al. 2016).

The metrics used to describe important aspects of invaded and not invaded communities showed similar values in both communities but the total extent of trophic diversity within the food webs was greater in the not invaded communities. Furthermore, the total carbon band exploited by the community reflected a greater abundance of resources exploited by local consumers in the invaded area (Layman et al. 2007; Jackson et al. 2012) which corroborates our hypothesis 1 that invaded communities present a lower degree of trophic diversity, with species characterized by similar trophic ecologies.. This was especially evident at IA which is located in the Cabo Frio upwelling region, and where primary productivity is high when seasonal upwelling occurs in austral spring-summer (September to November - December to February) and winter (June to August) (Moreira da Silva 1973; Valentin 1994) and thus differs from other study sites in terms of the amount of organic matter that can influence the basal resources. However, as we will discuss below, this does not seem to be a reflection of the absence of invaders, since *Tubastraea* spp. apparently occupies a specific and consistent niche in the three studied sites, which overlaps the niche of other functionally equivalent species, the suspension feeding species.

Although suspension feedingspecies occupy a wide isotopic niche space, invading corals occupy a specific and limited range within that niche. The likelihood that the invasion will be successful is increased if a new species niche requirements overlap little or not at all with species already resident in the receiving community (Tilman 2004). However, different from what we expected to find based on the empty niche hypothesis (hypothesis 2), *Tubastraea* spp. occupied a similar trophic niche space to that occupied by the native community, sharing resources already consumed by the receiving community. If, on the one hand, a non-native species that requires certain limiting resources to establish and spread is more successful in habitats where competition for these resources is reduced (Rilov 2009; Atkinson et al. 2011; Karlson et al. 2015), our results suggest that either food resources are not limiting compared to other resources or demands or that native species have been substituted by a superior competitor with regard to food; the outcome of coexistence may result from another type of competition. Another point worth bearing in mind is that for sessile suspension feeders in benthic communities the occupation or domination of space, per se, will directly affect its feeding success and *Tubastraea* spp. are well known for their arsenal of both allopathic chemical and physical defenses (Koh &Sweatman, 2000, Lages et al. 2010; Santos et al. 2013). We also confirm the only isotopic characterization ever carried out for the species of *Tubastraea* spp., which points to the same source or a similar mixture of food for the invasive corals and two other suspension feeders the bivalves *Leiosolenusaristatus* and *Crassostrea virginica* (Vinagre et al. 2018). In the Pacific the δ^{13}C and δ^{15}N values of *Tubastraea* sp. were similar to those found here, ranging from −21.1‰ to −19.9‰ and 8.6‰ to 9.2 ‰ respectively (Chang et al. 2018) were also similar to the δ^{13}C of *T. coccinea* in the North Atlantic, −20.27‰ (Muscatine et al. 1989), ranging frombetween −21‰ and −20‰ and δ^{15}N between 7‰ and 9‰ (Rezek et al. 2018).

The niche occupied by consumers in the invaded areas was similar in the three locations studied. The wide amplitude of the suspension feeder niche (Fig 4) suggests the consumption of different sources of resources; however, individuals of the same species grouped in different parts of the isotopic space (Fig 2) suggesting that the available resources are selected by some mechanism(s). The isotopic niches of *Tubastraea* spp., consistent in the three studied locations, were tight and occupied a characteristic range (*c*. -21 to -19‰ in δ^{13}C and *c*. 8 to 10‰ in δ^{15}N), confirming this observation. Sessile benthic suspension feeding consumers use a variety of foraging behaviors, from feeding on particles large enough to be seized individually to processing the surrounding water (filtering or capturing in mucus nets) for particles so small that they may only be obtained by these methods (Gili and Coma 1998; Riisgård and Larsen 2010). Ecological filtration functions performed by consumer suspension feeding species have previously been shown to be different in bivalve species that may select specific components of the suspended particulate material available in aquatic ecosystems (Atkinson et al. 2011). On the other hand, no selectivity has been observed regarding the size of the prey by species of tunicate and bryozoan suspension feeders (Whalen and Stachowicz 2017). The mechanisms used by *Tubastraea* spp. to select the consumed resources are still unknown and we suggest that further studies are needed to examine and evaluate food selection and uptake by these corals. Another aspect that would be enlightening, mainly for the purpose of comparison with our results, would be studies of the niche of *Tubastraea* spp. in it'snrange and communities.

In summary, using C and N isotopic analysis and isotopic niche diversity metrics this study provides the first trophic characterization of the invading corals *Tubastraea tagusensis* and *Tubastraea coccinea*. Our metrics derived from stable isotopes suggest that greater trophic diversity in a not invaded areas appears to be influenced not only by the community's resistance to invasion, but also by the abiotic factors involved (such as increased productivity due to upwelling events). In the light of the trophic niche we corroborate the hypothesis of biotic resistance, with regard to low abundance of native predators and low pressure of predation on NS prey and refute the empty niche hypothesis as there is some level of coexistence and substantial niche overlap of native and invasive. Our results suggest that *Tubastraea* spp. occupy a quite specific niche within the niche occupied by other functionally equivalent species, are successful competitors for food resources but are not desirable food items.

3.1.5 Acknowledgment

We are especially grateful to Augusto Machado, Bruno P. Masi, Edson Faria Jr., Katia Capel, Vanessa Bettcher and for help in the field. This work was supported by Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (JCC, FAPERJ E-26/010.003031/2014 and E26/203.002/2017) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (JCC, CNPq- 305924/2018-4) and received support for fieldwork logistics and equipment from the Brazilian Institute for Biodiversity (BrBio) as part of the Coral-sol Project funded through the Commitment to Conduct Adjustment Agreement signed by Chevron Brazil with the Brazilian Federal Prosecution Service (MinistérioPúblico Federal), with implementation by the Brazilian Biodiversity Fund (FUNBIO). LMPT acknowledges Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) that provided a PhD scholarship. VNL acknowledges the Universidade do Estado do Rio de Janeiro that provided the Teaching Support Scholarship (PAPD-UERJ). This study was carried out under the environmental license of the SISBIO (nº 59542/1). This article is no. 49 from the Projeto Coral-Sol.

3.1.6 References

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4 ANÁLISE DA DIVERSIDADE E ESTRUTURA TRÓFICA EM UM COSTÃO ROCHOSO RECENTEMENTE INVADIDO POR UM CORAL ZOOXANTELADO.

4.1 **Diversity analysis and trophic structure of a recently invaded tropical rocky shore.**

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Abstract

When a nonnative species remains in an invaded community for some time long-term effects on community diversity and ecosystem functioning are expected, as are changes in trophic interactions between species. The blue soft coral *Sansibia* sp., presumably of Indo-Pacific origin, was first detected in the wild in Brazil in 2017. This study provides the first information on the trophic relationship that has developed between *Sansibia* sp. and 29 other benthic marine species in a food web on shallow tropical rocky reefs which have been invaded in the tropical southeast Atlantic. The difference in species composition of invaded areas and control areas was also assessed. *Sansibia* sp. shown δ^{15}N values close to those of macroalgae, suggesting that its symbiosis with zooxanthellae represents an essential source of energy in addition to the suspension feeding. A possible opportunist-generalist consumer, the arrow crab *Stenorhynchusseticornis* showed values of δ^{13}C and δ^{15}N aligned as a possible consumer of *Sansibia* sp. The difference in species composition between invaded and control areas and an increase in the abundance of *Sansibia* sp. in shallow areas suggests an available settlement

mechanism to further expand distribution to more favorable locations, which leads us to encourage continuous monitoring of the invaded area along with actions for management and eradication.

Keywords: Nonnative species, trophic web, stable isotopes, trophic relationships, community.

4.1.1 Introduction

Trophic webs are particularly useful for understanding the multiple impacts of biological invasions on an ecosystem (Thomsen et al. 2014; David et al. 2017). Nonnative species (NS) inevitably create new trophic connections because they consume and/or are consumed by species residing in the invaded community (Byers 2000; David et al. 2017). Nonnative species can thus cause negative effects in the invaded community by competing for resources with native species at the same trophic level (Top-down effects) (Byers 2000; Mollot et al. 2017; Eddy et al. 2020). Furthermore, the introduction of a new species may also represent the formation of a novel habitat and the provision of food resources previously unavailable to native species (Troost 2010; Van Riel et al. 2006; Vinagre et al. 2018). As well as change in the trophic interactions of the species, when an NS remains in the invaded community for some time, long-term effects on ecosystem diversity and functioning are also to be expected (Strayer et al. 2006; Wallentinus and Nyberg 2007; Pires-Teixeira et al. 2021).

The blue soft coral *Sansibia* sp., presumably of Indo-Pacific origin, was first detected in the benthos in natural communities in Brazil in 2017 along a 170m extension of shallow subtidal tropical rocky reefs at Vermelha Beach, Ilha Grande Bay, Rio de Janeiro (Mantelatto et al. 2018). All evidence indicates that the introduction occurred due to release by an aquarist, possibly for *in situ* coral farming and currently *Sansbia* sp. is considered a NS (Mantelatto et al. 2018; Carpinelli et al. 2020). Species of the genus *Sansibia* which is still little-known (Alderslade 2000) have zooxanthellae, photosynthetic algae which represent an additional trophic resource (source of energy) for some corals in addition to those gained by suspension feeding. Predation of blue coral at the site of introduction has not yet been observed and no studies have shown what resources *Sansibia* sp. consumes. According to recent surveys carried out at the site invaded by *Sansibia* sp. the soft coral has dominated deeper communities (positively associated with macroalgae and negatively associated with the zoantharian *Palythoacaribaeorum* (Mantelatto et al. 2018).

The aim of this study is to provide a trophic characterization of the food web on the recently invaded rocky reefs by using $\delta^{13}C$ and $\delta^{15}N$ analyses to describe its general trophic structure, identify the trophic level of consumers and investigate any trophic relationships between the NS soft coral *Sansibia* sp. and native species. An additional objective is to verify whether there is a difference between invaded and control areas without NS.

4.1.2 Methods

4.1.2.1 Sampling

This study was carried out at Praia Vermelha (PV), located in Angra dos Reis, in the inner part of the Ilha Grande Bay, southwest Atlantic (23º01'34"S, 44º30'05"W). PV is a sheltered site with little wave action and typical of the region with warm, shallow waters (reef maximum depths from 4 -7m where sand plain begins. The main local activities are nautical tourism and fishing. *Sansibia* sp. was detected along the rocky shore in 2017 together with two other NS *Clavularia* cf. *viridis* (Mantellato et al. 2018) and *Erythropodiumcaribaeorum* (Duchassaing and Michelotti, 1860) (Carpinelli et al. 2020).

The survey of the benthic community was carried out in December 2018 using methods of Mantelatto et al. (2018). Sampling was carried out in three 20 m transects placed parallel to the rocky shore at three depths: shallow (~ 1–1.9 m), intermediate (~ 2–2.9 m) and at the sandy bottom / rocky interface - bottom (~ 5–7 m), along an extension of approximately 20m invaded by *Sansibia* sp. (IS) and in two control areas with the same extension in which *Sansibia* sp. was naturally absent (C1 and C2). We used a Canon PowerShot G16 digital camera with a waterproof case attached to a quadrat 90 cm away from the digital camera to sample twenty 50 × 50 cm photoquadrats at 1 m intervals alternately above and below each transect.

At the same time, we sampled the more abundant of primary producers and macroconsumers for C and N isotopic analysis. From one-to-ten replicate individuals / colonies were sampled for each species. The encrusting benthic species were removed with the help of a hammer and chisel (corals and bryozoans), scissors (sponges and algae) and spatulas (turf algae, soft corals, ascidians and anemones). The multi-species turf forming algae were separated after collection to be analyzed individually. Plankton was collected with 68 µm nylon plankton net mounted in a trapezoidal shape with a threaded PVC cup at the bottom. All samples were frozen immediately after collection and sent for screening and preparation in the laboratory.

4.1.2.2 Laboratory analysis

In the laboratory the samples were defrosted naturally, the muscle tissue of the macroconsumers (echinoderms, crustaceans, gastropods and polychaetes) were removed. Marine sponges, sea squirts, anemones, zoanthids and soft corals had their soft tissues selected. Any epiphyte or epizoa were removed and all samples were washed with distilled water so that any contaminants that could influence the isotopic compositions were excluded. The samples were dried in an oven for 48 hours at 60°C and then macerated and reduced to a fine powder. Calcareous macroalgae, zooplankton, bryozoans, hydrozoans and small crustaceans were acidified (only for $\delta^{13}C$) according to Pires-Teixeira et al. (2020). The samples were then inserted into tin capsules, weighed on a digital balance and analyzed for the isotopic composition of carbon and nitrogen at the Centro de Energia Nuclear na Agricultura da Escola Superior de Agricultura Luiz de Queiroz da Universidade de São Paulo (CENA-USP).

Stable isotope analyzes were performed using a Delta Plus continuous flow isotope ratio mass spectrometer (CF-IRMS, Finnigan MAT, Bremen, Germany) coupled to an elemental analyzer (CE Instruments Wigan, United Kingdom). The isotopic composition is expressed in terms of a delta value (δ) in parts per thousand (‰) and is obtained by dividing the sample's isotopic ratio by the isotopic ratio of an internationally accepted standard multiplied by one thousand, according to the formula: $\delta X = [(R_{sample}/R_{standard}) -1] .10^3$, where δX is $\delta^{13}C$ or $\delta^{15}N$ and R the ratio ^{13}C: ^{12}C or ^{15}N: ^{14}N. The standard material for carbon was Pee Dee Belemnite limestone and the standard material for nitrogen was atmospheric air (Fry 1988). The standard deviation of isotopic measurements was estimated at 0.09 for $\delta^{13}C$ and 0.21 for $\delta^{15}N$ through repeated measures of the internal standard (sugar cane).

4.1.2.3 Data analysis

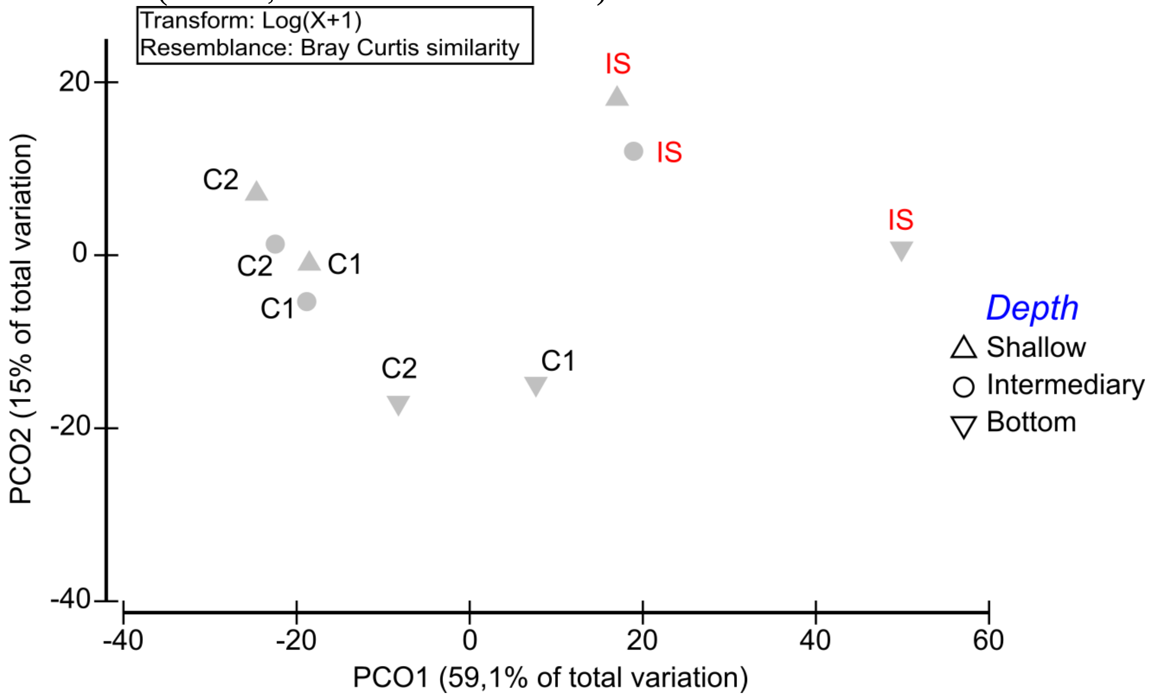
A biplot of the $\delta^{13}C$ and $\delta^{15}N$ values of the basal resources and consumers with the presence of potential predators was used to provide an overview of the trophic structure and identify possible trophic relationships between food sources and consumers through the SIMMR package (Parnell 2019) in the R Program (R Core Team 2020). To estimate the cover of benthic species for community analyses we used the Coral Point Count with Excel Extensions Software (Kohler and Gill 2006) to distribute 35 points on each image and to identify the organism below each point at the lowest possible taxonomic level. All species followed the nomenclature of the World Register of Marine Species (WoRMS) database (http://www.marinespecies.org/, accessed on 12 April 2021).

To describe the difference between areas invaded by *Sansibia* sp. (IS) and the control areas (C1 and C2) we used the Permutational MANOVA (PERMANOVA) based on Bray-Curtis similarity measures of the square root of percentage of cover of each taxon of the sessile macrobenthos + 1. Principal Coordinates Analysis (PCoA) was used to visualize the similarities or dissimilarities of composition data between areas (IS, C1 and C2) and depth (shallow, intermediate and bottom). The program PERMANOVA+ add-on for Primer v6 was used to for PERMANOVA and PCoA (Anderson et al. 2008).

4.1.3 Results

The invaded area (IS) had different species composition than the control areas (C1 and C2) (PERMANOVA: F= 5.065; $p < 0.05$). The PCoA plot confirmed that areas C1 and C2 grouped together and differ from IS mainly along first axis (PCO1 = 60% of variation) (Figure 17). In addition to the NS coral *Sansibia* sp., the main difference between the invaded and control areas was the composition of algae species, including the Rhodophyta *Asparagopsistaxiformis*, *Gelidium* sp. and the coralline alga *Janiaadhaerens* and the Phaeophyta *Dictyotaciliolata*, *Padina gymnospora* and *Sargassum* sp. The species composition of the areas was also varied over depth (PERMANOVA: F= 2.243; $p < 0.05$) and the NS infiltrated the community at all depths. The PCoA graph showed that the composition with depth varied along PCO2 (15% variation), especially the bottom communities (Figure 17).

Figure 17 - Variation in community composition between areas (IS, C1 and C2), and depth (shallow, intermediate and bottom)



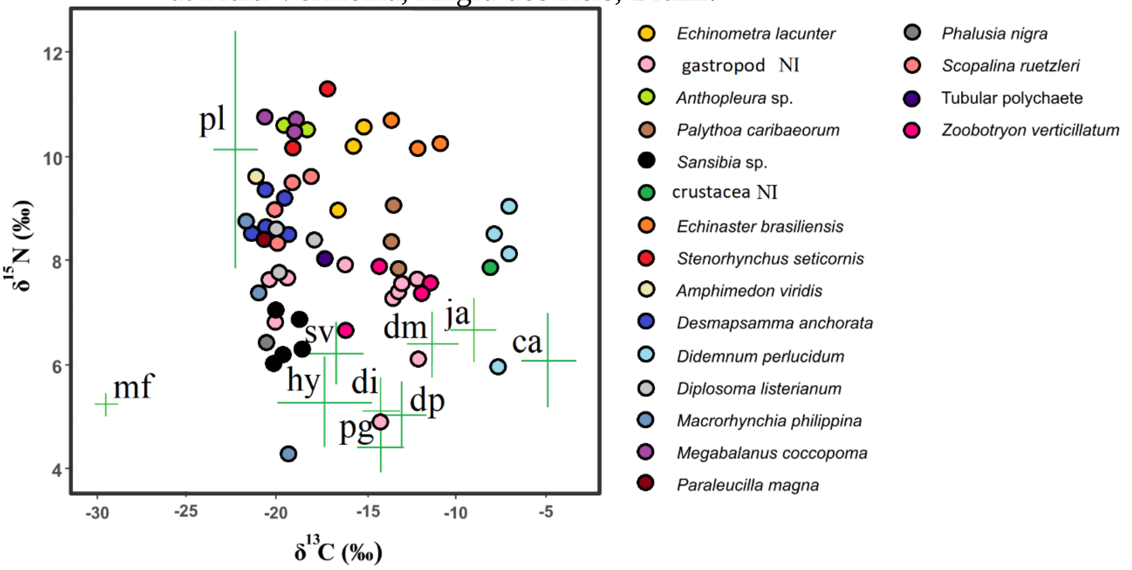
Source: PIRES-TEIXEIRA et al. (manuscript in preparation)

The control communities in the shallows and intermediate depths were similar and, especially in the shallows, the invaded community was richer and more diverse and dominated multi-species algal turfs and the zoantharian *Palythoacaribaeorum*, the most abundant species, both of which from mats. The invaded community was less dominated by these two taxons and thus richer, especially in the shallows but as *Sargassum* sp. increased its co-dominance with depth this difference disappeared on the bottom. *Sargassum* sp. was not recorded in controls. The coverage of *Sansibia* sp. was quite similar but slightly higher in the shallows (18.62%), followed by the bottom (15.86%) and intermediate (13.81%) (Table S11).

We analyzed the δ^{13}C and δ^{15}N of thirty species/groups, among them, twenty consumers and ten primary producers. The δ^{13}C value of the primary producers varied between -29.49‰ for the red alga *M. ferulaceus* and -4.87‰ for unidentified crustose coralline algae, representing respectively the lowest and highest mean value of δ^{13}C. The lowest mean values of δ^{15}N were from brown macroalgae *P. gymnospora* (4.41‰), *Dictyopteris* sp. (5.03‰) and *Dictyota* sp. (5.10‰). The highest mean value of δ^{15}N was from the generalist predator the arrow crab *S. seticornis* (10.77‰), followed by suspension feeding barnacle *M. coccopoma* (10.65‰) and mixotroph anemone *Anthopleura* sp. (10.53‰). The NS soft coral *Sansibia* sp. showed highly grouped values of δ^{15}N (6.31; 6.87; 7.05; 6.16; 8.47; 6.07‰) and δ^{13}C (-18.50; -18.79; -20.06; -19.64; -19.68; -20.07‰) in all collected samples (Figure 18).

Among the consumers, four species of crustaceans were analyzed including the zooplankton; however, among the species that move in search of food only the generalist predator *S. seticornis* (δ^{15}N: 10.16; 11.37‰; δ^{13}C: -19.02; -17.45‰) exhibited a trophic level considerably higher and close to the δ^{13}C values of *Sansibia* sp. We analyzed 10 unidentified gastropods with different δ^{13}C values; only two individuals (δ^{15}N: 7.62; 7.69‰; δ^{13}C: -20.46; -19.54‰) exhibited a trophic level above *Sansibia* sp. and similar δ^{13}C values. Among the primary producers, the macroalga Rhodophyta *Hypnea* sp. (δ^{13}C: -19.20; -15.43‰; δ^{15}N: 5.89; 4.65‰), collected as part of multi-species algal turf and separated later in the laboratory, presented values consistent with its consumption by the NS coral *Sansibia*sp (Figure 18).

Figure 18 - Biplot of the stable isotopic C and N of the community invaded by *Sansibia* sp. at Praia Vermelha, Angra dos Reis, Brazil.



Legend: Symbols (+) indicate the mean (± SD) of resources: unidentified crustose coralline algae (ca), *Janiaadhaerens* (ja), *Melanothamnusferulaceus* (mf), *Hypnea* sp. (hy), *Dictyota* sp. (di), *Dictyopteris* sp. (dp), *Dictyotamenstrualis* (dm), *Sargassum* sp. (sv), *Padina gymnospora* (pg) and plankton (pl). Circles of different colors indicate the isotopic values of consumers separated by species/rate.

Source: PIRES-TEIXEIRA et al. (manuscript in preparation)

4.1.4 Discussion

This study provides new information on the trophic relationship between an NS and other species in a food web on invaded shallow reefs in the tropical southeast Atlantic, and for the first time we provide isotopic values of C and N of the NS blue soft coral *Sansibia* sp., in addition to 29 other native benthic marine species. We also demonstrate that communities in invaded areas and control areas are different in terms of species composition, as well over different depths.

The presence of *Sansibia* sp. at different depths confirms the ability of this species to disperse and colonize from a sandy bottom to areas close to the surface (McFadden et al. 2014) and also proves its success as a NS that maintains high coverage rates two years after its initial invasion was documented (Mantelatto et al. 2018). Apparentl, there have been some changes in the benthic community since the last survey of the invaded community (Mantelatto et al. 2018). These changes may involve the seasonal variation in species (such as an increase in *Sargassum* sp., a macroalgae with an extensive distribution on the Brazilian coast and recognized for its sensitivity to variations in temperature, salinity and pollutants (Leite and Turra 2003). Compared to Mantelatto et al. (2018) there was also a decrease in multi-species algal turf and in the zoanthid *Palythoacaribaeorum*, both native mat forming taxons that can offer biological resistance to invasion. Although *Sansibia* sp. coverage seems to have decreased at depth since the last study (two years ago), in the shallows the coverage has increased. This suggest that after establishing in deeper waters it continued to expand its distribution to shallower areas, as the NS soft coral lives in association with photosynthetic microalgae and therefore needs light as an alternative source of energy.

Sansibia sp. showed δ^{15}N values close to macroalgal values, suggesting that the symbiosis with zooxanthellae represents an essential source of energy, in addition to suspension feeding. We observed that for resources, *Hypnea* sp., (Rhodophyta), part of the multi-species turf forming, presented the values of δ^{13}C and δ^{15}N consistent with its consumption by the NS coral *Sansibia* sp. and thus possibly represents a resource being consumed as a food source by *Sansibia* sp., probably captured as fragments of suspended debris after breakage by waves or herbivores. Interestingly the same source (*Hypnea* sp.) has previously been reported as a probable resource consumed by suspensivorous filter feeder corals *Tubastraea* spp. which are also invasive species at other sites in the region (Pires-Teixeira et al. 2021, manuscript in preparation). There was no relationship between the abundance of *Sansibia* sp. and other functionally similar species and our results for δ^{13}C and δ^{15}N show that *Sansibia* sp. occupies a specific portion of the isotopic space and is different from other mixotrophic species such as *P. caribaeorum* and some sponges. No consumer had isotopic values superimposed on the values of *Sansibia* sp., but the ascidian *Phalusia nigra* and the gastropod were the closest species. So far, no study on potential predation of the soft coral *Sansibia* sp. has been performed but one video observation filmed during a control experiment with salt filmed the arrow crab *Stenorhynchusseticornis* apparently eating retracted *Sansibia* sp. (Video S12) which lends support to predation by the arrow crab, an opportunistic generalist consumer that feeds according to the availability of the most abundant food in the environment (Cobo et al. 2019) showed values of δ^{13}C and δ^{15}N aligned as one possible consumer.

In conclusion we use here the analysis of δ^{13}C and δ^{15}N isotopes to characterize a trophic web and have provided evidence of the use of different energy sources in a NS zooxanthelate soft coral species, as well as identified trophic relationships between the NS *Sansibia* sp. and potential consumer and possible resources. Our study has also described changes in NS abundance at different depths in an invaded rocky shore community and suggests a potential mechanism for the further expantion to other favorable locations. We expect that that the NS soft coral *Sansibia* sp. will soon become the most abundant species in Praia Vermelha (Pires-Teixeira et al. 2021) and we encourage continuous monitoring of the invaded area along as well as action for control and eradication.

4.1.5 Acknowledgments

We are especially grateful to Amanda Guilherme, Herick Simas, Marcello Mantellato, and Vinícius Kerr for help in the field. Thisworkwassupportedby Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (JCC, FAPERJ E-26/010.003031/2014 and E26/203.002/2017) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (JCC, CNPq- 305924/2018-4). LMPT acknowledges Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) thatprovided a PhD scholarship. VNL acknowledgesthe Universidade do Estado do Rio de Janeiro thatprovided a TeachingSupportScholarship (PAPD-UERJ/2019).

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4.1.8 Supplementary material

Table S11 - Major space-occupying taxa/functional groups and their percentage cover (%) at Control sites (C1 and C2) and at Invaded site (IS) amongst different depths (Shallow, Intermediate and Bottom) in the Praia Vermelha, Ilha Grande Bay, Brazil (to be continued).

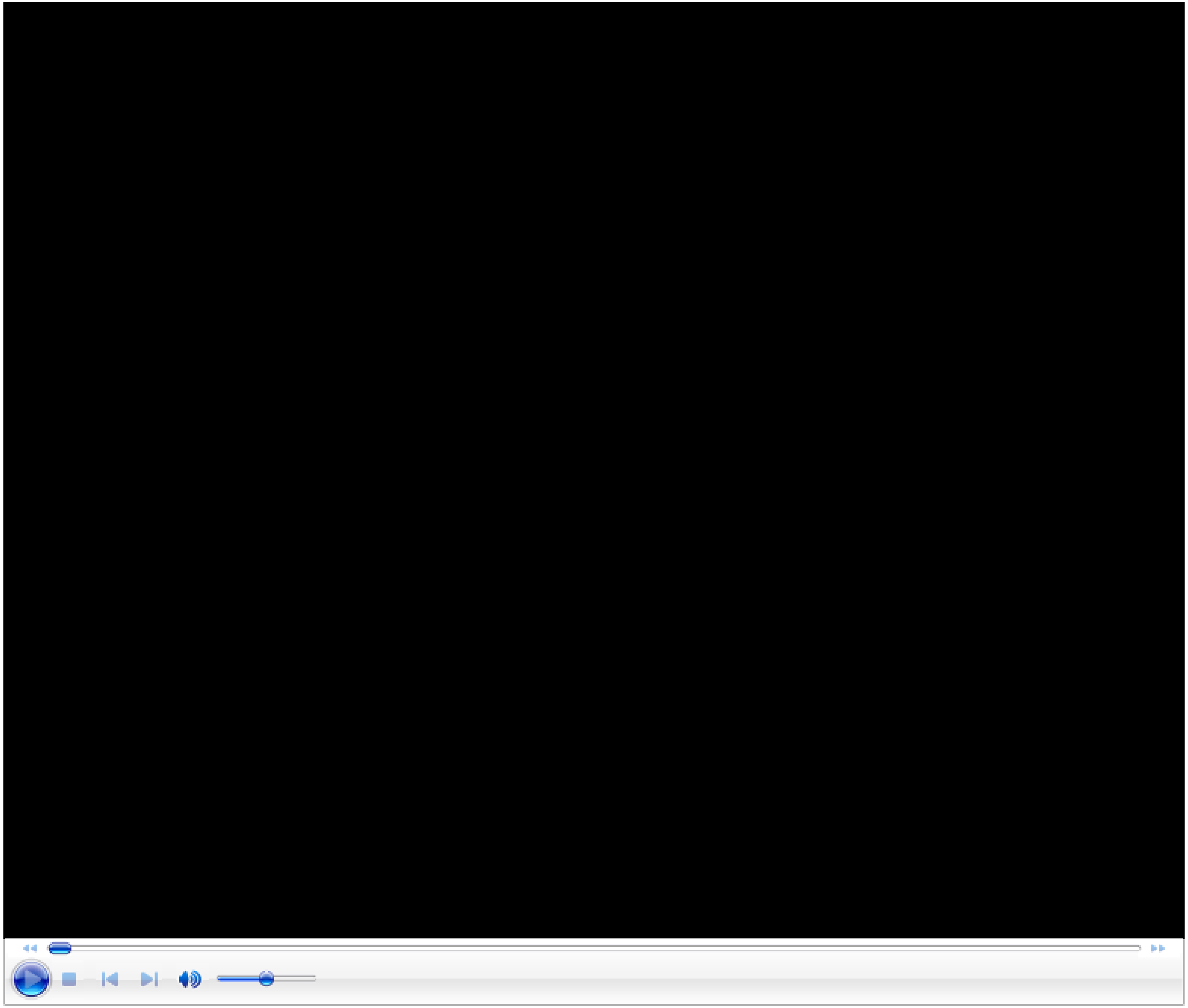
	Shallow			Intermediary			Bottom		
Taxa	C1	C2	IS	C1	C2	IS	C1	C2	IS
Multi-speciesturfforming	63.00	32.57	21.86	37.52	24.52	11.81	54.33	37.57	2.33
Crustosecorallinealgae	4.71	1.90	10.90	6.57	2.76	3.67	1.33	1.24	0.90
Asparagopsistaxiformis (Delile) Trevisan de SaintLéon, 1845			0.10	0.19		1.95			
Dichotomariamarginata (J.Ellis&Solander) Lamarck, 1816	0.19		1.43			6.76	17.52	5.38	18.52
Gelidium sp.			0.29						0.38
*Jania*J.V.Lamouroux, 1812	0.10		6.10	0.05	0.05	1.90	1.86		0.90
Colpomenia sinuosa (Mertensex Roth) Derbès&Solier, 1851			0.05						
*Dictyota*J.V.Lamouroux, 1809 sp. 1			2.57			1.52	0.90	0.19	2.71
Melanothamnusferulaceus(SuhrexJ.Agardh) Díaz-Tapia&Maggs, 2017 (Suhr ex J.Agardh) S.M.Guimarães&M.T.Fujii, 2004	2.95			15.38	2.05		5.29	15.29	0.57
Padinagymnospora (Kützing) Sonder, 1871			0.52			1.19	0.76		1.19
*Sargassum*C.Agardh, 1820			19.43			34.33			53.38
FilamentousAlgae	1.14								
Palythoacaribaeorum (Duchassaing&Michelotti, 1860)	26.19	64.67	13.24	37.38	69.76	21.76	12.62	37.57	0.62
Zoanthussociatus (Ellis, 1768)		0.14						0.19	
Sansibia Alderslade, 2000			18.62			13.81			15.86
Mussismilia hispida (Verrill, 1901)					0.05		0.71		
*Amphimedonviridis*Duchassaing&Michelotti, 1864	0.43		1.48	0.52	0.05	0.29	0.76		1.10
Desmapsammaanchorata (Carter, 1882)	0.57	0.62	1.33	1.38	0.24	0.48	1.29	0.67	0.76
*Iotrochota arenosa*Rützler, Maldonado, Piantoni&Riesgo, 2007				0.19			0.71		
Mycale (Aegogropila) *americana* van Soest, 1984			0.10						0.38
Scopalinaruetzleri (Wiedenmayer, 1977)	0.10		1.00	0.14	0.19	0.24	1.05	0.81	0.38
Tedania(Tedania) *ignis* (Duchassaing&Michelotti, 1864)			0.05			0.10		0.38	
*Paraleucilla magna*Klautau, Monteiro &Borojevic, 2004			0.10		0.10				
*Schizoporella*Hincks, 1877sp.				0.05	0.05			0.33	
*Botrylloidesnigrum*Herdman, 1886						0.05			
*Macrorhynchiaphilippina*Kirchenpauer, 1872			0.38		0.05				

Table S11 - Major space-occupying taxa/functional groups and their percentage cover (%) at Control sites (C1 and C2) and at Invaded site (IS) amongst different depths (Shallow, Intermediate and Bottom) in the Praia Vermelha, Ilha Grande Bay, Brazil (conclusion).

*Phallusianigra*Savigny, 1816									
*Didemnum*Savigny, 1816	0.05	0.05	0.14					0.19	
Mollusca	0.48	0.05		0.52	0.05		0.86	0.19	
Echinodermata	0.10		0.33	0.10	0.10	0.14			
TOTAL	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00

Source: PIRES-TEIXEIRA ET AL. (manuscript in preparation)

Video S12 - Video observation filmed the arrow crab Stenorhynchusseticornis apparently eating retracted Sansibia sp.



5 **EXTENSÃO UNIVERSITÁRIA COMO FERRAMENTA PARA PROMOVER A PROFISSÃO DO CIENTISTA.**

5.1 Promovendo a profissão do cientista a partir de um projeto de extensão universitária.

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Resumo

A ciência deve ser cada vez mais valorizada, incentivada e acessível dentro e fora do meio acadêmico. O apoio popular de quem não tem contato com a ciência no seu dia a dia, é fundamental nesse processo. O Projeto “Pra que Serve?” é um projeto de extensão universitária que tem como objetivo trazer a debate a importância da ciência, sobretudo em ambiente marinho, em uma cidade litorânea como o Rio de Janeiro, e contribuir para a valorização da pesquisa científica, possibilitando, de forma simples e acessível, vivências de pesquisa e acesso a conteúdo científico. A oficina que constitui a metodologia do Projeto pode ser aplicada de duas formas, visitas escolares programadas e eventos de ciência abertos ao público espontâneo. No presente trabalho, nós relatamos a experiência vivenciada no Espaço de Desenvolvimento Infantil Professora Solange Conceição Tricarico na comunidade da Maré, no Instituto Benjamin

Constant, escola que atende crianças e adolescentes cegos, surdocegos, com baixa visão e deficiência múltipla e nos eventos Bio na Rua 2018 e 2019, no Parque Madureira, localizado na zona norte carioca. Ao longo da oficina, foram registrados por meio de fotografias, momentos de interação, para que pudéssemos analisar diferentes dimensões de atuação do projeto e a resposta daqueles que participavam. A curiosidade sobre o material utilizado na pesquisa marinha foi fundamental para despertar o interesse do público, independente da faixa etária e do local da oficina. Detectamos diferentes interações durante as oficinas, sendo a observação e/ou atenção às explicações a mais recorrente. Responder "O que é?" e "Pra que serve?" a ciência, considerando as ações do Projeto despertou nos participantes grande engajamento nos temas científicos e curiosidade sobre a profissão do(a) cientista. A partir dos resultados positivos apresentados no presente trabalho daremos continuidade às ações do Projeto, buscando ampliar o desenvolvimento qualitativo de práticas como essa.

PALAVRAS-CHAVE: Ciência; Costão rochoso; Divulgação científica; Ecologia marinha; Popularização da ciência.

5.1.1 Introdução

A divulgação científica se refere à difusão de informações em ciência, tecnologia e inovação, voltada, principalmente, para aqueles que não têm, obrigatoriamente, formação técnico-científica que permita compreender conceitos científicos sem esforço (Bueno 2010). Difundir a ciência usando uma linguagem acessível aproxima a população dos trabalhos desenvolvidos no âmbito da ciência e tecnologia (C&T) o que, além de estender informações para um público maior, esclarece sobre os serviços que a ciência pode prestar e aumenta, também, a confiança por aqueles responsáveis por fazer ciência.

Albagli (1996) aponta diferentes objetivos que podem orientar o papel da divulgação científica, entre eles a ampliação do conhecimento e da compreensão a respeito do processo científico e sua lógica (educação), o desenvolvimento de uma opinião pública informada sobre os impactos do desenvolvimento científico e tecnológico sobre a sociedade, particularmente em áreas críticas do processo de tomada de decisões (cívico), e a ampliação da possibilidade e da qualidade de participação da sociedade na formulação de políticas públicas e na escolha de opções tecnológicas (mobilização popular).

O interesse de brasileiros e brasileiras por C&T pode ser considerado satisfatório. No entanto, na mídia, o acesso aos conteúdos que envolvem esse tema ainda é escasso e as pessoas que afirmam ser interessadas em C&T não assistem por exemplo, a programas de TV que abordem a temática. Tais dados mostram haver uma associação significativa entre manifestar-se interessado em C&T e ter algum acesso à informação sobre tais temas (Velho 2017). Resultados como esses nos fazem questionar quais ações são necessárias para popularizar a ciência.

As Instituições de Ensino Superior (IES) desempenham papéis importantes emcultivar conhecimento e colocá-lo em benefício da sociedade (Schwartzman eChristophe, 2008). No entanto, o conhecimento gerado raramente atravessa os limitesda academia. A falta de um diálogo constante entre aqueles que fazem ciência e a sociedade gera dúvidas quanto à profissão do cientista e à importância do mesmo. A falta de informação do público leigo é o que o torna vulnerável a pseudociência, a manipulação e o artificialismo político. A maior parte das pesquisas no âmbito acadêmico é financiada com dinheiro público, o que torna ainda mais imprescindível o diálogo entre ciência e sociedade (Tostes 2006). Ainda que a importância e o impacto das descobertas científicas e de suas aplicações através da tecnologia como meio de desenvolvimento e de promoção do bem-estar sejam reconhecidos, a pesquisa científica ainda é encarada com apreensão e importantes dúvidas são levantadas com relação ao papel da ciência na sociedade (Sala 2017).

A divulgação científica, na prática, não está restrita aos meios de comunicação demassa, inclui também o uso de livros didáticos, palestras de Ciências, histórias em quadrinhose folhetos para veiculação de informações científicas (Bueno 2010). Aeducação em Ciências faz com que o aluno interprete o mundo desde o ponto de vista dasciências, maneje conceitos, leis e teorias científicas, e aborde problemas raciocinando,cientificamente, identificando aspectos históricos, epistemológicos, sociais e culturais dasCiências (Moreira 2004). Independentemente do método adotado, a educação emciências pode inspirar futuros cientistas e despertar nas pessoas atitudes típicas de umcientista: curiosidade intelectual, dúvida metódica, observação dos fatos e busca de relações causais (Schwartzmane Christophe 2009).

5.1.1.1 “Projeto Pra Que Serve?” O que faz um cientista que trabalha com o mar.

A ciência deve ser cada vez mais valorizada, incentivada e estar acessível para todos, dentro e fora do meio acadêmico. O apoio da população que não tem contato com a ciência no seu dia a dia, é fundamental nesse processo. A ciência funciona como ferramenta transformadora em termos sociais e econômicos, mas, em uma sociedade que, majoritariamente, desconhece o desenvolvimento dos saberes científicos, esse processo fica distante de uma realidade de avanços nesses mesmos termos. O Projeto “Pra que Serve?” é um projeto de extensão universitária que tem como principal objetivo divulgar a profissão do cientista que trabalha com o mar, enriquecendo o conhecimento que o público não acadêmico possui acerca da ciência, das etapas do trabalho de um cientista e da importância do desenvolvimento de pesquisas científicas. O projeto foi elaborado para diferentes públicos, desde o ambiente escolar até espaços públicos. Relatamos aqui a experiência que vivenciamos durante as oficinas de extensão, a avaliação acerca da resposta do público, os desafios que encontramos e as perspectivas futuras para dar continuidade ao projeto.

5.1.2 Procedimentos Metodológicos

Para trazer à debate a importância da ciência, sobretudo no ambiente marinho emuma cidade litorâneo como o Rio de Janeiro, e reverter a atual situação desfavorável aciência, contribuindo para a valorização da pesquisa científica no Brasil, o projeto “Pra queserve?” foi organizado de forma simples e plástica, adaptado a qualquer tipo de local epúblico com diferentes idades, deficientes visuais ou com baixa visão e pessoas nãoalfabetizadas. Desta forma, pretendemos alcançar locais com carência de centros e deinstituições de pesquisa e de ensino, como comunidades periféricas e violentas.

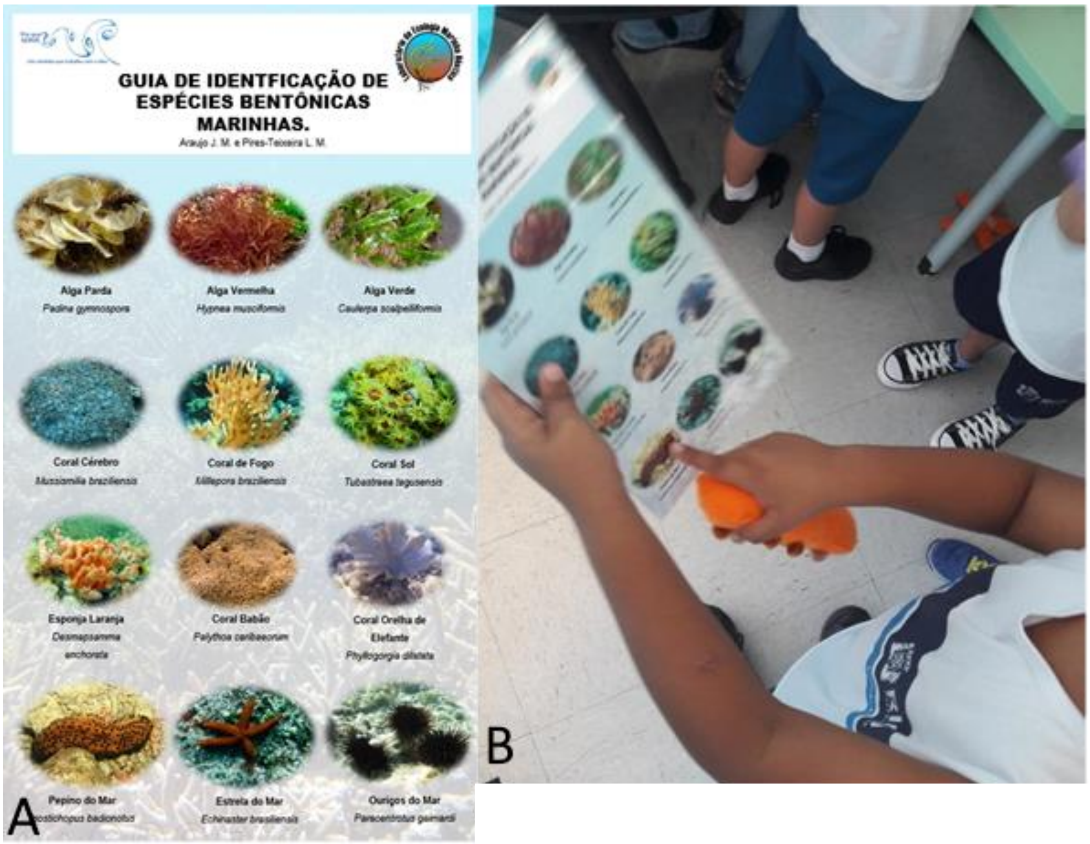
5.1.2.1 Material utilizado

Inicialmente, nós produzimos material audiovisual e material permanente com o tema “pesquisa no mar”, confeccionado em feltro, EVA e materiais de texturas diferentes. Os modelos didáticos de organismos marinhos (Figura 19) representam suas principais características morfológicas e são acessíveis ao manuseio pelo público, não dependendo somente do recurso visual. Produzimos um guia de identificação de espécies marinhas bentônicas, encontradas no litoral brasileiro, com foto e nome popular/científico de cada espécie (Figura 20).

Figura 19 – Modelos didáticos dos organismos marinhos confeccionados em feltro e EVAe tirinha em quadrinho sobre o trabalho de um cientista que trabalho com o mar.

Fonte: TEIXEIRA ET AL. 2021

Figura 20 – (A) Guia de espécies marinhas bentônicas encontradas no litoralbrasileiro;(B) Guia sendo utilizado por alunoda pré-escola do Espaço de Desenvolvimento Infantil Professora SolangeConceição Tricarico.



Fonte: TEIXEIRA et al. 2021

Elaboramos uma tirinha em quadrinhos para ser pintada, relatando as atividadesrealizadas por um cientista que trabalha com o mar (Figura 3). Esperamos atingir não sóquem participou daoficina, mas também outras pessoas, com o manuseio desse material,que pode ser levadopelos participantes/alunos. A tirinha contém o endereço eletrônicodas redes sociaisvinculadas ao laboratório de pesquisa e o contato para agendamento daoficina.

Figura 21 - Tirinha em quadrinho mostrando o trabalho de uma cientista que trabalha com o mar.

Nota: Durante a oficina ela é distribuída em preto e branco para que os participantes possam colorir e assim perceber detalhes nos diálogos e peculiaridades dos organismos marinhos.
Fonte: TEIXEIRA ET AL. 2021

5.1.2.2 Desenvolvimento da oficina

A oficina pode ser aplicada de duas formas, sendo elas, visitas escolaresprogramadas e eventos de ciência abertos ao público espontâneo. No presente trabalho,nós relatamos a experiência vivenciada no Espaço de Desenvolvimento Infantil ProfessoraSolange Conceição Tricarico na comunidade da Maré (maio de 2019); no InstitutoBenjamin Constant (IBC), escola que atende crianças e adolescentes cegos, surdocegos,com baixa visão e deficiência múltipla localizada no bairro da Urca (novembro de 2018); enos eventos Bio na Rua 2018 (novembro de 2018) e Bio na Rua 2019 (dezembro de2019), ambos no Parque Madureira, localizado no bairro de Madureira na zona nortecarioca.

Nos eventos de divulgação científica, Bio na Rua, condensamos a oficina eminformações rápidas e materiais lúdicos para manuseio do público. No IBC, apresentamos diferentes materiais, texturas, roupas de Neoprene (tecido usualmente usado para omergulho) e material de mergulho, para que os alunos pudessem experimentar o trabalhodo cientista e se vestir como cientistas em um trabalho de campo no ambiente marinho.No Espaço de Desenvolvimento Infantil Professora Solange Conceição Tricarico, a oficinafoi adaptada para crianças da creche a pré-escola, com idade entre 3 e 6 anos, sendoutilizados, principalmente, os modelos didáticos dos organismos marinhos, espécimesfixados de animais marinhos (Coleção zoológica da Seção de Assistência ao Ensino – SAE,setor educativo do Museu Nacional – MN/UFRJ), figuras, leituras e recursos como pinturae desenho.

Inicialmente, para nos aproximarmos e despertarmos o interesse do público pelotema principal, questionamos qual o conhecimento prévio dos participantes com relação aalgum(a) cientista, para que, em seguida, nos apresentemos como um(a) cientista. Paraengajar os participantes na discussão do importante papel da ciência na sociedade,exemplificamos parte do trabalho que realizamos no âmbito da pesquisa em IES,descrevemos atividades de campo e de laboratório, apresentando de forma sucinta nossodia a dia como cientistas. Durante esse diálogo, expomos utensílios que um(a) cientistamarinho(a), ou seja, que trabalha com o mar, utiliza. Entre eles, materiais de mergulhoautônomo como nadadeiras, máscaras de mergulho, colete e regulador de mergulho,amostradores e tubos de anotação submersíveis[1], sempre possibilitando que osparticipantes vistam e manuseiem os materiais.

5.1.2.3 Registro fotográfico e análise de dados

Ao longo da oficina, foram realizados registros fotográficos dos momentos de interação dos participantes, para que pudéssemos analisar diferentes dimensões de atuação do projeto e a resposta daqueles que participavam da oficina. Também analisamos a diferença das interações nas propostas pedagógicas da oficina, quando aplicadas em ambiente escolar e para o público espontâneo em feiras e eventos de ciências, na perspectiva da antropologia visual (Banks 1998). Para tal, foi feita uma abordagem quali-quantitativa com base na análise fotográfica das interações nas oficinas realizadas. Na Oficina realizada no IBC, não foi possível o registro fotográfico tão amplo por motivos logísticos, portanto, as imagens não serão usadas na análise de interações.

[1] Para escrever dentro d’água, os mergulhadores utilizam lápis sobre um tubo de PVC (polímero de adição policloreto de vinila), um tipo de material usado em encanamentos de água e esgoto.

As análises foram feitas no software Dedoose (Version 8.3.35, 2021), que auxilia naanálise de imagens com base na codificação de cenas que apresentem atitudes einterações dosparticipantes. Nós avaliamos a ocorrência de atividades de leitura,interação com materialdidático, observação/atenção às explicações, interação com os(as)pesquisadores(as)/professores(as) e emoções. As emoções foram analisadas pelo registrodeexpressões faciais. Utilizando uma planilha no Microsoft Excel 2016, organizamos aquantidade com que cada tipo de interação foi observado e calculamos a porcentagem decadainteração.

5.1.3 Resultados e Discussão

A curiosidade sobre o material utilizado em pesquisa subaquática foi fundamentalpara despertar o interesse do público, independente da faixa etária e do local da oficina. Otubo de anotação submersível foi o material mais manuseado pelas crianças de formageral (Figura4), e participantes adultos que visitaram o estande do Projeto se mostraramsurpresos com a possibilidade de escrever enquanto submersos. Em todos os ambientesque a oficina foi oferecida, ainda que o público fosse diferente, tanto a parte teóricaquanto a parte prática foram realizadas, mantendo informações que despertassem acuriosidade e o interesse, linguagem clara e informal, recursos táteis e possíveis demanusear, associados a informações do dia a dia.

Figura 22 - Aluno da pré-escola do Espaço de Desenvolvimento Infantil Professora Solange Conceição Tricaricomanuseando o tubo de anotação submersível.

Fonte: TEIXEIRA et al. 2021

Com as figuras e os modelos didáticos mostramos parte da diversidade que existeno fundo do mar, engajamos os participantes em discussões acerca da biologia e ecologiade diferentes organismos marinhos, levantamos curiosidades envolvendo ocomportamento e anatomia desses organismos, diferença entre grupos de animais e algase a importância da preservação dos ambientes marinhos, como praias, costões rochosos,recifes de coral, mangues e restingas. São exemplos das questões levantadas com maiorfrequência: Entre os organismos apresentados, quais são animais e quais são plantas?

Onde fica a boca? Como se locomovem e se alimentam? Existe animal sem olho? O quesão e qual a importância de animais sésseis? Por que precisamos preservar o ambientemarinho?

Um recurso que utilizamos durante a oficina no Instituto Benjamin Constant (IBC), além dos organismos em feltro, foram tipos diferentes de esponja para manuseio e observação da diferença de uma esponja sintética, utilizada para lavar louça, uma esponja vegetal e um esqueleto de esponja marinha verdadeiro. Fizemos o mesmo com uma folha de árvore e uma alga marinha. Os alunos ficaram surpresos com a possibilidade de tocar em organismos que habitam o fundo do mar, e animados em adivinhar qual era o organismo e seu respectivo ambiente. Para alunos da pré-escola, tentar identificar a espécie do organismo em feltro, observando a ficha de identificação foi uma forma divertida para eles exercerem o trabalho de um cientista marinho e, ao mesmo tempo, aprender sobre cada um dos organismos e suas características básicas. Para o público que frequentou o stand durante a feira de divulgação científica, observar figuras nos livros de fotografia marinha foi um recurso importante para um diálogo não só sobre a profissão do cientista, mas sobre o ambiente marinho, a importância da preservação desses ambientes, e a biologia de alguns organismos, como por exemplo, saber que o coral é um animal e não uma planta, e a importância das algas marinhas como produtoras de oxigênio.

Quanto às interações avaliadas nas imagens fotográficas obtidas durante as oficinas, distinguimos duas modalidades oferecidas, público escolar (n=50) e público espontâneo (n=50). Identificamos 148 diferentes ocorrências das interações que mapeamos, sendo a observação e/ou atenção às explicações a mais recorrente (n=53) seguida das interações com os(as) pesquisadores(as)/professores(as) e monitores(as) (n=34) e com o material didático (n=33). A leitura ocorreu em maior número nas oficinas direcionadas ao público espontâneo (n=17), que incluía adultos nas interações, o que pode ser reflexo do caráter menos aprofundado da modalidade de oficina de divulgação, e como consequência, os participantes buscaram por conta própria, ler o material disponível sobre os assuntos abordados. Em contrapartida, com as crianças em ambiente escolar, as atividades participativas se destacaram, com grande número de interações com o material didático (n=20) e observação das explicações dadas pelos (as) pesquisadores(as)/professores(as) (n=35) (Tabela 1). Destacamos, também, as emoções, que ocorreram, apenas, no ambiente escolar (N=11), todas positivas, representando alegria e surpresa, demonstrando que a proposta imersiva da oficina pode promover o engajamento aos temas científicos de forma lúdica, e proporcionar aprendizados a partir de respostas no campo afetivo.

Tabela 8 - Proporções de ocorrência das interações observadas nas oficinas do Projeto Pra queServe?

Interações observadas	n	Visita escolar	Público espontâneo	Contribuição relativa de cada interação
Emoção	11	100%		7%
Interação com material didático	33	61%	42%	22%
Interação com professores	34	56%	38%	23%
Observação e/ou atençãoáesxplicação	53	66%	34%	36%
Leitura	17	29%	71%	11%
Total	148			100%

Fonte: TEIXEIRA et al. 2021

Segundo Gohn (1999), a concepção ampla de educação está associada ao conceito de cultura e apresenta perfil multidimensional relacionado à aprendizagem política de direitos coletivos e individuais e a aprendizagem de conteúdos escolares, ambos em formas e espaços diferenciados. Sendo assim, conseguimos perceber a importância de práticas sociais para o aprendizado, sobretudo, daqueles com baixo ou nenhum acesso à informação. Partindo desse pressuposto, podemos colocar como primeiro resultado relevante do projeto “Pra que serve?” o acesso de diferentes grupos sociais a conteúdos técnico-científicos, muitas vezes sendo o primeiro contato do público com o tema abordado. Não tivemos problemas de comunicação para exposição dos conceitos básicos e a estrutura da oficina se adequou muito bem aos diferentes públicos até o momento, acreditamos que o perfil prático e dinâmico tenha contribuído para a resposta positiva mencionada.

Em nossas atuações com ensino infantil, educação especial e creche fomos surpreendidas pela quantidade de perguntas e pelo envolvimento dos alunos, e recebemos mensagens de mães e de professores, reforçando a resposta que os alunos apresentaram após as atividades, principalmente, em relação ao contato com material exposto e novas informações acerca da profissão do cientista. Tivemos interessantes discussões com os alunos que questionaram: “Por onde ele faz o número dois?” – aluna de educação infantil se referindo a excreção dos corais; “Mas como ele é bicho se não tem olho” “Você já montou em um cavalo marinho?” – aluna deficiente visual interessada e relatando a sua perspectiva sobre o tamanho dos cavalos marinhos, que, na verdade, são bem pequenos; “Os corais são meio pedras e meio plantas né?” - aluna de ensino infantil demonstrando seu conhecimento empírico sobre animais bentônicos marinhos; “Meu pai tem essas coisas também” - aluno de ensino infantil, identificando materiais de mergulho que são utilizados pelo pai na rotina de trabalho com pesca.

A apresentação dos materiais de mergulho autônomo, aparatos de pesquisa e os modelos didáticos confeccionados com detalhes biológicos e cores chamativas, sem dúvida, despertaram a curiosidade do público que questiona e se engaja desde o início na oficina, interessados em compreender como funcionam os equipamentos e que organismos tão diferentes estão representados ali.

Outro ponto relevante é a nossa apresentação inicial que rompe, sem dúvida, o pré-conceito em relação ao perfil do cientista que é construído no imaginário popular, figura masculina, de jaleco e óculos, que trabalha dentro de um laboratório. Ouvimos relatos como: “Nossa! Nunca tinha visto uma cientista assim de perto.”; “Você é cientista? Como faz para ser também?”.

Após a oficina, os participantes demonstraram interesse na profissão do cientista marinho por meio de perguntas acerca das etapas necessárias para se tornar um cientista. Não só o público infantil, mas também os adultos durante a feira de divulgação científica se interessaram pelo trabalho e relataram o interesse pelo mergulho. Identificamos esse retorno como mais um ponto positivo na realização das oficinas, que representa uma possibilidade para muitos que não sabiam que existia essa linha de trabalho disponível. A ausência de um discurso positivo e esperançoso, o pouco prestígio da imagem social do cientista e a deficiência na comunicação pelos profissionais são alguns fatores que contribuem para a falta de motivação dos jovens para seguirem carreira profissional na área de pesquisa em C&T (Carrapatoso et al. 2005). Apresentar informações sobre a profissão do cientista não só contribuiu para a divulgação científica, tornando a sociedade no geral mais informada e crítica, mas também inspirou os participantes a seguirem a carreira de cientista.

5.1.4 Considerações finais

O projeto de extensão aqui apresentado busca a princípio difundir conceitos básicos de ciência e do trabalho do cientista, trabalhando no âmbito da divulgação científica com oficinas versáteis e adaptadas a diferentes públicos, sobretudo para escolas e em comunidades afastadas ou com difícil penetração em centros de pesquisa, como periferias, escolas com público majoritariamente de estudantes portadores de deficiência e em locais de risco. Até o momento, de acordo com os resultados apresentados, nosso retorno foi positivo e pudemos perceber a desconstrução de muitos conceitos prévios sobre o que é ser cientista, no Brasil, o que nos torna mais próximos do nosso público e, por conseguinte, nosso público demonstra vontade de fazer e conhecer a ciência.

É fundamental responder “O que é?” e “Pra que serve?” todo tipo de ciência bemcomo os cientistas. Portanto, as ações do projeto continuarão e se aprimorarão no âmbitoda extensão universitária e da divulgação científica, buscando ampliar o desenvolvimentoqualitativo de práticas como essa.

5.1.5 Referências

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CONSIDERAÇÕES FINAIS

Toda a pesquisa realizada no presente trabalho está inserida no contexto da bioinvasão marinha, que, como mostramos aqui, está aumentando exponencialmente com o passar dos anos (capítulo 1). De acordo com a lista atualizada que fornecemos juntos aos resultados, em dez anos o número de espécies exóticas (EE) no litoral brasileiro aumentou 160% e atualmente conta com cento e trinta e oito EE marinhas em 15 classes ou grupos funcionais. Entre as EE, chama atenção o aumento no número de espécies estabelecidas e a diminuição de espécies detectadas, que mostra não só a ineficiência em controlar completamente o movimento das EE mas também apoia o que diferentes estudos vem demonstrando, a capacidade que as EE têm para aumentar sua abundância, colonizar novas áreas e dominar as áreas invadidas (Meinesz et al. 2001; Piazzi et al. 2001; Branch et al. 2004; Zabin et al. 2007). Neste caso, há alguns peculiaridades do Atlântico sudeste quando comparado com as demais regiões da planeta (Bailey et al. 2020 – ANEXO B).Outros resultados desse estudo sugerem o mesmo, já que mostramos queo estabelecimento de um EEI afeta a comunidade invadida não apenas por representar mais uma espécie, mas também porimpactar consideravelmente a uniformidade (a abundância relativa das outras espécies) (capítulo 2).

Todas as EEI marinhas avaliadas nesse estudo estão estre as espécies mais abundantes nas suas respectivas comunidades invadidas(capítulo 2). Os corais *Tubastraea* spp. são um exemplo de EEI bem-sucedida e mostramos aqui quea pressão de predação não é um fator forte o suficiente para evitar a rápida expansão desse corais, ao mesmo tempo que os recursos alimentares não são limitantes e *Tubastraea* spp. é um competidor alimentar de sucesso que ocupa um nicho específico dentro do nicho ocupado por outras espécies funcionalmente equivalentes (capítulo 3).

Outro coral que representa uma invasão recente e que também foi nosso objeto de estudo parece estar, da mesma forma, ampliando sua área de cobertura. Nossos resultados mostram que o coral mole *Sansibia* sp. mantém altas taxas de cobertura dois anos após sua invasão inicial e está se expandindo para locais próximos da superfície e consequentemente mais favoráveis para sua sobrevivência como coral zooxantelado (capítulo 4). Além disso, assim como sugerimos um potencial predador de *Tubastraea* spp. a partir das análises de $\delta^{13}C$ e $\delta^{15}N$, também o fazemos para *Sansibia* sp. A partir dos valores de $\delta^{13}C$ e $\delta^{15}N$e de observação in situ (ver material suplementar S12) trazemos evidências de que *Sansibia* sp. faz parte da dieta do consumidor generalista oportunista *Stenorhynchus seticornis* (parte 4). Toda via, ainda não sabemos se ao contrário da poliqueta *Hermodice carunculata* que parece não oferecer pressão de predação forte o suficiente para evitar a rápida expansão de *Tubastraea* spp.(capítulo 3), *S. seticornis* pode representar uma resistência biótica que afete a abundância de *Sansibia* sp. Ainda, houve fortes indícios que ambas *Tubastraea* spp. e *Sansibia* sp. utilizam como fonte de alimento, fragmentos (detritos) das macroalgas formadores de *turf* (grupo funcional de um tapete multiespecífica de algas muito comum em recifes) em suas respectivas comunidadese que ficam em suspensão após a quebra por ondas ou pela ação de herbívoros.

Nos estudos de ecologia de comunidades, a diversidade de espécies constitui um tema central, que inicialmente era avaliado a partir da análise de riqueza e uniformidade e atualmente é complementado com estudos que consideraram também o papel de cada espécie e suas características morfológicas, fisiológicas e traços ecológicos (Villéger et al. 2010). Aqui nós testamos ambas as ferramentas para avaliar comunidades invadidas e consideramos os índices de diversidade taxonômica e de diversidade funcional ferramentas úteis para identificar processos que determinam a diversidade biológica, pois parecem obedecer a um padrão que reflete a maior diversidade nas comunidadesnão invadidas, ainda que as características funcionais das espécies tenham refletido melhor o número e a biomassa de EEI(capítulo 2). Da mesma forma, ao utilizarmos métricas isotópicas para descrever aspectos importantes das comunidades invadidas e não invadidas, observamos que a extensão total da diversidade trófica dentro da teia alimentar e as fontes de recurso exploradas pelos consumidores foram menores nas áreas invadidas por *Tubastraea* spp. (capítulo 3).

Responder perguntas que permeiam os estudos em bioinvasão marinha representa um longo caminho que precisa ser percorrido. A partir de novos *insights* sobre relações tróficas, incluindo interações entre EEI e espécies nativas, acreditamos ter contribuído para o preenchimento de uma lacuna ainda pouco explorada. Nós apresentamos o primeiro trabalho sobre relações tróficas envolvendo predação e competição por recursos alimentares dasEEI do gênero *Tubastraea* spp. no Brasil (capítulo 3) e a primeira caracterização de uma teia trófica em um costão rochoso de uma área invadida pelo coral mole invasor *Sansibia* sp. (capítulo 4). Buscamos compreender também particularidades da comunidade invadida e para isso utilizamos um tipo de análise pouco aplicada a ambientes marinhos invadidos, as análises de diversidade funcional(capítulo 2). Por fim, entendemos que promover o diálogo entre academia e sociedade é uma parte adicional mas também fundamental para divulgar problemáticas ambientais como a bioinvasão marinha e ressaltar a importância do desenvolvimento de pesquisas científicas. Desta forma, parte desse trabalho também foi dedicada para relatar o retorno positivo com um projeto de extensão universitária e a desconstrução de muitos conceitos prévios sobre o que é ser cientista no Brasil (capítulo 5).

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GLOSSÁRIO

Aquariofilia	Manter ou comercializar, para fins de lazer ou de entretenimento, indivíduos vivos em aquários, tanques, lagos ou reservatórios destinados para este fim (Brasil 2020)
Atributos funcionais (‘*Functional attributes*’)	Valor do traço funcional em um dado lugar e tempo (Petchey et al. 2009).
Azooxantelado (‘*Azooxanthellate*’)	Organismos marinhos heterotróficos que não vivem em associação com zooxantelas (Pereira e Soares-Gomes 2019)
Bioinvasão (‘*Bioinvasion*’)	Ato ou efeito de um ou mais organismos invadirem e se estabelecerem em ambientes onde não havia registros anteriores para a espécie, que após a introdução, passa a ocorrer fora da sua distribuição natural, em locais onde não seria possível chegar sem a interferência das atividades humanas (Pereira e Soares-Gomes 2009)
Biodiversidade (‘*Biodiversity*’)	Variedade e abundância de espécies em uma área de estudo definida (Magurran 2013)
Comunidade (‘*Community*’)	Coleções de espécies ocorrendo em um lugar e tempo específicos (Magurran 2013)
Competição (‘*Competition*’)	Interação entre dois organismos que afeta adversamente o crescimento e a sobrevivência (Odum 2012)
Costão Rochoso (‘*Rocky shore*’)	Interface entre terra, ar e mar, constituída por uma série de limites ou gradientes cuja extensão varia de centímetros a quilômetros, bem como no tempo e no espaço (Pereira e Soares-Gomes 2009)
Detritívoros (‘*Scavengers*’)	Organismos que se alimentam de organismos mortos ou de matéria orgânica parcialmente em decomposição (Brusca e Brusca 2003)

Depositívoros (‘*Depositing organisms*’)	Animais que capturam alimento depositado no substrato marinho, de lagos e de rios, no ambiente aquático (Pereira e Soares-Gomes 2009)
Diversidade funcional (‘*Functional diversity*’)	O valor e a variação das características funcionais das espécies que influenciam o funcionamento das comunidades (Tilman 2001)
Diversidade taxonômica (‘*Taxonomic diversity*’)	Diversidade de táxons presentes em uma comunidade (Magurran 2013)
Ecossistema (‘E*cosystem*’)	Unidade que abrange todos os organismos que funcionam em uma comunidade biótica em uma dada área, interagindo com o ambiente físico de tal modo que um fluxo de energia produza estruturas bióticas claramente definidas e uma ciclagem de materiais entre as partes vivas e não vivas (Odum 2012)
Espécie exótica (‘*Non-indigenous species*’)	É definida como espécie,subespécie ou táxon de hierarquiainferior ocorrendo fora de sua áreade distribuição natural passada oupresente. Inclui qualquer parte,como gametas, sementes, ovos oupropágulos que possam sobreviveresubsequentemente reproduzir-se (Lopes 2009)
Espécie exótica invasora (‘*invasive species*’)	É definida como espécie exótica cuja introdução e/ou dispersão ameaçam a diversidade biológica (Lopes 2009)
Espécie nativa (‘*native species*’)	Espécie que vive em sua região de origem (em contraste à espécie exótica) (Lopes 2009)
Filtradores suspensívoros (‘*suspension filter feeders*’)	Organismosheterotróficos que removem do meio circundante partículas e alimento em suspensão, por intermédio de algum mecanismo de captura, aprisionamento ou filtração (Brusca e Brusca 2003)
Hipótese de Aceitação Biótica (‘*Biotic acceptance hypotheses*’)	Ecossistemas queapresentam condições ambientais favoráveis para espécies nativas também oferecem oportunidades decolonização para espécies não nativas,

	de forma que a diversidade de espécies covariam com os gradientes ambientais (Fridley et al. 2007)
Hipótese de Resistência Biótica (‘*Biotic resistence hypotheses*’)	É esperado que comunidades mais diversas apresentem maior resistência ao ingresso de novas espécies por competição (Elton 1958).
Impactos antrópicos (‘*Anthropic impacts*’)	Toda ação realizada pelo homem na qual resulta em um desequilíbrio ao meio ambiente (Andriolo et al. 2018)
Isótopos estáveis (‘*Stable isotopes*’)	Espécies atômicas de um mesmo elemento químico que possuem o mesmo número de prótons, mas diferentes números de nêutron no núcleo atômico e não alteram a massa ao longo de sua existência (Martinelli et al. 2009)
Métricas de nicho isotópico (‘*Isotopic niche metrics*’)	Abordagemanalítica que consistem utilizar métricas derivadas de valores isotópicos $\delta^{13}C$ e $\delta^{15}N$ que refletem aspectos importantes da estrutura trófica em uma comunidade (Layman et al. 2007)
Métricas de Layman (‘*Layman metrics’)*	Ver Métricas de nicho isotópico
Nicho ecológico (‘*Ecological niche’)*	Hiper volume em um espaço n-dimensionalque considera as condições e recursos necessários para a sobrevivência de uma espécie ou população de forma indefinida (Leibold 1995)
Onívoros (‘*Omnivores*’)	Consumidores que possuem capacidade anatômica e fisiológica para capturar, manipular e digerir tanto plantas quanto matéria animal (Brusca e Brusca 2003)
Paradoxo da Invasão (‘*Invasion Paradox*’)	O paradoxo se baseia nos pressupostos de existe uma associação positiva entre espécies nativas e não nativas em amplas escalas espaciais (Hipótese de Aceitação Biótica) e associação negativa frequentemente encontrada em menores escalas espaciais (Hipótese de resistência Biótica) (Fridley et al. 2007)
População (‘*Population*’)	Qualquer grupo de organismos da mesma espécie (ou grupos dentro dos quais os indivíduos podem intercambiar informações genéticas) que ocupa um

	espaço determinado e funciona como uma parte de uma comunidade biótica (Odum 2012)
Predação (‘*Predation*’)	Quando uma população afeta adversamente a outra por um ataque direto, dependendo, entretanto, da outra (Odum 2012)
Produção Primária (‘*Primary production’*)	Fixação de carbono do ambiente através de atividade biológica (Pereira e Soares-Gomes 2009)
Produtores Primários (‘*Primary producers’*)	Organismos capazes de converter energia solar em energia química (Pereira e Soares-Gomes 2009)
Recursos (‘*Resources*’)	Qualquer substância ou fator consumido por organismos e usado para suas manutenções e crescimentos, e que sustenta taxas populacionais crescentes à medida que sua disponibilidade no ambiente aumenta (Ricklefs 2010)
Ressurgência marinha (‘*Marine resurgence*’)	Afloramento de massa d’água que promovem consideráveis variações nas condições químicas, físicas e biológicas do ambiente costeiro (Pereira e Soares-Gomes 2009)
Sedimento marinho (‘*Marine sediment*’)	Partículas de diferentes tamanhos depositados no fundo dos oceanos derivados de uma variedade de fontes (Pereira e Soares-Gomes 2009)
Teia trófica (‘*Trophic web*’)	Representação das relações alimentares entre predadores e presas numa comunidade ecológica (Pimm 1982)
Teoria de nicho (‘*Niche Theory*’)	Espécies diferem entre si exibindo certa diferenciação de nicho, de forma que os recursos são utilizados diferencialmente por cada espécie, que para coexistirem em uma comunidadese especializam na obtenção de um determinado tipo de recurso normalmente acompanhado de uma diminuição na eficiência com relação a outro (Pianka 1974)
Traços funcionais (‘*Functional trait*’)	Características do organismo que estão relacionadas à aptidão e desempenho de um organismos (Laureto et al. 2015)

Uniformidade (‘*Uniformity*’)	Variabilidade da abundância das espécies em uma comunidade (Magurran 2013)
Vetor de introdução de EE (‘*NS introduction vector*’)	Veículo ou atividade pela qual uma espécie é transportada e introduzida em um novo habitat (Pereira e Soares-Gomes 2019).
Zona costeira (‘*Coastal zone*’)	Ver costão rochoso
Zooxantelas (‘*Zooxanthella*’)	Microalgas vivem em endossimbiose com corais, nudibrânquios e outros animais heterotróficos marinhos, realizando fotossíntese e liberando compostos orgânicos nutritivos (Pereira e Soares-Gomes 2019).
Zooxantelado (‘*Zooxanthelate*’)	Corais, nudibrânquios e outros animais heterotróficos marinhos que vivem em associação com zooxantelas, podendo sobreviver por meses só com a nutrição por elas produzida (Pereira e Soares-Gomes 2019).

APÊNDICE – Valores de δ^{13}C e δ^{15}N de produtores primários e consumidores analisados no presente estudo.

Situação	Local	Taxa	Group	n	δ^{15}N		δ^{13}C	
					value/ mean value	SD	value/ mean value	SD
invaded	PV	*Janiaadhaerens*J.V.Lamouroux*, 1816*	rhodophyta	8	6.67	0.62	-9.03	1.27
invaded	PV	crustosecorallinealgae	rhodophyta	4	6.08	0.9	-4.87	1.52
invaded	PV	*Melanothamnusferulaceus*(SuhrexJ.Agardh) Díaz-Tapia&Maggs, 2017	rhodophyta	4	5.57	0.7	-25.33	8.34
invaded	PV	*Hypnea*J.V.Lamouroux, 1813	rhodophyta	2	5.27	0.87	-17.31	2.66
invaded	PV	*Dictyota* J.V.Lamouroux	phaeophyceae	5	5.1	0.65	-14.18	1.04
invaded	PV	*Dictyopteris*J.V.Lamouroux, 1809	phaeophyceae	1	5.03		-13.08	
invaded	PV	*Dictyotamenstrualis* (Hoyt) Schnetter, Hörning& Weber-Peukert	phaeophyceae	1	6.38		-11.33	
invaded	PV	*Sargassumvulgare*C.Agardh, 1820	phaeophyceae	6	6.21	0.61	-16.69	1.58
invaded	PV	*Padinagymnospora*(Kützing) Sonder, 1871	phaeophyceae	2	4.41	0.48	-14.19	1.30
invaded	PV	*Didemnumperlucidum*Monniot F., 1983	ascidiacea	4	7.91	1.36	-7.44	0.46
invaded	PV	*Diplosomalisterianum*(Milne Edwards, 1841)	ascidiacea	3	8.22	0.43	-19.16	1.17
invaded	PV	*Desmapsammaanchorata*(Carter, 1882)	porifera	5	8.83	0.41	-20.33	0.77
invaded	PV	*Paraleucilla magna* Klautau, Monteiro &Borojevic, 2004	porifera	1	8.43		-20.61	
invaded	PV	*Amphimedonviridis*	porifera	1	9.61		-21.12	
invaded	PV	*Scopalinaruetzleri*(Wiedenmayer, 1977)	porifera	4	9.09	0.58	-19.30	0.88
invaded	PV	*Anthopleura*Duchassaing de Fonbressin&Michelotti, 1860	anemone	2	10.53	0.05	-18.89	0.79
invaded	PV	*Phallusianigra*Savigny, 1816	ascidiacea	1	6.43		-20.47	
invaded	PV	*Megabalanuscoccopoma*(Darwin, 1854)	crustacea	1	10.74		-20.56	
invaded	PV	*Amathiaverticillata*(delleChiaje, 1822)	bryozoa	4	7.39	0.51	-13.54	2.12
invaded	PV	*Macrorhynchiaphilippina*Kirchenpauer, 1872	hydrozoa	3	6.77	2.27	-20.64	1.10
invaded	PV	tubular polychaete	polychaeta	1	8.05		-17.19	

invaded	PV	*Palythoacaribaeorum*Duchassaing&Michelotti, 1860	zoanthidea	3	8.41	0.60	-13.43	0.18
invaded	PV	gastropod NI	gastrophoda	10	7.09	0.93	-15.43	3.36
invaded	PV	zooplankton	crustacea	2	9.66	0.52	-22.27	1.61
invaded	PV	*Stenorhynchusseticornis*(Herbst, 1788)	crustacea	2	10.77	0.86	-18.23	1.11
invaded	PV	*Megabalanuscoccopoma*(Darwin, 1854)	crustacea	2	10.6	0.12	-18.94	0.06
invaded	PV	crustacea NI	crustacea	1	7.86		-8.05	
invaded	PV	*Sansibia*Alderslade, 2000	cnidaria	6	6.82	0.90	-19.46	0.66
invaded	PV	*Echinometralucunter*(Linnaeus, 1758)	echinodermata	3	9.88	0.85	-15.73	0.70
invaded	PV	*Echinaster*(Othilia) *brasiliensis* Müller &Troschel, 1842	echinodermata	3	10.36	0.25	-12.19	1.41
invaded	IC	*Centroceras*Kützing, 1842 '1841'	rhodophyta	1	6.683		-19.206	
invaded	IC	corallinealgae	rhodophyta	3	7.02	0.38	-12.9	0.68
invaded	IC	zooplankton	crustacea	1	12.471		-21.553	
invaded	IC	*Croniusruber*(Lamarck, 1818)	crustacea	2	10.1	0.767917964	-19.75	0.47517576
invaded	IC	*Pachychelesmonilifer*(Dana, 1852)	crustacea	1	10.539		-18.054	
invaded	IC	shrimp NI	crustacea	2	8.75	0.076367532	-19.52	0.03
invaded	IC	*Perna perna*(Linnaeus, 1758)	gastrophoda	3	8.08	0.97	-18.21	0.56
invaded	IC	*Leiosolenusaristatus*(Dillwyn, 1817)	gastrophoda	3	8.3	0.27	-19.02	0.06
invaded	IC	*Bunodosomacaissarum*Corrêa in Belém, 1987	anemone	3	10.91	0.25	-19.34	0.43
invaded	IC	*Obeliadichotoma*	hydrozoa	3	8.37	0.64	-19.4	0.23
invaded	IC	*Schizoporellaunicornis*(Johnston in Wood, 1844)	brydrozoa	3	7.59	0.54	-10.8	3.84
invaded	IC	*Diplosomalisterianum*(MilneEdwards, 1841)	ascidiacea	3	7.23	0.1	-20.66	0.2
invaded	IC	*Paraleucilla magna* Klautau, Monteiro &Borojevic, 2004	porifera	3	7.79	0.46	-6.02	1.88
invaded	IC	*Scopalinaruetzleri*(Wiedenmayer, 1977)	porifera	3	8.64	0.1	-21.03	0.43
invaded	IC	*Tubastraea tagusensis* Wells, 1982	cnidaria	3	9.5	0.05	-18.43	0.78
invaded	IC	*Echinometralucunter*(Linnaeus, 1758)	echinodermata	3	11.35	0.73	-16.59	0.28
notinvaded	IC	corallinealgae NI	rhodophyta	3	6.81	0.33	-10.56	0.65

notinvaded	IC	*Obeliadichotoma*	hydrozoa	3	8.8	0.17	-19.59	0.36
notinvaded	IC	*Schizoporellaunicornis*(Johnston in Wood, 1844)	bryozoa	3	7.43	0.46	-8.7	4.69
notinvaded	IC	*Megabalanuscoccopoma*(Darwin, 1854)	crustacea	3	10.46	0.11	-18.52	1
notinvaded	IC	*Pachychelesmonilifer*(Dana, 1852)	crustacea	1	10.104		-18.786	
notinvaded	IC	*Croniusruber*(Lamarck, 1818)	crustacea	2	10.03	0.27	-18.97	0.54
notinvaded	IC	shrimp NI	crustacea	3	8.36	0.42	-19.28	0.85
notinvaded	IC	gastrophoda NI	gastrophoda	3	10.92	0.27	-17.21	0.49
notinvaded	IC	*Leiosolenusaristatus*(Dillwyn, 1817)	gastrophoda	3	7.42	0.24	-20.91	0.04
notinvaded	IC	*Perna perna*(Linnaeus, 1758)	gastrophoda	3	7.89	0.32	-20.23	0.5
notinvaded	IC	*Mytilastersolisianus*(d'Orbigny, 1842)	gastrophoda	3	8.89	0.18	-18.71	0.1
notinvaded	IC	*Scopalinaruetzleri*(Wiedenmayer, 1977)	porifera	3	9.08	0.07	-20.01	0.94
notinvaded	IC	*Dysideaetheria*de Laubenfels, 1936	porifera	3	9.16	0.2	-20.01	0.32
notinvaded	IC	*Bunodosomacaissarum*	anemone	3	10.55	0.29	-20.01	0.53
notinvaded	IC	*Didemnumperlucidum*Monniot F., 1983	ascidiacea	3	9.62	0.46	-6.86	0.95
notinvaded	IC	*Echinometralucunter*(Linnaeus, 1758)	echinodermata	3	10.38	0.3	-16.26	1.84
notinvaded	IC	ofiuroidea NI	echinodermata	1	9.496		-17.981	
notinvaded	IC	*Carijoariisei*(Duchassaing&Michelotti, 1860)	cnidaria	3	9.16	0.25	-18.88	1.72
invaded	IA	*Janiaadhaerens*J.V.Lamouroux*, 1816*	rhodophyta	3	7.25	0.51	-6.17	2.77
invaded	IA	*Hypnea*J.V.Lamouroux, 1813	rhodophyta	2	5.78	0.25	-19.35	0.29
invaded	IA	*Codiumintertextum*Collins &Hervey, 1917	chlorophyta	3	6.56	0.62	-9.02	0.49
invaded	IA	*Dictyopteris*J.V.Lamouroux, 1809	phaeophyceae	3	6.31	0.36	-16.92	0.11
invaded	IA	*Padinagymnospora*(Kützing) Sonder, 1871	phaeophyceae	3	7.06	0.17	-12.51	0.6
invaded	IA	*Dictyotamenstrualis*(Hoyt) Schnetter, Hörning& Weber-Peukert, 1987	phaeophyceae	3	6.48	0.11	-17.17	1.12
invaded	IA	*Dictyota* J.V.Lamouroux	phaeophyceae	3	5.67	0.18	-14.59	3.04
invaded	IA	*Obeliadichotoma*(Linnaeus, 1758)	hydrozoa	3	7.47	0.15	-21.41	0.4
invaded	IA	*Macrorhynchiaphilippina*Kirchenpauer, 1872	hydrozoa	2	6.84	0.11	-20.39	0.12
invaded	IA	*Milleporaalcicornis*Linnaeus, 1758	hydrozoa	3	7.99	2.19	-6.98	1.03

invaded	IA	*Schizoporellaunicornis*(Johnston in Wood, 1844)	bryozoa	3	7.11	0.52	-4.85	0.5
invaded	IA	*Leptogorgiapunicea*(Milne Edwards &Haime, 1857)	gorgoniidae	3	8.96	0.22	-14.18	1.8
invaded	IA	*Tubastraeacoccinea*Lesson, 1830	cnidaria	3	8.32	0.14	-19.92	0.54
invaded	IA	*Tubastraea tagusensis* Wells, 1982	cnidaria	3	9.18	0.43	-19.53	0.37
invaded	IA	*Diplosomalisterianum*(Milne Edwards, 1841)	ascidiacea	3	6.94	0.41	-14.69	4.18
invaded	IA	*Didemnumperlucidum*Monniot F., 1983	ascidiacea	3	8.38	0.35	-14.75	1.72
invaded	IA	*Scopalinaruetzleri*(Wiedenmayer, 1977)	porifera	3	9.11	0.06	-18.81	0.59
invaded	IA	*Guitarra sepia*Lerner, Hajdu, Custodio & van Soest, 2004	porifera	3	8.49	0.11	-18.52	1.15
invaded	IA	*Arenosclera brasiliensis* Muricy & Ribeiro, 1999	porifera	3	9.05	0.09	-20.81	1.96
invaded	IA	gastropod NI	gastrophoda	3	11.51	0.35	-17.12	0.79
invaded	IA	*Leiosolenusaristatus*(Dillwyn, 1817)	gastrophoda	3	9.16	2.65	-18.93	2.37
invaded	IA	tubular polychaete NI	polychaeta	3	10.26	1.84	-19.65	0.4
invaded	IA	ofiuroidea NI	echinodermata	1	9.222		-13.364	
invaded	IA	*Echinaster brasiliensis*	echinodermata	3	8.98	0.48	-21.21	0.2
notinvaded	IA	*Janiaadhaerens*J.V.Lamouroux*, 1816*	rhodophyta	3	6.94	0.32	-20.31	0.67
notinvaded	IA	corallinealgae	rhodophyta	3	7.23	0.22	-9.22	3.24
notinvaded	IA	*Hypnea*J.V.Lamouroux, 1813	rhodophyta	3	6.3	0.42	-20.35	2.4
notinvaded	IA	*Sargassumvulgare*C.Agardh, 1820	phaeophyceae	3	6.52	0.32	-14.46	0.19
notinvaded	IA	*Dictyota*J.V.Lamouroux, 1809 sp.	phaeophyceae	3	6.7	0.16	-27.18	0.02
notinvaded	IA	*Codiumintertextum*Collins &Hervey, 1917	chlorophyta	3	6.81	0.77	-8.13	1.51
notinvaded	IA	*Obeliadichotoma*(Linnaeus, 1758)	hydrozoa	3	7.81	0.58	-20.56	0.4
notinvaded	IA	*Milleporaalcicornis*Linnaeus, 1758	hydrozoa	3	7.04	1.82	-3.25	0.75
notinvaded	IA	*Macrorhynchiaphilippina*Kirchenpauer, 1872	hydrozoa	3	7.8	0.28	-16.31	7.58
notinvaded	IA	*Ophiothelamirabilis*Verrill, 1867	hydrozoa	1	9.14		-19.437	
notinvaded	IA	ofiuroidea NI	echinodermata	1	10.275		-10.118	
notinvaded	IA	*Siderastreastellata*Verrill, 1868	cnidaria	3	8.11	0.78	-7.26	1.28

notinvaded	IA	*Madracisdecactis*(Lyman, 1859)	cnidaria	3	8.92	1.52	-8.7	4.61
notinvaded	IA	*Poritesbranneri*	cnidaria	3	8.62	0.69	-11.19	2.64
notinvaded	IA	*Echinometralucunter*(Linnaeus, 1758)	echinodermata	3	10.13	0.62	-15.21	0.08
notinvaded	IA	*Leptogorgiapunicea*(Milne Edwards &Haime, 1857)	gorgoniidae	3	9.89	0.09	-19.46	0.83
notinvaded	IA	*Palythoacaribaeorum*Duchassaing&Michelotti, 1860	zoanthidea	3	7.99	0.36	-13.1	0.69
notinvaded	IA	*Arenosclera brasiliensis* Muricy & Ribeiro, 1999	porifera	3	7.08	0.23	-10.64	0.6
notinvaded	IA	*Aplysina fulva* (Pallas, 1766)	porifera	3	7.25	0.53	-19.37	0.37
notinvaded	IA	crustacea NI	crustacea	1	9.783		-17.474	
notinvaded	IA	gastropod NI	gastrophoda	3	11.54	0.35	-16.33	0.06
notinvaded	IA	tubular polychaete	polychaeta	2	11.3	0.3	-20.28	1.38
invaded	IG	corallinealgae	rhodophyta	3	8.23	0.32	-16.4	0.36
invaded	IG	*Janiaadhaerens*J.V.Lamouroux*, 1816*	rhodophyta	2	5.58	0.78	-10.14	3.67
invaded	IG	*Hypnea*J.V.Lamouroux, 1813	rhodophyta	3	6.42	0.21	-19.99	0.48
invaded	IG	chlorophyta NI	chlorophyta	3	7.49	0.41	-10.91	0.6
invaded	IG	*Acetabulariaschenckii*Möbius, 1889	phaeophyceae	3	7.33	0.9	-15.43	0.91
invaded	IG	*Dictyota* J.V.Lamouroux	phaeophyceae	2	6.47	0.38	-16.37	0.15
invaded	IG	hydrozoa NI	hydrozoa	3	7.56	0.1	-21.56	0.45
invaded	IG	*Schizoporellaunicornis*(Johnston in Wood, 1844)	bryozoa	2	8.43	0.41	-5.46	0.42
invaded	IG	*Bugulaneritina*(Linnaeus, 1758)	bryozoa	3	8.51	0.66	-7.73	1.47
invaded	IG	zooplankton	bryozoa	1	7.5		-22.395	
invaded	IG	*Stenorhynchusseticornis*(Herbst, 1788)	crustacea	3	7.91	0.31	-15.34	1.45
invaded	IG	*Mithraculus forceps* A. Milne-Edwards, 1875 [in A. Milne-Edwards, 1873-1880]	crustacea	3	7.6	0.27	-16.61	1.59
invaded	IG	*Leiosolenusaristatus*(Dillwyn, 1817)	crustacea	3	8.32	0.66	-18.21	1.75
invaded	IG	*Iotrochotabirotulata*(Higgin, 1877)	porifera	3	9.13	0.25	-18.01	3.23
invaded	IG	*Desmapsammaanchorata*(Carter, 1882)	porifera	3	9.69	0.63	-22.17	0.49
invaded	IG	*Phallusianigra*Savigny, 1816	ascidiacea	3	8.66	0.98	-20.84	0.63

invaded	IG	*Tubastraeacoccinea*Lesson, 1830	cnidaria	3	9.84	0.31	-21.39	0.25
invaded	IG	*Tubastraea tagusensis* Wells, 1982	cnidaria	3	9.88	0.23	-20.8	0.16
invaded	IG	*Carijoariisei*(Duchassaing&Michelotti, 1860)	cnidaria	3	9.43	0.37	-12.63	0.76
invaded	IG	*Palythoacaribaeorum*Duchassaing&Michelotti, 1860	zoanthidea	3	8.88	0.48	-13.46	1.16
invaded	IG	tubular polychaete	polychaeta	1	9.076		-19.803	
invaded	IG	*Hermodicecarunculata*(Pallas, 1766)	polychaeta	3	12.19	0.3	-19.3	0.38
invaded	IG	*Haemulonsteindachneri*(Jordan & Gilbert, 1882)	fish	3	12.42	0.5	-16.62	0.66
invaded	IG	*Haemulonaurolineatum*Cuvier, 1830	fish	3	12.7	0.43	-17.15	0.2
invaded	IG	*Stephanolepis hispida* (Linnaeus, 1766)	fish	1	12.013		-15.589	
invaded	IG	*Sphoeroidesspengleri*(Bloch, 1785)	fish	2	10.86	0.34	-15.34	0.09

ANEXO A – Artigos científicos que compõem o presente trabalho.

Aquatic Invasions (2020) Volume 15, Issue 1: 30–43

Special Issue: Proceedings of the 10th International Conference on Marine Bioinvasions
Guest editors: Amy Fowler, April Blakeslee, Carolyn Tepolt, Alejandro Bortolus, Evangelina Schwindt and Joana Dias

Research Article

A decade on: an updated assessment of the status of marine non-indigenous species in Brazil

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Co-Editors' Note: This study was first presented at the 10th International Conference on Marine Bioinvasions held in Puerto Madryn, Argentina, October 16–18, 2018 (http://www.marinebioinvasions.info). Since their inception in 1999, the ICMB meetings have provided a venue for the exchange of information on various aspects of biological invasions in marine ecosystems, including ecological research, education, management and policies tackling marine bioinvasions.

Citation: Teixeira LMP, Creed JC (2020) A decade on: an updated assessment of the status of marine non-indigenous species in Brazil. *Aquatic Invasions* 15(1): 30–43, https://doi.org/10.3391/ai.2020.15.1.03

Received: 6 January 2019
Accepted: 21 August 2019
Published: 4 November 2019

Handling editor: Evangelina Schwindt
Thematic editor: Amy Fowler

Abstract

In order to prevent the introduction, control or eradicate non-indigenous species (NIS) which threaten native species, habitats or ecosystems, an essential first step is that countries have and keep up-to-date lists of species non-indigenous to the region. The last list of marine NIS for Brazil was published a decade ago. We compiled an updated list of marine NIS and revised the species' statuses. One-hundred-thirty-eight marine species in 15 classes or functional groups are NIS in Brazil. Brazilian states with greater maritime commerce (greater market share) had more marine NIS. From the period between the 1950s to 2010, the number of NIS at least doubled each decade. We identified a significant mismatch (underestimation) between the previous list and this study, which seemed to be due to improved scientific knowledge and an often considerable lag between first record (detection), identification and communication of new marine NIS. Currently Brazil has 19 invasive, 76 established and 43 detected marine NIS, an increase of 160% in ten years compared to the previous national list. We recommend that Brazil implements a national database as a rapid, appropriate, flexible and cost effective method of monitoring trends in NIS introductions.

Key words: class/functional groups, geographical variation, historical change, invasive, national checklist, non native species

Introduction

The Convention on Biological Diversity (to which Brazil is a party, Brasil 1998) states that consenting parties should prevent the introduction, control or eradicate those alien species which threaten ecosystems, habitats or native species. In Brazil this convention was ratified in 1994, with the Ministry of the Environment being the principal entity responsible for planning and decision making with regard to non-indigenous species (NIS) and biological invasion (Lopes et al. 2009). An essential first step is that countries have and keep up-to-date lists of NIS recorded for their region. According to Sliwa et al. (2009) once lists are adopted into the

diversity

Article

How Do Biological and Functional Diversity Change in Invaded Tropical Marine Rocky Reef Communities?

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Abstract: Evidence so far shows that most alien species (AS) have negative impacts on native biodiversity and are changing biodiversity in almost all environments. Here, we study eight rocky shores at four sites containing reefs with invaded communities and other not-invaded (control) communities, to evaluate the effects of four marine invasive species on biological and functional diversity. We used the adjustment and selection approach of species abundance distribution models (SAD), taxonomic diversity indices and functional diversity indices based on hierarchical grouping matrices (FD—Functional Diversity). In addition to comparing invaded and not-invaded communities, we also performed the same analysis, but removed the invaders (AS removed) from the matrices. The geometric-series model was best adjusted to the majority of communities. The diversity indices suggest that the taxonomic diversity is lower in invaded communities, while the functional diversity indices suggest a change in the functional space of invaded and not-invaded communities, with a greater amount of functional space filled by species in the not-invaded communities. Taxonomic and functional diversity indices were successful in identifying processes that determine the biological diversity of invaded communities, as they seem to obey a pattern that reflects the reduced diversity of invaded communities.

Keywords: diversity indices; functional diversity; invasive; alien species; rank abundance plots; species abundance distribution models

Citation: Pires-Teixeira, L.M.; Neres-Lima, V.; Creed, J.C. How Do Biological and Functional Diversity Change in Invaded Tropical Marine Rocky Reef Communities?. *Diversity* 2021, *13*, 353. https://doi.org/10.3390/d13080353

Academic Editor: Bert W. Hoeksema

Received: 6 July 2021
Accepted: 28 July 2021
Published: 31 July 2021

1. Introduction

The introduction of new species into a new habitat represents a change and adjustment in the pre-existing state of the receiving community. These changes can occur at different intensities and affect one or more species that already make up part of the receptor community [1]. Alien species (AS) can transform marine environments, displacing native species, changing community structure and food webs, as well as impacting the dynamics of nutrients and sedimentation rates [2]. In the marine environment the number of documented biological invasions is increasing in the tropical southwest Atlantic Ocean [3], which reflects a worldwide trend in marine ecosystems [4], and the evidence shows that most AS have negative impacts on native biodiversity and human well-being, and are changing the biodiversity of almost all environments [5–7].

Native and AS often have different biological characteristics and interactions with the community, for example chemical defenses or the high reproductive output of the AS or escape from predators within the new community. Such factors can favor their dominance in the community invaded by AS, as they become more abundant than the other species [8]. The abundance of a species, at least to some extent, reflects its success in competing for limited resources [9], so the effects of an AS will increase with its abundance and vary

e-Mosaicos
Revista Multidisciplinar de Ensino, Pesquisa, Extensão e Cultura
do Instituto de Aplicação Fernando Rodrigues da Silveira (CAp-UERJ)
V. 10 - N. 23 - Janeiro-Abril de 2021 - ISSN 2316-9303

DOI: 10.12957/e-mosaicos.2021.47898

PROMOVENDO A PROFISSÃO DO CIENTISTA A PARTIR DE UM PROJETO DE EXTENSÃO UNIVERSITÁRIA.

PROMOTING THE SCIENTIST'S PROFESSION THROUGH A UNIVERSITY EXTENTION PROJECT.

TEIXEIRA, Larissa Marques Pires[1]
ARAUJO, Juliana Magalhães[2]
CREED, Joel Christopher[3]

RESUMO

A ciência deve ser cada vez mais valorizada, incentivada e acessível dentro e fora do meio acadêmico. O apoio popular de quem não tem contato com a ciência no seu dia a dia, é fundamental nesse processo. O Projeto "Pra que Serve?" é um projeto de extensão universitária que tem como objetivo trazer a debate a importância da ciência, sobretudo em ambiente marinho, em uma cidade litorânea como o Rio de Janeiro, e contribuir para a valorização da pesquisa científica, possibilitando, de forma simples e acessível, vivências de pesquisa e acesso a conteúdo científico. A oficina que constitui a metodologia do Projeto pode ser aplicada de duas formas, visitas escolares programadas e eventos de ciência abertos ao público espontâneo. No presente trabalho, nós relatamos a experiência vivenciada no Espaço de Desenvolvimento Infantil Professora Solange Conceição Tricarico na comunidade da Maré, no Instituto Benjamin Constant, escola que atende crianças e adolescentes cegos, surdocegos, com baixa visão e deficiência múltipla e nos eventos Bio na Rua 2018 e 2019, no Parque Madureira, localizado na zona norte carioca. Ao longo da oficina, foram registrados por meio de fotografias, momentos de interação, para que pudéssemos analisar diferentes dimensões de atuação do projeto e a resposta daqueles que participavam. A curiosidade sobre o material utilizado na pesquisa marinha foi fundamental para despertar o interesse do público, independente da faixa etária e do local da oficina. Detectamos diferentes interações durante as oficinas, sendo a observação e/ou atenção às explicações a mais recorrente. Responder "O que é?" e "Pra que serve?" a ciência, considerando

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ANEXO B - Artigo científico produto adicional do presente trabalho.

Received: 25 March 2020 | Revised: 20 August 2020 | Accepted: 5 September 2020
DOI: 10.1111/ddi.13167

BIODIVERSITY RESEARCH

Diversity and Distributions WILEY

Trends in the detection of aquatic non-indigenous species across global marine, estuarine and freshwater ecosystems: A 50-year perspective

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Funding information
Commonwealth Scientific and Industrial Research Organisation; Environmental Protection Agency; Fundação para a Ciência e a Tecnologia; Fisheries and Oceans Canada; Consejo Nacional de Investigaciones Científicas y Técnicas; Strategic Science Investment Fund (SSIF), New Zealand; Natural Sciences and Engineering Research Council of Canada; National Natural Science Foundation of China, Grant/Award Number: 31622011; Biosecurity New Zealand; European Regional Development Fund; North Pacific Marine Science Organization (PICES); United States Coast Guard; Galapagos Conservancy

Editor: Nigel Hussey

Abstract

Aim: The introduction of aquatic non-indigenous species (ANS) has become a major driver for global changes in species biogeography. We examined spatial patterns and temporal trends of ANS detections since 1965 to inform conservation policy and management.

Location: Global.

Methods: We assembled an extensive dataset of first records of detection of ANS (1965–2015) across 49 aquatic ecosystems, including the (a) year of first collection, (b) population status and (c) potential pathway(s) of introduction. Data were analysed at global and regional levels to assess patterns of detection rate, richness and transport pathways.

Results: An annual mean of 43 (±16 *SD*) primary detections of ANS occurred—one new detection every 8.4 days for 50 years. The global rate of detections was relatively stable during 1965–1995, but increased rapidly after this time, peaking at roughly 66 primary detections per year during 2005–2010 and then declining marginally. Detection rates were variable within and across regions through time. Arthropods, molluscs and fishes were the most frequently reported ANS. Most ANS were likely introduced as stowaways in ships' ballast water or biofouling, although direct evidence is typically absent.

Main conclusions: This synthesis highlights the magnitude of recent ANS detections, yet almost certainly represents an underestimate as many ANS go unreported due to limited search effort and diminishing taxonomic expertise. Temporal rates of detection are also confounded by reporting lags, likely contributing to the lower detection rate observed in recent years. There is a critical need to implement standardized, repeated methods across regions and taxa to improve the quality of global-scale comparisons and sustain core measures over longer time-scales. It will be fundamental to fill in knowledge gaps given that invasion data representing broad regions of the world's oceans are not yet readily available and to maintain knowledge pipelines for adaptive management.

KEYWORDS
aquatic non-indigenous species, biological invasions, detection rate, inventory, long-term dataset, population status, richness, spatial patterns, temporal trends, transport pathways

1 | INTRODUCTION

Analyses of long-term datasets on species introductions can provide insights into past and future trends to inform conservation management (Seebens et al., 2017; van Kleunen et al., 2015), yet such studies are relatively rare, particularly for aquatic ecosystems where species introductions are often more difficult to detect and study (Ojaveer et al., 2015). A recent study examining more than 45,800 records of mainly terrestrial non-indigenous taxa showed a continuous rise in the rate of detection during the time period 1800–2000 and a strong correlation between detection rates and trade values for taxa associated with transport pathways (Seebens et al., 2017). Moreover, the growth of trade and worldwide transport of goods by shipping is predicted to lead to a surge in the translocation of both terrestrial taxa (as stowaways in cargo and packing materials) and marine taxa (within ships' ballast water and biofouling) (Sardain et al., 2019). Despite the expected surge in species delivery to novel aquatic ecosystems, prior studies examining detection rates and/or pathways of aquatic non-indigenous species (ANS) have been conducted at local or regional scales (e.g. Galil, 2009; Katsanevakis et al., 2013; Ojaveer et al., 2017) and/or have focused on a single taxonomic group (e.g. Carlton, 2011; Darrigran et al., 2020). As introductions of many different ANS have occurred and continue to occur worldwide, studies are needed at a global scale to provide a robust understanding of invasion dynamics, identify needed management strategies and evaluate policy effectiveness in aquatic ecosystems.

The introduction of species across biogeographic barriers by human activities is a key component of global biodiversity loss and subsequent environmental change (Lewis & Maslin, 2015; Pyšek et al., 2020; Simberloff et al., 2013). The importance of coastal marine diversity was highlighted as part of the Convention on Biological Diversity (CBD) Ministerial Statement at the Conference of the Parties meeting in Jakarta in 1995 (the Jakarta Mandate) (UNEP, 2000). It is widely accepted that management of non-indigenous species introductions should be based on the precautionary approach and focus primarily on management of invasion pathways (e.g. Finnoff et al., 2007; Hewitt, Willing, et al., 2004; Lodge et al., 2016). In recognition of the urgent need to address the impacts of non-indigenous species, the CBD states that each contracting party shall, as far as possible and as appropriate, "prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species" (UNEP, 1994). The CBD revised Strategic Plan for 2011–2020 proposes that "By 2020, invasive alien species and pathways are identified and prioritized, priority species are controlled or eradicated, and measures are in place to manage pathways to prevent their introduction and establishment" (UNEP, 2011). New goals for 2021–2030 are currently being drafted, with prevention and pathway management likely to remain important components of the strategy.

Despite efforts to establish reporting mechanisms (e.g. Pagad et al., 2018), reliable inventories worldwide of non-indigenous species and their pathways are still relatively few in the published literature, especially for aquatic environments. Here, we assembled an extensive dataset of first records of detection of ANS to assess patterns of detection rate, richness, population status and transport pathways during a 50-year time period across 49 global ecosystems, including marine and estuarine habitats as well as the freshwater Laurentian Great Lakes. This synthesis is intended to provide a baseline of current knowledge, a baseline largely built on a multi-decade and perhaps in some cases a century or more, backlog of undetected invasions, to identify and support prioritization of pathways and to guide recommendations for policy and management in support of biological conservation objectives.

2 | METHODS

We assembled an extensive dataset of primary detection events of ANS (i.e. the first recorded collection of each species in each region) across global (primarily coastal marine, but also estuarine and freshwater) aquatic ecosystems for the period 1965–2015 using online ANS databases as primary data sources, including AquaNIS (http://www.corpi.ku.lt/databases/index.php/aquanis/), GLANSIS (https://www.glerl.noaa.gov/glansis/), Marine Biosecurity Porthole (https://www.marinebiosecurity.org.nz/) and NEMESIS (http://invasions.si.edu/nemesis/). In addition, we conducted a literature search using the Web of Science to locate published datasets not available online, using the search terms "nonindigenous" or "non-indigenous" or "nonnative" or "non-native" or "alien" AND "aquatic" or "marine" AND "database" or "dataset" or "list" or "inventory". Datasets were included only if dedicated, expert research on ANS had been conducted such that an up-to-date comprehensive and reliable inventory exists; datasets comprised of only a single taxonomic group, or not listing dates of first collection, or covering a shorter time period than this analysis were not included. As the geographic scale of different studies varied, we compiled data at the scale of Large Marine Ecosystem (Sherman, 1991; http://lme.edc.uri.edu), but also included available data for smaller marine ecosystems (i.e. Galápagos Islands and Madeira Archipelago). We excluded records from inland or freshwater habitats but included the Laurentian Great Lakes as a large freshwater ecosystem accessible to global shipping (Pagnucco et al., 2015).

At least one co-author with extensive regional knowledge of ANS carefully reviewed and edited each regional dataset for accuracy, checking scientific peer-reviewed publications, reports, books and personal collections to confirm: (a) year of first collection; (b) current population status and; (c) potential pathway(s) of introduction (as known up to July 15, 2020; Table 1). Records were compiled only for ANS collected from the natural environment while those reported exclusively on or within pathways were excluded (e.g. taxa sampled during surveys of ships' ballast water and biofouling, tsunami debris and other marine litter). Only species considered fully aquatic were counted, including marine stenohaline, marine euryhaline, diadromous and freshwater euryhaline species, but excluding, for example, shoreline plants and aquatic birds. Freshwater stenohaline species were included for the Laurentian Great Lakes and Baltic Sea but excluded from all other estuarine and marine ecosystems as being "inland" introductions. We also excluded records for cryptogenic species (whose status as indigenous or non-indigenous is unresolved) and taxa poorly studied or otherwise presenting challenges for taxonomic identification and assessment of historical biogeographic origin (e.g. fungi, protists, parasitic and free-living flatworms, viruses and microbes). Scientific names of ANS were standardized according to the Integrated Taxonomic Information System (www.itis.gov), the World Register of Marine Species (www.marinespecies.org) or AlgaeBase (www.algaebase.org), or more recent literature when available.

We acknowledge that the date of first collection is likely to lag behind the actual date of introduction and that we do not know for most of these species when the introduction occurred nor when a reproducing population became established. The majority of the records analysed here resulted from the onset of ANS inventories that by and large did not commence worldwide until the last decades of the 20th century, thus resulting in first reports of species that may have been present much earlier. For example, of the 141 ANS species reported from Hawaii between 1965 and 2015, at least 101 may have been present prior to World War II, and many could have arrived in the 19th century; more than half of the remaining 40 species likely arrived after WWII but prior to 1965 (J. T. Carlton, Williams College—Mystic Seaport, personal communication). We thus take a conservative approach and define the date of first record as the *date of detection*, thus yielding a *detection rate*, rather than an introduction

TABLE 1 Categories and definitions of population status and pathways utilized in the analyses

Population Status[a]	Definition
Established	Species has been repeatedly collected and/or there is evidence of successful reproduction (found in two separate locations or in two collections in separate years in the same location)
Extinct	Reproducing populations appear to have existed in a location for a length of time but appear to have subsequently died out
Failed	Species was introduced to a location, but there was no evidence of any prolonged survival or reproduction
Unknown	Insufficient data to assign to one of the above three categories

Pathways[b]	Sub-pathways[b]	Description
Corridor	Interconnected Waterways/ Basins/Seas	Species spreading to new regions along infrastructure such as canals or other artificial waterways interconnecting previously unconnected water bodies, basins and seas
Escape from confinement	Aquaculture/Mariculture	Species that have escaped from confinement or controlled situations in either freshwater or marine environments to produce food or other agricultural type products including bioenergy products
	Botanical garden/zoo/aquaria	Species that have escaped from confinement and that were kept for public display, public education or conservation breeding programmes
	Horticulture	Species that have escaped from confined or controlled environments where they were commercially cultivated for purposes other than aquaculture/mariculture
	Live food and live bait	Species that have escaped from confinement or controlled environments where they were kept and/or transported as live food or live bait
	Ornamental	Species that have escaped from confined or controlled environments where they were introduced for decorative or ornamental reasons excluding commercial horticulture
	Pet/Aquarium Species	Species that have escaped confinement or controlled environments where they were kept by private collectors or hobbyists for recreation
	Research	Species that have escaped confinement or controlled environments where they were kept and/or bred for use in research
Release in nature	Biological Control	Species released into the (semi)natural environment with the purpose of controlling the population(s) of one or more organisms
	Erosion Control	Species released into the (semi)natural environment to control the environment or to act as physical barriers
	Fishery in the Wild	Fish and other aquatic animals (e.g. invertebrates) released into the (semi)natural environment to provide additional or alternative subsistence and/or commercial or recreational fishing opportunities
	Other Intentional Release	Species released into the natural environment for reasons other than those covered in any other release in nature pathways
Transport (Contaminant)	Contaminant on Animals	Species introduced unintentionally as contaminants on animals transported through human related activities (e.g. aquaculture)
	Contaminant on Plants	Species introduced unintentionally as contaminants on plants or plant products transported through human related activities
	Contaminated Bait	Species introduced unintentionally as contaminants in/of bait
	Parasites on Animals	Unintentional introduction of parasitic species transported by a host animal or an animal that acts as a vector
Transport (Stowaway)	Angling/Fishing Gear	Species introduced unintentionally as stowaways on equipment used by recreational anglers or commercial/professional fishermen, including aquaculture gear
	Ballast Water	Species that have been introduced unintentionally via the ballast tanks of ships and boats, within ballast water, ballast sediments or solid ballast materials
	Container/Bulk	Species introduced as accidental stowaways in or on shipping containers and bulk cargo
	Hitchhikers on Plane	Species that have been introduced unintentionally by being a hitchhiker in or on airplanes and other aircraft

(Continues)

TABLE 1 (Continued)

Pathways[b]	Sub-pathways[b]	Description
	Hitchhikers on Ship	Species that have been introduced unintentionally by being a hitchhiker in or on ships, boats or other watercraft but excluding species transported in ballast tanks or via ship fouling
	Organic packaging material	Species that have been introduced unintentionally by being a stowaway in or on packing materials such as wooden pallets
	Ship Fouling	Species that have been introduced unintentionally as biofouling organisms on underwater surfaces of ships including the hull and niche areas
Unaided	Rafting on Anthropogenic Debris	Species that spread to new regions attached to marine litter and other anthropogenic materials drifting in natural water currents

[a] Adapted fromFofonoff et al. (2018).

[b] Adapted from Harrower et al. (2018).

rate. This date encompasses the relatively few cases where a species is known to have been intentionally planted or released; such cases are rare after the 1960s, as there was rapid growth in environmental awareness about the potential negative outcomes of deliberate introductions. Distinguishing between a date of detection and a date of introduction is critical. We emphasize that there should be no confusion between our use of detection and the concept of the rate of species discovery resulting from a given effort or type of sampling (which in classical community diversity studies is used to establish a probable species discovery asymptote).

We chose the timeframe 1965–2015 with the assumption that there has been increasing awareness and more comprehensive reporting since 1965, with time-lags presumably being smaller compared to reports prior to 1965. In cases of multiple records of the same ANS, the first record within each region was used. The year of first collection was typically recorded as a single year, but when only time ranges were provided (e.g. "2012–2015"), the first year of the range was taken as the earliest possible date. For a small number of records (<0.01%), the year of first report (the year of publication) was recorded when the date of collection was not provided. Population status was recorded for each introduced species as "established," "extinct," "failed" or "unknown" following definitions used by the NEMESIS database (see Table 1) which account for uncertainty associated with limited search effort. We acknowledge that established populations are more likely to be observed and documented and that, without regular surveillance programmes, many detections are recorded only as single records and the population status may be highly uncertain. Seven ANS populations were successfully eradicated after detection—these were labelled with the population status observed prior to eradication efforts.

We assigned pathways of introduction using categories and sub-categories proposed as part of the Convention on Biological Diversity following guidance in Harrower et al. (2018), with small modifications (Table 1). Ship fouling (rather than the more limited "hull" fouling) included organisms attached or associated with any underwater surfaces of ships (defined as a vessel of any type operating in the aquatic environment, including fixed or floating platforms) including the hull and niche areas (e.g. sea chests, seawater inlets and inlet grates, anchors and anchor chain) (as per IMO, 2011). Ships' ballast water also included stowaways within ballast sediments as well as solid ballast materials used historically. We considered aquaculture equipment as angling/fishing equipment.

Pathway information was initially taken from source online databases and published literature, if stated, and was then critically evaluated for completeness and standardization across regions/data sources based on our own expertise and knowledge. Many references implicate commercial shipping as a possible mechanism of introduction without assessing specific pathways. Therefore, we designated shipping pathways primarily based on our own prior biological surveys of ballast water and ship fouling combined with knowledge of life history characteristics of the species. Ballast water can be a possible transport pathway for a wide variety of aquatic species, not only those with pelagic life stages, as virtually any sessile organism may be drawn into ballast tanks (or floodable cargo holds) on floating pieces of debris, wood chips, algae or seagrass bearing a biofouling community of attached species. While this aspect of ballast-able biota is rarely studied, the potential for species associated with floating material to be taken into ballast tanks was suggested as early as the 1920s (Carlton, 1985). Conversely, ship fouling can be a possible transport pathway not only for encrusting or fouling species on a ships' main hull, but also for sedentary and mobile species associated with more protected underwater niche areas such as sea chests (Coutts & Dodgshun, 2007). As a result, both ballast water and ship fouling were assigned as potential pathways for the majority of taxa, excepting purely pelagic free-swimming taxa (such as shrimps, planktonic copepods and ctenophores) associated only with ballast water. We standardized the assignment of shipping pathways for related taxa across regions, typically at the level of Family or Order, except where there was no geographic correlation between shipping activity and the site of first collection (e.g. where pathways such as aquaculture were more likely). As there is uncertainty associated with all pathway assignments, we tallied records where documented or direct evidence existed (e.g. species was observed within a pathway at the time of introduction to a particular location).

When a single detection was linked to multiple possible pathways of introduction, we tallied each pathway using an unweighted approach to identify the maximum number of detection events per pathway (as in Williams et al., 2013). In this analysis, canals, such as the Suez Canal, were evaluated both as a pathway through which ANS may move naturally (i.e. as species with pelagic life stages) and as a route used by ships. In cases where species have pelagic behaviour and are possibly associated with shipping, they were assigned multiple pathways. Although unassisted pathways, such as water currents, can be an important pathway for the movement of ANS (see Discussion), if the first report of an ANS within an ecosystem was considered solely due to natural spread from a neighbouring ecosystem (e.g. range expansion or range shift), it was excluded from this analysis because unassisted movement was not documented consistently across regional datasets. Transport associated with anthropogenic debris, however, was included (considering Carlton et al., 2017).

Data were analysed at global and regional levels to explore trends in the rate of detection, ANS richness, population status and pathways of introduction. A ten-year moving average was used in temporal plots to decrease variability across years due to inconsistent search effort (see Discussion).

3 | RESULTS

3.1 | Global patterns

The assembled comprehensive dataset comprises 2209 records of primary detections of ANS (1442 unique species belonging to 17 phyla) across 49 aquatic ecosystems, including ten ecosystems found to have zero confirmed records during the period of study (Figure 1; Table S1). Considering all regions combined, an annual mean of 43 (±16 *SD*) primary ANS detections occurred. This translates to roughly one new detection every 8.4 days for this 50-year era. The rate of detections was relatively stable during 1965–1995, with a ten-year mean detection rate of about 32 ANS per year (Figure 2a). After this time, the rate increased, reaching 51 primary detections of ANS annually by the year 2000 and peaking at roughly 66 primary detections of ANS per year during 2005–2010. In the last five years, the rate of detection declined marginally, with about 59 primary detections per year.

A variety of ANS taxa were reported, with Arthropoda (*n* = 522, 23.6% of total), Mollusca (*n* = 373, 16.9%) and Chordata (Pisces) (*n* = 279, 12.6%) being most frequent, followed by Rhodophyta (*n* = 209, 9.5%), Annelida (*n* = 200, 9.1%), Chordata (Tunicata)

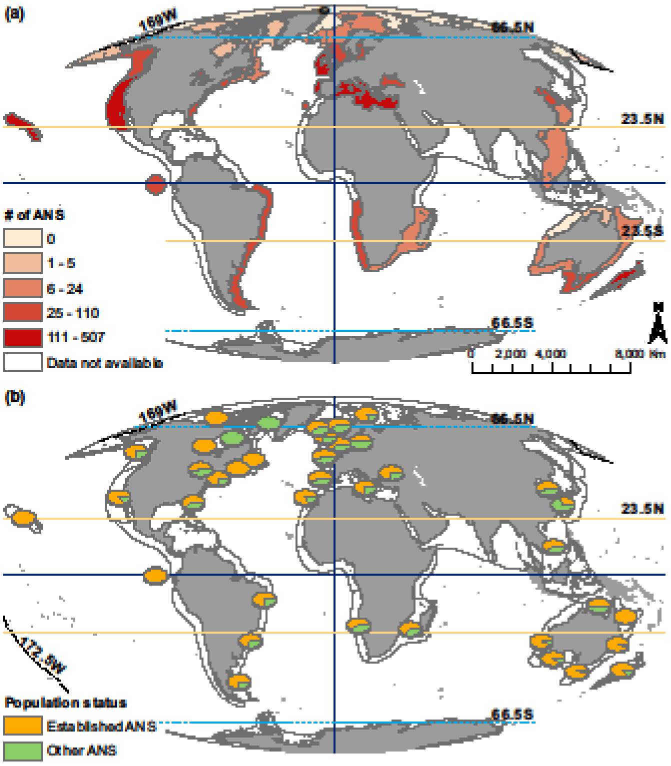


FIGURE 1 Records of primary detections of aquatic non-indigenous species (ANS) between 1965 and 2015 in each of 49 coastal marine, estuarine and freshwater ecosystems. Panels (a) and (b) show total number of detections and proportion of populations with established status, respectively. Comparable data were not available for regions in white, though ANS may be present, and are documented from a number of these regions

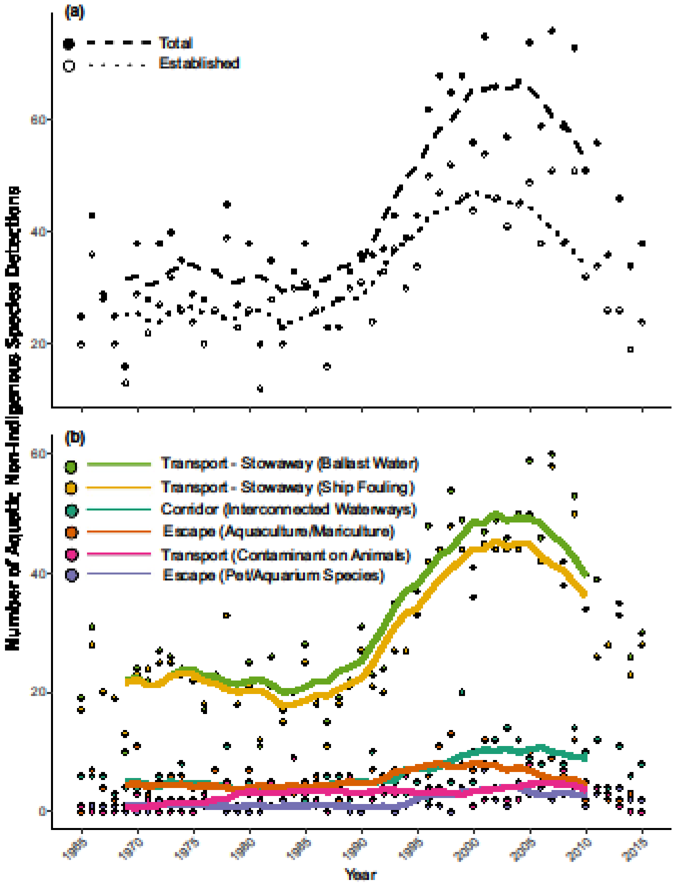


FIGURE 2 Chronology of primary detection events of aquatic non-indigenous species (ANS) across 49 coastal marine, estuarine and freshwater ecosystems during 1965–2015. Panel (a) shows trends by population status, where the dashed and dotted lines denote the ten-year moving averages for the annual number of detection events for total and established populations, respectively. Panel (b) shows trends in the number of primary detection events of ANS by pathway, for the top six pathways (96% of records)

(*n* = 160, 7.2%), Bryozoa (*n* = 148, 6.7%) and Cnidaria (*n* = 131, 5.9%) (Table S2). Ochrophyta (*n* = 57, 2.6%), Chlorophyta (*n* = 51, 2.3%) and Porifera (*n* = 26, 1.2%) were reported relatively infrequently, while Tracheophyta, Echinodermata, Ctenophora, Kamptozoa, other Chordates (e.g. Amphibia and Reptilia), Phoronida, Brachiopoda and Charophyta were seldom reported (each having fewer than 20 detection events, cumulatively representing 2.4% of all records).

Most ANS were reported as having established (74.2%) or unknown population status (19.9%)—few records exist for ANS with failed (5.4%) or extinct (0.5%) populations (Table S1). Most ANS were likely introduced as stowaways in ships' ballast water or biofouling, although direct evidence is typically absent, particularly for ballast water (direct evidence cited for 42/1468 ship fouling vs. 4/1595 ballast water records, respectively). The temporal trends for these two pathways were similar to or are largely responsible for the overall pattern of detections through time (Figure 2b). Escape of aquaculture/mariculture species follows a similar pattern, although much lower in magnitude, while the corridor pathway and escape of pet/aquarium species seem to have increased in importance/rate since the late 1990s. Nearly one-third of ANS primary detections were associated with a single pathway (32.7%), while most were associated with at least two (52.6%) or three (14.1%) pathways. Movement through connected waterways/seas/basins (193 records), stowaways in ballast water (162 records) and escape of aquaculture/mariculture species (144 records) were the most important pathways for single-pathway primary detection events. When two pathways were possible, stowaway as ship fouling and/or in ballast water were overwhelmingly implicated (91.5% of two-pathway events).

3.2 | Regional patterns

Patterns of primary detection were variable across regions, as would be expected due to differences in pathway strength (i.e. introduction

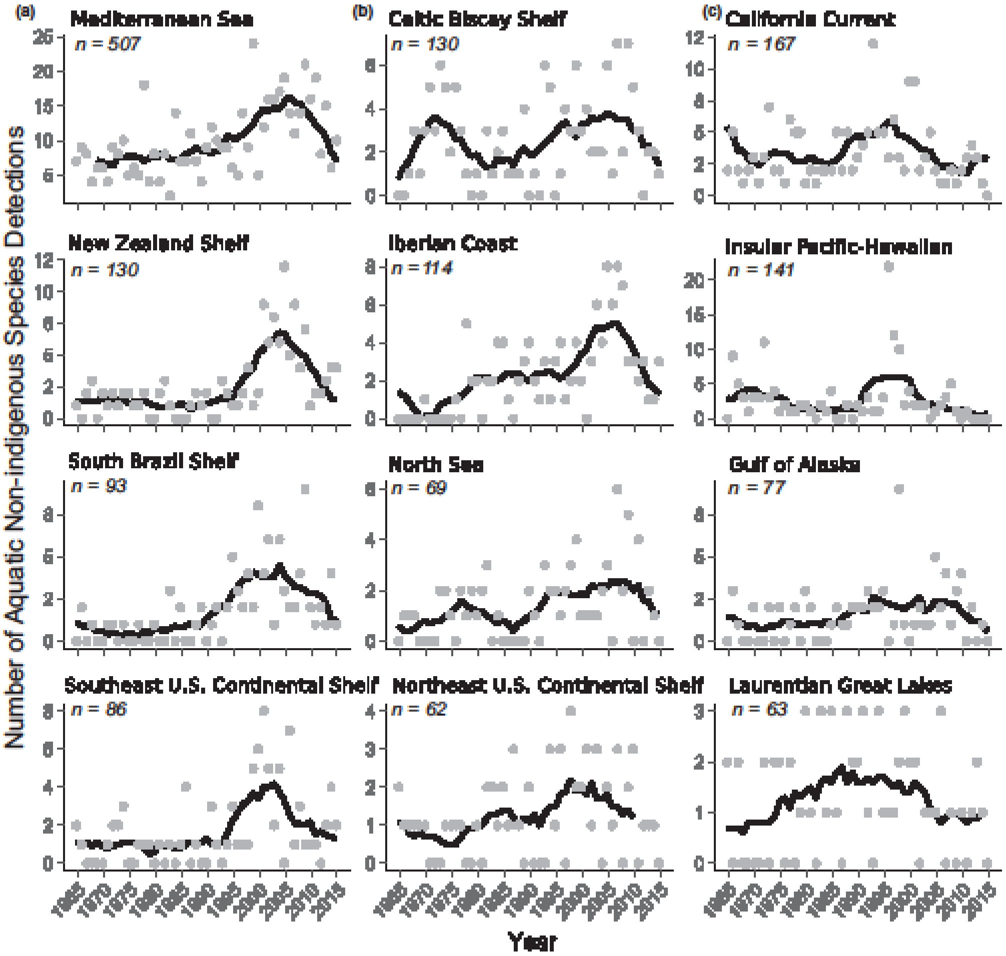


FIGURE 3 Temporal trends in primary detections of aquatic non-indigenous species across the top 12 ecosystems studied. Trend lines show ten-year moving average of the annual number (dots) of detections. Plots are arranged in columns to show (a) ecosystems having a strong peak in detections between 1995 and 2015; (b) ecosystems having an overall trend of increased rate of detections through time; and (c) ecosystems having relatively stable detection rate through time. Note differences in scale of y-axes across plots

effort), environmental conditions, ecosystem size, survey effort and taxonomic expertise. The cumulative number of primary detection events during the 50-year period ranged from zero to more than 500 per ecosystem, with variable levels of population establishment success across regions (Figure 1, Table S1). Inter-regional temporal trends varied with three patterns being typical: a distinct peak of ANS primary detections in the 1995–2015 timeframe, an overall trend (positive slope) of increased detections through time or a relatively stable rate of detections (Figure 3).

A majority (76.6%) of the 1442 unique ANS records were reported from a single ecosystem, while the 25 most reported ANS were reported from at least seven different ecosystems (Table 2). Regions having at least 10 primary detection records during the study period exhibited a diverse assemblage of ANS from at least five phyla, with any one phylum typically comprising no more than 30% of species within a location (exceptions being Arthropods and Pisces, which comprised 40%–50% of ANS in some regions) (Figure 4, Table S2).

TABLE 2 List of the 25 most common aquatic non-indigenous species reported as new primary detections across the studied ecosystems during 1965–2015

Species Name	Ecosystems	Potential Pathways of Introduction
Caprella mutica	13	BW, SF, AFG
Botrylloides violaceus	10	BW, SF, AFG, EAM, TCA
Palaemon macrodactylus	10	BW, EAM, CIW
Styela clava	10	BW, SF, EAM, AFG, TCA
Agarophyton vermiculophyllum	9	BW, SF, EAM, TCA
Grateloupia turuturu	9	BW, SF, EAM, TCA, OPM
Mytilus galloprovincialis	9	BW, SF, EAM
Amphibalanus amphitrite	8	BW, SF
Antithamnionella spirographidis	8	BW, SF, TCA, UAD
Carcinus maenas	8	BW, SF, AFG, TCB, ELF
Crassostrea gigas	8	EAM, SF
Dasysiphonia japonica	8	BW, SF, AFG, TCA
Didemnum vexillum	8	BW, SF, EAM, AFG, TCA, CIW
Molgula manhattensis	8	BW, SF, EAM
Paracerceis sculpta	8	BW, SF
Pseudopolydora paucibranchiata	8	BW, SF, EAM, TCA
Boccardia proboscidea	7	BW, SF, TCA
Grandidierella japonica	7	BW, SF, EAM
Diadumene lineata	7	SF, EAM
Polyandrocarpa zorritensis	7	BW, SF
Polycera hedgpethi	7	BW, SF, TCA
Ruditapes philippinarum	7	EAM, RFW
Ulva australis	7	BW, SF, TCA
Undaria pinnatifida	7	BW, SF, TCA, EAM OPM
Watersipora subtorquata complex	7	BW, SF

Note: The number of studied ecosystems reporting the species is given, as well as a cumulative list of possible pathways of introduction (pathways may differ for the same species introduced to different regions).

Abbreviations: AFG, Transport stowaway in angling/fishing gear; BW, Transport stowaway in ballast water, sediments or solid ballast; CIW, Corridor through interconnected waterways; EAM, Escape from aquaculture/mariculture; ELF, Escape of live food/live bait; OPM, Transport stowaway in organic packing materials; RFW, Release for fishery in the wild; SF, Transport stowaway in ship biofouling; TCA, Transport contaminant on animals; TCB, Transport contaminant in bait; UAD, Unaided rafting on anthropogenic debris.

Transport stowaway in ship fouling and ballast water tended to be the dominant pathways in most regions, typically responsible for at least 40% of primary detection events (Figure 5). Exceptions are the corridor pathway (Suez Canal) in the Mediterranean Sea and escape of aquaculture/mariculture species in the East China, South China and Yellow Seas (Table S3).

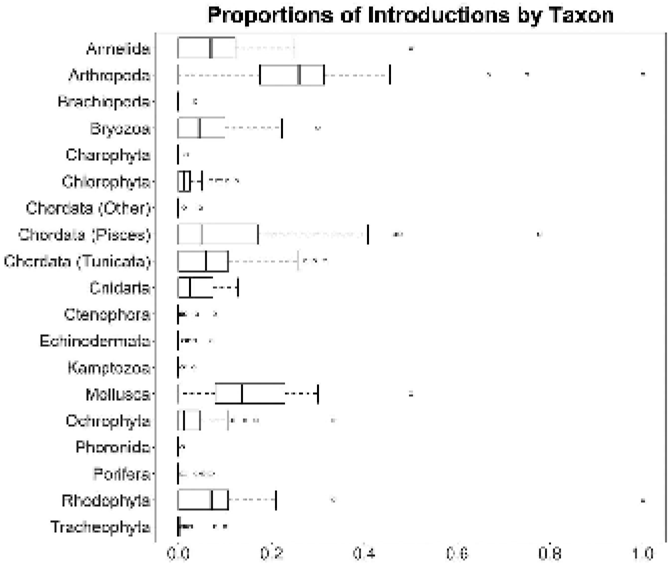
4 | DISCUSSION

Our analyses identified 2209 primary detection events of 1442 unique ANS over the past 50 years which, although confounded by time-lags between actual introduction and detection, likely is an underestimate of the actual number of introductions during this time period. It is widely recognized that ANS are frequently under-reported due to limited search effort, uncertainty about historical biogeography and an insufficiency of taxonomic expertise (Carlton & Fowler, 2018; Ojaveer et al., 2017), especially for smaller-bodied organisms (Carlton, 2009; Lohan et al., 2020). Our study also does not consider secondary introductions (spread) of ANS neither within an ecosystem nor between ecosystems, which will further contribute to this underestimation. Although our dataset represents an extensive collection of global detection records, it includes only ~73% of the world's large marine ecosystems, with very limited coverage of Africa, Central and South America and Asia. Introductions of ANS have undoubtedly occurred in these areas; the cost of ANS surveys can be prohibitive in regions with limited resources and a dearth of expertise across many taxa, which could explain why data were not accessible for this study.

The results of this study highlight a possible under-representation of taxa in global datasets of non-indigenous species: the 1442 unique species recorded here is more than ten-fold lower than the number of non-indigenous species (vascular plants, mammals, insects, birds, molluscs and fishes) observed in terrestrial ecosystems (Seebens et al., 2017). While land biodiversity is vastly higher than both marine and aquatic diversity combined (Grosberg et al., 2012; Vermeij & Grosberg, 2010), and thus more NIS would be proportionally expected in terrestrial systems, the documentation of the diversity of invasions in marine, estuarine and freshwater habitats has significantly lagged behind similar research on land. For example, extensive documentation of terrestrial invasions in the Hawaiian Islands and the Galápagos Islands commenced decades before the first investigations of marine invasions in those archipelagos (Carlton, & Eldridge, 2009, 2015; Carlton et al., 2019). We thus suspect that we may be at the tip of an invasion iceberg in understanding the scale of introductions in coastal environments (see also Byers et al., 2015).

Cumulatively, over the past 50 years, one ANS was reported as a primary detection within the evaluated ecosystems every 8.4 days (on average), and the rate of detection exhibits changes across years both within and across regions. While changes in the rate of ANS primary detections through time may reflect the actual introduction rate, this relationship is uncertain and confounded by variable survey effort and species detectability (Hewitt, Campbell, et al., 2004; Hewitt, Willing, et al., 2004; Ruiz et al., 2000). The rate of ANS primary detections appeared to increase in the 1990s and 2000s, possibly related to increased global trade (e.g. Sardain et al., 2019), but it is also likely influenced by increasing scientific, government and public awareness, and increased funding for surveys, monitoring and other assessments. For example, peaks in detection rate for Insular Pacific-Hawaii, New Zealand and Southeast

FIGURE 4 Relative importance of taxonomic groups (as a proportion of total primary detections) for aquatic non-indigenous species detected across 49 coastal marine, estuarine and freshwater ecosystems, from 1965 to 2015. In the box plots, the boundary of the box closest to zero indicates the 25th percentile, the black line within the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers above and below the box indicate the 10th and 90th percentiles. Points left and right of the whiskers indicate outliers outside the 10th and 90th percentiles



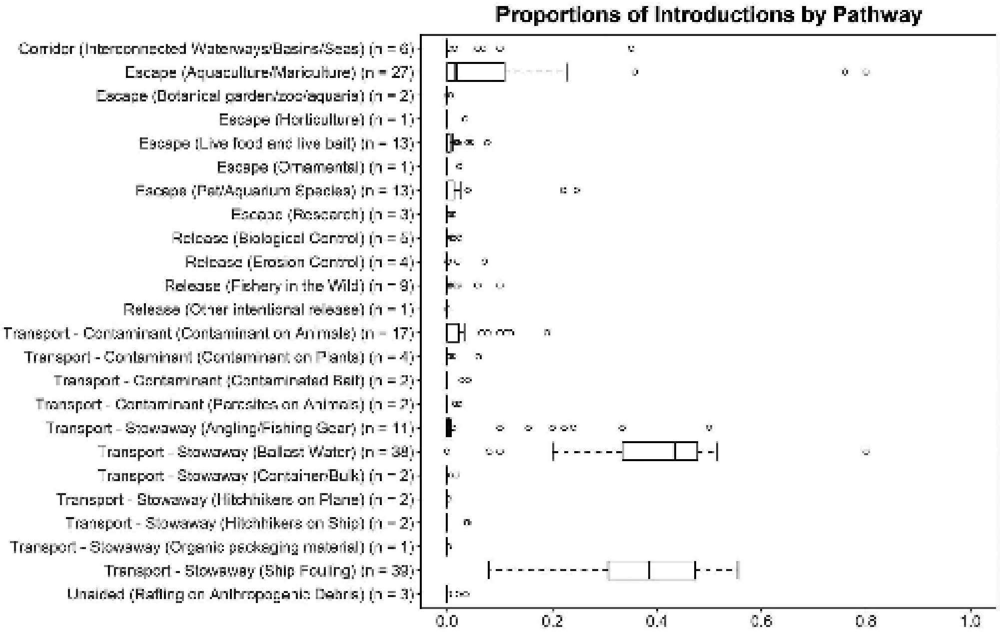


FIGURE 5 Relative importance of introduction pathways (as a proportion of total pathway records) associated with aquatic non-indigenous species detected across 49 coastal marine, estuarine and freshwater ecosystems, from 1965 to 2015. In the box plots, the boundary of the box closest to zero indicates the 25th percentile, the black line within the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers above and below the box indicate the 10th and 90th percentiles. Points left and right of the whiskers indicate outliers outside the 10th and 90th percentiles

Australian Shelf correspond with dedicated scientific surveys aiming to document ANS beginning in the 1990s (Carlton & Eldridge, 2009; Hewitt, 2002; Hewitt, Campbell, et al., 2004) and in the 2000s (Inglis & Seaward, 2016). Comparatively, these areas receive just a small proportion of global shipping but account for much greater numbers of recorded ANS than regions that are global centres for shipping (e.g. China, SE Asia, Japan, NW Atlantic), appearing to challenge predictions that invasion hot spots should be strongly correlated with modern shipping activity (Kaluza et al., 2010; Sardain et al., 2019; Seebens et al., 2016). In fact, for Hawaii (and for many of the regions reviewed here), the majority of introductions may have occurred long before the first reports. Similarly, regions with apparent increasing rate of primary detections since the 1990s (Patagonian Shelf, East Brazil Shelf and Madeira Archipelago) are likely reflective of recent, dedicated research (Canning-Clode et al., 2013; Schwindt et al., 2020; Teixeira & Creed, 2020).

The apparent decline in primary detections of ANS since 2005 in many regions may correspond with preventative measures implemented to reduce biological introductions, such as requirements to manage ships' ballast water (e.g. Hayes et al., 2019), and to diminish the risks associated with the intentional introduction and transfer of aquatic organisms via aquaculture and fisheries (e.g. Cook et al., 2008; Hewitt et al., 2006). However, given uncertainty due to inconsistent and often insufficient search effort leading to time-lags between introduction and first collection, any inferences about ANS introduction rate based on collection dates must be made cautiously and, ideally, consider multiple lines of evidence (see Costello & Solow, 2003). For example, Bailey et al. (2011) inferred that a declining rate of ANS detections in the Great Lakes could be due to management efforts (i.e. new ballast-tank flushing regulations) only after reviewing direct cause-and-effect studies of the management technique and evaluating compliance rates by the shipping industry. Even after such detailed analysis, the relative contribution of management versus search effort is not clear. Seebens et al. (2017) found similar declines in records of recent detections of terrestrial taxa and fishes consistent with a decline in deliberate introductions due to increasing awareness of impacts of biological introductions, but also cautioned that data collected after the year 2000 may be incomplete due to time-lags. We therefore suggest that future assessments should consider long-term averages and associated levels of search effort to evaluate invasion dynamics of ANS.

Most regions do not have regular surveillance programmes with consistent long-term funding or are pursuing generalized surveys to generate baseline inventories rather than targeted early detection of ANS. In the absence of standardized, targeted and repeated methods for surveillance, the true date of introduction could be years or even decades earlier than the date of first detection (e.g. Galil, 2008; Hewitt, Campbell, et al., 2004; Zenetos et al., 2019). One example of time-lags within these data is the collection and reporting of four beach-dwelling isopods from Hawaii between the 1970s and 1990s (*Halophiloscia couchii* (Kinahan, 1858), *Littorophiloscia culebrae* (H. F. Moore, 1901), *Porcellio lamellatus* (Budde-Lund, 1885) and *Armadilloniscus ellipticus* (Harger, 1878)), thought to have been introduced in solid ballast materials such as rock and sand (Carlton & Eldridge, 2009); as solid ballast was phased out of use in the 1800s (National Research Council, 1996), these isopods may have been introduced one hundred years (or more) prior to their published collection date.

Where surveillance is designed specifically to detect targeted taxa and is implemented regularly, ANS can be detected at relatively small population sizes, reducing time-lags between introduction and detection (Hayes et al., 2019). More often, ANS are collected as "by-catch" during non-surveillance research activities (Ruiz et al., 2000). Additional lags then occur because time is required to detect, positively identify and report new species once collected in a sample (Azzurro et al., 2016; Stanislawczyk et al., 2018). A lack of taxonomic expertise can cause significant delays in reporting, particularly if individuals are first misidentified as native species (Campbell et al., 2007; Carlton, 2009; Mienis, 1992). Furthermore, without standardized and targeted surveillance programmes in place, many years may pass before a new ANS is collected because introduced populations are likely to be rare (both in spatial coverage and abundance) until several generations contribute to population growth and spread (Azzurro et al., 2016; Harvey et al., 2009). Similarly, it is difficult to ascertain the population status (established, failed or extinct) without repeated surveys in the location of introduction, and many introductions are likely to occur unnoticed if populations fail or go extinct within a short time-scale. The high proportion of records with unknown population status (19.9%) and low number of "failed" populations (5.4%) in this study indicate a need to better design or implement surveillance programmes with repeated measures.

Most detection events in this dataset are comprised of Arthropoda, Mollusca and Pisces. The reporting of certain taxa (such as Annelida, Rhodophyta, Bryozoa, Cnidaria and Tunicata) in only a subset of the studied ecosystems may reflect different active pathways (anthropogenic transport mechanisms and source regions of ANS) and species adaptations to different recipient conditions (Cardeccia et al., 2018). However, it is likely that the pattern is also heavily influenced by the availability of taxonomic specialists focusing on these groups and the different sampling methods used across studies. Interestingly, Echinodermata comprise only 12 ANS reported in six of the 49 estuarine and marine ecosystems studied. Given that this phylum is globally well studied, abundant and widely distributed (e.g. Lebrato et al., 2010), it is unlikely that the low number of echinoderm invasions can be attributed solely to the group's prevalence or to lack of taxonomic expertise, suggesting other factors also influence the frequency of ANS reports. Further, many experts argue that the biogeography and taxonomy of microscopic species in the Chlorophyta and Ochrophyta are so poorly understood that new reports of these taxa should be considered cryptogenic (sensu Carlton, 1996; see also De Clerck et al., 2013; Gómez, 2008, 2019) with few exceptions where forensic assessment clearly demonstrates introduction of ANS (e.g. Bolch & Hallegraeff, 1990; Hallegraeff et al., 1988).

The true rate of recent introductions (since 1965) is undoubtedly much greater than documented here for many small-bodied taxa.

More specifically, the magnitude of organism transfer (both in abundance and species richness) is inversely proportional to body size, yet relatively few ANS are recognized for fungi, protists, parasitic and free-living flatworms, viruses and microbes, likely reflecting high uncertainty in taxonomic identification and geographic origin (Lohan et al., 2020). The investigation of lesser-studied and cryptogenic taxa will be a fruitful avenue of future research, particularly as molecular tools, reference databases and museum collections advance (e.g. Darling et al., 2017), noting that both conventional and molecular biological surveys are dependent on taxonomic expertise—a skill set rapidly diminishing without dedicated funding and training programmes (Bik, 2017; Coleman, 2015; Costello et al., 2010; Kim & Byrne, 2006).

Assessment of the pathways of introduction of ANS is fundamental for biological invasion risk assessments and for prioritizing management, monitoring and surveillance activities (Barry et al., 2008; Essl et al., 2015). For many non-indigenous species, more than one introduction pathway is possible based on human activities occurring in or near the locality of first collection; hence, the assignment of the responsible pathway is uncertain (Ojaveer et al., 2018). As a result, many studies report only "commercial shipping" as the mechanism of introduction, without differentiating between the various pathways associated with this activity (e.g. ballast water and biofouling of underwater surfaces), making it difficult to quantify introduction likelihood and evaluate the efficacy of pathway-based management actions. Our study also indicates that commercial shipping activities are often inferred as the responsible pathway(s) of introduction without direct evidence (nor critical examination of alternate possibilities). Research examining commonly neglected or understudied pathways, such as the aquarium and bait trades, Internet commerce and anthropogenic marine litter (e.g. Campbell et al., 2017; Carlton et al., 2017; Chan et al., 2020; Fowler et al., 2015; Lenda et al., 2014), could lead to new insights and priorities for management of ANS. It is vital that future work transparently consider uncertainties in pathway assignments, describe the level of confidence and critically evaluate all possible pathways (Essl et al., 2015; Ojaveer et al., 2018).

National regulations requiring ballast water to be exchanged mid-ocean, thereby purging coastal species for presumably less harmful oceanic species and reducing viability of remaining coastal species via osmotic shock, have been implemented in multiple locations around the world since the early 1990s (Bailey, 2015). While there is evidence that ballast water exchange has effectively reduced ballast-mediated introductions to the Laurentian Great Lakes where there is a high level of enforcement (Bailey et al., 2011), there is greater uncertainty about the degree of protection offered to coastal marine ports (e.g. Casas-Monroy et al., 2015; Scriven et al., 2015) and locations lacking performance measures. For some marine ports, there have been trade-driven compensatory changes in the total ballast water and organism delivery (Carney et al., 2017), and biofouling remains a largely unmanaged source of ANS (Williams et al., 2013). It is notable that the declining trend in detections associated with ship fouling occurs after the entry-into-force of the International Convention on the Control of Harmful Anti-Fouling Systems on Ships (IMO, 2001) in 2008 which banned the use of the anti-fouling compound tributyltin (TBT). This ban raised concerns that in the absence of effective replacements for TBT, introductions via ship fouling would escalate (Drake & Lodge, 2007; Faasse & Ligthart, 2007; Lewis et al., 2004); however, there is no evidence of this in our study. Further research is needed to disentangle the risk associated with ballast water versus biofouling and to evaluate if international measures (IMO, 2004, 2011) intended to curtail introductions by these pathways are effective or if additional measures are needed (ICES, 2019).

When species are introduced and become established in a new geographic region, they often spread beyond the initial site of invasion, expanding the area occupied and increasing the potential magnitude of impacts (Parker et al., 1999). Such secondary spread beyond the initial site of introduction results from a combination of natural processes (e.g. active swimming, passive larval transport or drifting) and human-mediated dispersal mechanisms (e.g. recreational vessels, aquaculture, fishing and restoration). Although excluded from this study due to a lack of consistent data across studied regions, secondary spread is known to be a very important component of invasion dynamics, at multiple scales within and among adjacent ecosystems. For example, the Japanese wireweed, *Sargassum muticum* (Yendo) Fensholt, is believed to have been introduced initially to the coasts of northern France through oyster aquaculture activities and to have subsequently spread via drifting plants to the English south coast and the Netherlands. It has now spread to most coastal countries in Europe, likely through a combination of natural dispersal, ships' ballast water or biofouling and oyster aquaculture activities (Gollasch et al., 2009).

A recently published study on the Baltic Sea indicates that secondary spread of ANS from the adjacent North Sea is responsible for around 50% of introductions when both natural dispersal and human-mediated pathways are considered (Ojaveer et al., 2017). In a previous analysis of 257 ANS established in California, 57% of these species were known from multiple bays along the coast with some occurring all the way to Alaska, suggesting secondary spread attributed primarily to shipping (ballast water and/or ship fouling) and aquaculture (Ruiz et al., 2011). There is mounting evidence that global warming has enabled ANS to expand into regions where previously they were not able to survive and reproduce (Canning-Clode & Carlton, 2017; Occhipinti-Ambrogi, 2007; Walther et al., 2009). Given the impressive rates of dispersal of ANS, it is likely that the unaided pathway is significantly underestimated (Hulme et al., 2008). This stresses the need for regional cooperation, as unaided spread is an important pathway to grasp both from a management perspective and in terms of fundamental invasion ecology (Faulkner et al., 2020; Schwindt & Bortolus, 2017).

This study indicates that introductions of ANS have occurred at an alarming rate on a global scale for the past 50 years. Coordinated actions are urgently needed to prevent new introductions and further spread of ANS, one of the top drivers of biodiversity change (IPBES, 2019; IUCN, 2017). While there have been significant advances over the past 30 years in policies to reduce ballast water-mediated invasions, including those by the International Maritime Organization and regulations in several nations (e.g. Government of Canada, 2006; U.S. Coast Guard, 1998), these are still being implemented, and ship fouling is largely unregulated but gaining increased attention (e.g. Department of Agriculture and Water Resources, 2019; Georgiades et al., 2020; Ulman et al., 2019). Further regional actions, such as those to address introductions via the Suez Canal, will have substantial benefits for the Mediterranean Sea and across associated global trade networks (Galil et al., 2017).

Despite the good intentions of the CBD to evaluate non-indigenous species as a key indicator and recent efforts to establish a mechanism for reporting (Pagad et al., 2018), this is still at an early stage for aquatic and marine species, and synthetic inventories of ANS and associated invasion pathways are still very limited, inhibiting prioritization and control activities in aquatic environments. While numerous policies and strategies have been put in place that aim to reduce the introduction and spread of non-indigenous species as conservation measures, the coverage is piecemeal, taxonomically biased and focused only on a subset of pathways—implementation and enforcement is often lacking (see Ojaveer et al., 2018) and international treaties may be in conflict (Campbell et al., 2009). For example, the CBD and the World Trade Organization's General Agreement on Tariffs and Trade 1994 (GATT) apply the precautionary approach from different contexts, with the GATT able to utilize "gateway" provisions (Campbell et al., 2009). The end result is that Sanitary and Phytosanitary Measures may be cancelled out by the World Trade Organization if trade is blocked as a result of ANS. The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services recently reported that, based on past and ongoing rapid declines in biodiversity, goals for conserving nature and achieving sustainability cannot be met without urgent and concerted efforts fostering transformative change to reduce drivers of biodiversity loss (IPBES, 2019). In our view, this requires robust and reliable inventories of ANS introductions and their introduction pathways, needed to both evaluate performance of management measures and accelerate the rate of adaptive management to achieve desired outcomes.

Studies such as this one, based on national and/or regional inventories of non-indigenous species, are only reliable if local experts can maintain and continually update lists considering new records, range expansions and evolving knowledge of nomenclature, population status and responsible pathways (Marchini et al., 2015). It is vital to continue and to expand research and survey efforts across marine, estuarine and large freshwater ecosystems to better inform both regional and global policy development and management activities, such as the European Water Framework Directive (Cardoso & Free, 2008). Inventories of ANS frequently suffer from a number of uncertainties in species identification (taxonomic uncertainty) and inferred pathways of introduction, inconsistent or uneven search effort (leading to low spatial, temporal and taxonomic resolution), poor documentation of data and knowledge and inadequate baseline information (Marchini & Cardeccia, 2017; McGeoch et al., 2012). These are all critical gaps that impair our ability to fully understand invasion dynamics, their drivers and performance of policies and management actions. Addressing these gaps requires standardized and repeated measures for detection, in order to improve the core data quality and inferences that can be drawn (e.g. Ruiz & Hewitt, 2002). While this need is well recognized and several research groups have sought to advance this within their region, it is also the case that: (a) somewhat different methods and approaches are used among regions and (b) such efforts are usually short-term and limited by funding available to an individual researcher or group.

We call for standardized, targeted and repeated methods across regions in order to improve the quality of global-scale comparisons and sustain core measures over longer time-scales. Future studies should include key human activities/pressure trends over time in helping to interpret the temporal dynamics of new introductions. It will be fundamental to fill in existing knowledge gaps given that invasion data representing broad regions of the world's oceans are not yet readily available and to maintain knowledge pipelines for adaptive management. We hope that the baseline provided here will be updated in the future as pathway management is implemented and, ideally, becomes evidence of associated positive changes (fewer introductions of ANS).

ACKNOWLEDGEMENTS

The authors thank the joint Working Group on Ballast and Other Shipping Vectors (WGBOSV) of the International Council for the Exploration of the Sea (ICES), Intergovernmental Oceanographic Commission of UNESCO (IOC) and International Maritime Organization (IMO) for facilitating this research and the ICES Working Group on Introductions and Transfers of Marine Organisms (WGITMO) for contributing to the AquaNIS database. Financial support was provided by Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grants to SAB and NEM, a NSERC Visiting Fellowship at Fisheries and Oceans Canada to FTC and a National Natural Science Foundation of China (grant no. 31622011) to AZ. The Atlantic Canada contribution was partly supported by Fisheries and Oceans Canada, Aquatic Invasive Species Science Program. Australia's National Port Survey Program was funded through the CSIRO Centre for Research on Introduced Marine Pests and individual port investments through Ports Australia; ongoing marine biosecurity surveillance is funded by State Governments. The Baltic Sea contribution was partly supported by the COMPLETE project (Completing management options in the Baltic Sea region to reduce risk of invasive species introduction by shipping), co-financed by the European Union's funding Programme Interreg Baltic Sea Region (European Regional Development Fund). The Gulf of Alaska contribution was partially supported by Fisheries and Oceans Canada and the North Pacific Marine Science Organization (PICES). New Zealand's marine biosecurity surveillance programmes were funded by Biosecurity New Zealand; GJI and KS were supported by the NZ Government's Strategic Science Investment Fund (SSIF) through NIWA Coasts & Oceans Programme 6. NC was funded by a doctoral grant (SFRH/BD/146881/2019) awarded by Fundação para a Ciência e Tecnologia (FCT). JCC is funded by national funds through FCT

– Fundação para a Ciência e a Tecnologia, I.P., under the Scientific Employment Stimulus - Institutional Call - [CEECINST/00098/2018]. The support and cooperation of the Allochthonous Species Group of the Italian Society of Marine Biology (S.I.B.M.) are acknowledged. Partial funding by CONICET-PIP 508 and ANPCyT-PICT 2016-1083 to ES is acknowledged. IK would like to thank the Galapagos National Park for granting authorization to carry out this research as well as Galapagos Conservancy, Lindblad Expedition/National Geographic Fund, Galapagos Conservation Trust, Paul M. Angell Foundation and Ecoventura for research funding provided for the CDF marine invasive species programme. This publication is contribution number 2355 of the Charles Darwin Foundation for the Galapagos Islands. The United States Coast Guard provided support to GR and PF for collection and analysis of invasions in coastal marine waters of North America. The United States Environmental Protection Agency, through its Office of Research and Development, supported the research described here. Though it has been subjected to Agency administrative review and approved for publication, its content does not necessarily reflect official Agency policy. The authors have no conflict of interest to declare concerning the subject matter discussed in this manuscript.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13167.

DATA AVAILABILITY STATEMENT

The full dataset of primary detection events of aquatic non-indigenous species collected for this study (and associated references) is available at https://doi.org/10.5061/dryad.msbcc2fwk.

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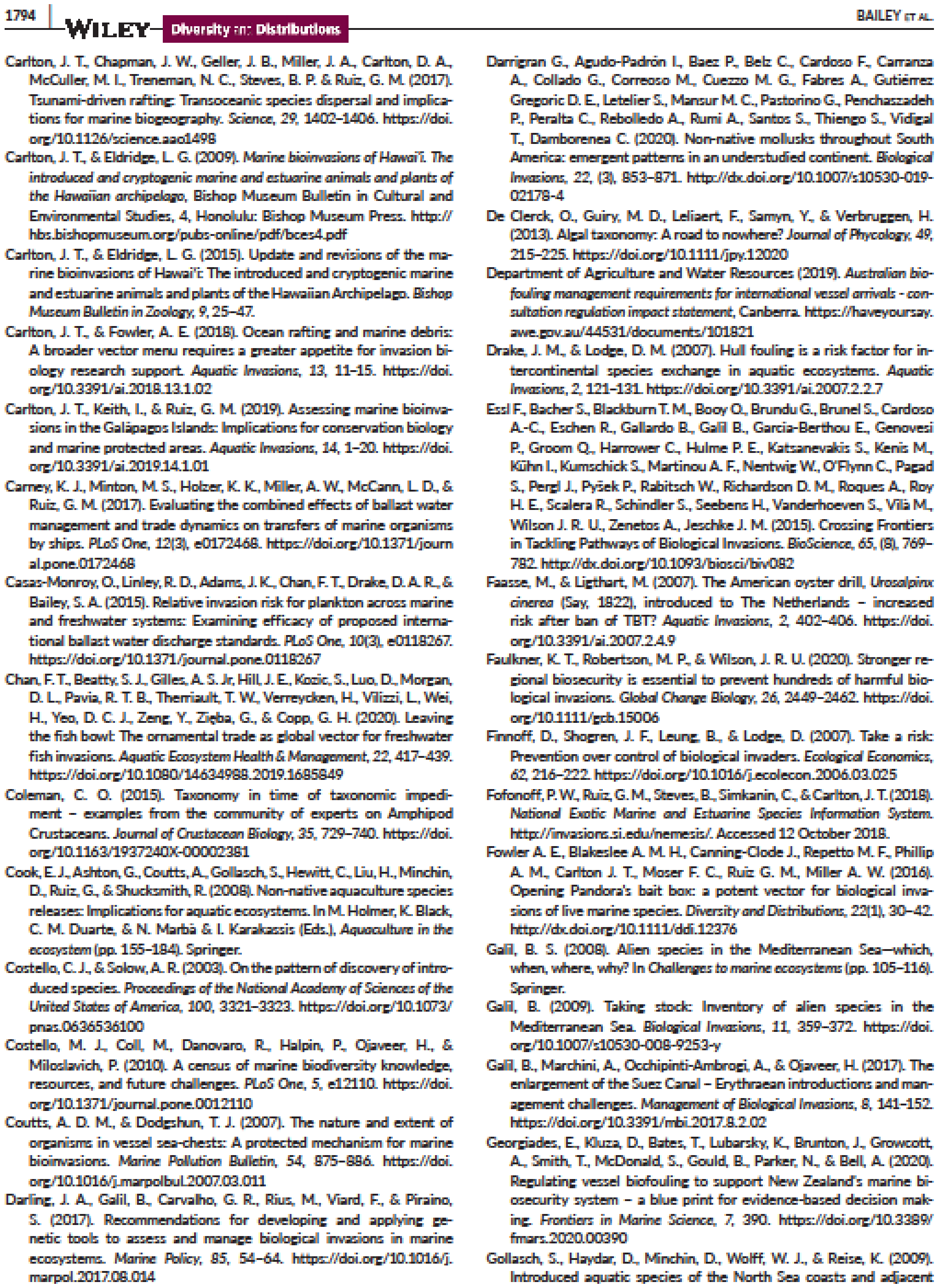

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BIOSKETCH

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Author contributions: S.B. conceived the study, led data analysis and drafting of the manuscript. All authors compiled and critically reviewed data. S.B., J.T.C and P.F. conducted final standardization of data including pathway assignments. A.C., F.C. and J.D. contributed to data analysis. J.T.C., J.D., B.G., G.I., H.O. and G.R. made significant contributions to early drafts of the manuscript. All authors contributed to editing the final manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Bailey SA, Brown L, Campbell ML, et al. Trends in the detection of aquatic non-indigenous species across global marine, estuarine and freshwater ecosystems: A 50-year perspective. *Divers Distrib*. 2020;26:1780–1797. https://doi.org/10.1111/ddi.13167

Fonte: Bailey SA, Brown L, Campbell ML, Canning-Clode J, Carlton JT, Castro N, Chainho P, Chan FT, Creed JC, Curd A, Darling J, Fofonoff P, Galil BS, Hewitt CL, Inglis GJ, Keith I, Mandrak NE, Marchini A, McKenzie CH, Occhipinti-Ambrogi A, Ojaveer H, Pires-Teixeira LM, Robinson TB, Ruiz GM, Seaward K, Schwindt E, Son MO, Therriault TW, Zhan A. 2020. Trends in the detection of aquatic non-indigenous species across global marine, estuarine and freshwater ecosystems: A 50-year perspective. DiversityandDistributions. 26(12): 1780-1797. https://doi.org/10.1111/ddi.13167