

Universidade de Brasília
Instituto de Ciências Biológicas
Programa de Pós Graduação em Ecologia

A importância do tempo no estudo de peixes recifais: métodos, interações e comunidades

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Dissertação de Mestrado

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Dissertação de Mestrado

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Métodos, Interações e Comunidades

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"No que diz respeito à física, a flecha do tempo é apenas uma propriedade da entropia."

Arthur Eddington

"Diante da vastidão do tempo e da imensidão do universo, é um imenso prazer para mim dividir um planeta e uma época com você."

Carl Sagan

"São os mecanismos interligados e interativos de evolução e ecologia, cada um dos quais é ao mesmo tempo um produto e um processo, que são responsáveis pela vida como a vemos e como ela tem sido."

James Valentine

"Alegre-se com a vida, porque ela lhe dá a chance de amar, trabalhar, brincar e olhar para as estrelas."

Henry van Dyke

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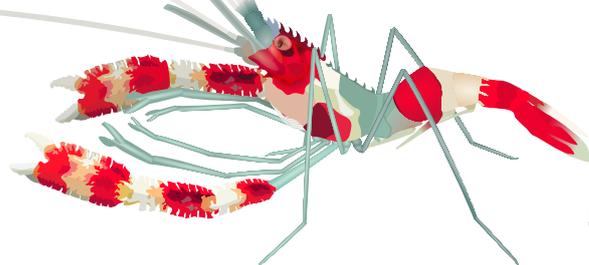
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Resumo geral

Comunidades biológicas são dinâmicas e mudam constantemente no tempo. No entanto, abordagens temporais costumam ser escassas e a maioria dos estudos na ecologia marinha brasileira usam amostragens em escalas de tempo curtas. Pensando nisso, nesta dissertação realizei três estudos focados no tempo, usando as assembleias de peixes recifais do Atlântico Sudoeste como organismos modelo.

No primeiro capítulo eu descrevi o histórico de mudanças das assembleias de peixes recifais em quatro ilhas oceânicas brasileiras usando mais de uma década de informações coletadas por um programa de monitoramento a longo prazo (PELD-ILOC). As assembleias de peixes são variáveis, onde o tempo *per se* explica de 30% a 50% das mudanças na composição. Entretanto, essas mudanças não apresentam uma direção clara e parecem ser flutuações estocásticas provenientes das oscilações populacionais de diferentes espécies. Além disso, cada ilha teve um histórico de mudanças próprio que sugere a atuação de um mecanismo ecológico diferente em cada local, que incluem cenários estabilidade dinâmica, substituições de espécies intraguilda, cascatas tróficas e distúrbios provavelmente ligados a floração de macroalgas. Toda essa variabilidade fornece um indicativo das vantagens trazidas pelo acompanhamento a longo prazo.

No segundo capítulo, eu avaliei como interações de limpeza — uma relação mutualística característica de ambientes recifais, na qual uma espécie (limpador) remove parasitas, muco ou pele morta de uma outra espécie (cliente) — variaram no período de dois anos em uma enseada de Arraial do Cabo. As redes de interações dependem prioritariamente de um limpador especializado, *Elacatinus figaro* e de um facultativo, *Pomacanthus paru*, que atendem a conjuntos de espécies semelhantes. Cardumes de juvenis de *Haemulon* também atuaram como limpadores facultativos quando juvenis, mas atendem principalmente a um cliente, *Pseudupeneus maculatus*. No entanto, o engajamento de *Haemulon* na interação variou entre anos, oferecendo uma oportunidade de limpeza temporária. Ainda assim, a maior parte das redes de interações se manteve semelhante entre os anos devido à presença constante de *E. figaro* e *P. paru*, mostrando que se as espécies centrais forem mantidas, o restante da rede permanece estável.

Por fim, o objetivo do terceiro capítulo foi avaliar como amostragens de peixes por vídeos podem se beneficiar ao incluir o tempo de gravação, buscando identificar estratégias de amostragem mais eficientes. O capítulo foca em dois tipos de amostragens: se ter mais réplicas com vídeos curtos ou poucos vídeos mais longos. Usando recifes da costa leste do Rio Grande do Norte como modelo, foi encontrado que a maioria das espécies é detectada nos primeiros minutos de filmagem, onde cinco vídeos de cinco minutos foram suficientes para detectar boa parte da riqueza de espécies do estado. Para atingir um mesmo número de espécies, tempo e réplicas podem ser intercambiáveis, mas essa relação não é linear, de modo que a taxa de detecção de novas espécies por minuto cai drasticamente quando a duração dos vídeos aumentou. Dessa forma, muitas réplicas de vídeos mais curtos são mais eficientes por unidade de tempo que poucas réplicas de vídeos mais longos.

Nesta dissertação, eu espero ter demonstrado como a ecologia recifal brasileira pode se beneficiar ao incluir o tempo para responder padrões, demonstrando que perspectivas temporais permitem um entendimento mais profundo dos mecanismos determinantes da estrutura das assembleias marinhas recifais.

Palavras-Chave: Atlântico Sudoeste, Monitoramento, Ilhas Oceânicas, Limpeza, Filmagens Remotas Subaquáticas

Abstract

Biological communities are dynamic and changes constantly through time. Still, surveys within the Brazilian marine ecology counts on few temporal assessments. In an attempt to inspire the spread of temporal perspectives in the field, in this dissertation I conducted three surveys using a temporal framework, taking the Southwestern Atlantic reef fishes as target organisms.

The first chapter goal was to describe how reef fish assemblages changed within the last decade in four Brazilian oceanic islands, using data recorded by a long-term monitoring program since 2007 (PELD-ILOC). The fish assemblages rearranged constantly through time, with time itself accounting from a third to half the variability in species composition. However, those changes were mostly non-directional, likely resulting from random fluctuations on fish populations. Each island had their own set of changes, suggesting a distinct mechanism could explain changes in each island. Those ranged between a dynamic stability scenario to a within-group turnover, a trophic cascade and a disturbance-recover dynamics (probably linked to algal blooms). This diversity of processes shows how temporal perspectives can improve our current understanding about biological communities by suggesting new ideas on community functioning.

Beyond tracking changes of composition, time assessments may be useful to characterize other topics within community ecology. Minding these applications, the second chapter attempted to describe cleaning interactions — a mutualistic relation common in reefs in which a cleaner species remove parasites and dead skin from a client species — in a rocky reef in Southwestern Brazil using a two years temporal perspective. The local cleaning networks rely mostly on two species, *Elacatinus figaro* and *Pomacanthus paru*. Schools of juvenile *Haemulon* also engaged as second-party cleaners, though attending mostly a single client (*Pseudupeneus maculatus*). Cleaning activities of *Haemulon* species decreased substantially between years, such that their importance on the 2020 network was almost negligible. The cleaning networks still changed little between years, such that as long as the central species *E. figaro* and *P. paru* remain on the reef, the cleaning interaction shall remain stable.

The last chapter was dedicated to unravel how a time perspective could be applied to harvest field samples. The main goal was to evaluate the trade-offs associated to methodological decisions in recording fish richness and composition through remote filming. Particularly, the focus lied upon identifying which strategy record more species under a smaller effort, if either using several replicates of short videos or a few replicates of longer videos. The analysis took place on reefs in Northeastern Brazil. Most of the local richness was detected within the video first minutes, such that as few as 5 videos lasting for as short as 5 min could reveal most of the local richness. Time and replicates were interchangeable in order to reach a same species number, though this relation was non-linear, such that new records per minute dropped quickly towards longer videos. So, using shorter videos provide a more efficient way to record more species within less sampling time.

By exploring these distinct issues, I expect to have shown how community ecology on reef systems would benefit from including a temporal perspective, allowing for a deeper understanding about the mechanisms regulating the structure of marine reef communities.

Keywords: Southwestern Atlantic; Monitoring; Oceanic Islands; Cleaning Interactions; Remote Underwater Videos

Introdução geral

Comunidades biológicas são dinâmicas e podem ser estudadas em várias escalas de tempo (MURPHY et al., 1988; OTTERSEN et al., 2010). Estudos envolvendo variação temporal costumam ser escassos, mas permitem um entendimento mais profundo das espécies e de como elas interagem entre si e com o ambiente (MAGURRAN et al., 2010). Uma mesma comunidade pode ser acompanhada por minutos, meses ou anos e revelar diferentes facetas da sua estrutura e funcionamento em cada tempo. Abordagens na escala de dias e semanas mostram um recorte instantâneo das comunidades, que costumam ser úteis para descrever a composição de espécies e como elas interagem entre si e com o ambiente (AUED et al., 2018; FONTOURA et al., 2020; MORAIS; FERREIRA; FLOETER, 2017; QUIMBAYO et al., 2018). Na escala de anos ou décadas, temos mais detalhes sobre o caminho que as comunidades tomaram recentemente para chegar em seu estado atual, trazendo um conhecimento mais detalhado sobre sua estabilidade no tempo (BATES et al., 2014; KELMO; ATTRILL, 2013; WOLFF; RUIZ; TAYLOR, 2012).

Estudos com comunidades biológicas possuem escalas temporais bem variadas, de alguns dias até milhões de anos (BONTHOUX; BALENT, 2012; CONDAMINE; ROLLAND; MORLON, 2013). Por exemplo, as filogenias de comunidades acompanham o histórico evolutivo das espécies, detalhando quais processos geológicos e biogeográficos moldaram a composição local no tempo geológico (NARWANI et al., 2015). Por outro lado, as comunidades também podem ser descritas usando janelas de tempo curtas, de apenas alguns dias ou semanas, que permitem realizar inferências ecológicas ao custo de assumir que as comunidades são estáticas (AUED et al., 2018; FONTOURA et al., 2020; LONGO et al., 2019; MORAIS; FERREIRA; FLOETER, 2017). Na prática, as comunidades biológicas dificilmente permanecem constantes no tempo porque as espécies são dinâmicas, sofrendo flutuações populacionais em resposta às mudanças de outras espécies ou mesmo das condições ambientais.

O ambiente está sempre suscetível a sofrer alterações, sejam elas graduais, como as mudanças no clima (CONDAMINE; ROLLAND; MORLON, 2013), ou abruptas (também chamados de distúrbios), como em tempestades ou incêndios florestais (BURKLE et al., 2019; DUFOUR et al., 2019; REAGAN, 1991). Os distúrbios garantem que as comunidades sejam dinâmicas ao provocar mortalidade de indivíduos, seja ela seletiva ou não, abrindo oportunidades para que outras espécies aumentem em abundância (COLLINS, 2000). Os impactos da perda de indivíduos podem ser instantâneos ou persistir ao longo do tempo, impedindo que as comunidades se aproximem de um equilíbrio (JACQUET; ALTERMATT, 2020). Acompanhar as comunidades no tempo consiste em uma das melhores estratégias para entender os efeitos imediatos e tardios dos distúrbios (MAGURRAN et al., 2010). As mudanças demográficas, como nascimento e mortalidade

**Comunidades
no tempo**

**Escalas de
tempo**

**Por que
monitorar?**

costumam ser mais aparentes e por isso são o alvo da maioria dos estudos de monitoramento (MAGURRAN et al., 2010).

Amostrar comunidades periodicamente demanda esforços e recursos que frequentemente não estão à disposição, tornando abordagens a longo prazo mais raras, especialmente nos trópicos (MAGURRAN et al., 2010). Métodos indiretos podem ser usado para extrair dados com relevância biológica a exemplo do acervo fossilífero e de amostragens de gases atmosféricos em núcleos de gelo (CHEVALIER et al., 2020; STOLPER et al., 2016), mas acabam não fornecendo dados tão precisos quanto os obtidos pela amostragem direta. Assim, para suprir a demanda de informações temporais, redes de monitoramento foram estabelecidas em várias paisagens naturais em especial nas nações desenvolvidas do hemisfério norte, com intuito de mostrar qual o estado atual da biota nesses sítios e suas mudanças ao longo do tempo (MAGURRAN et al., 2010; PROENÇA et al., 2017).

Custo vs vantagens

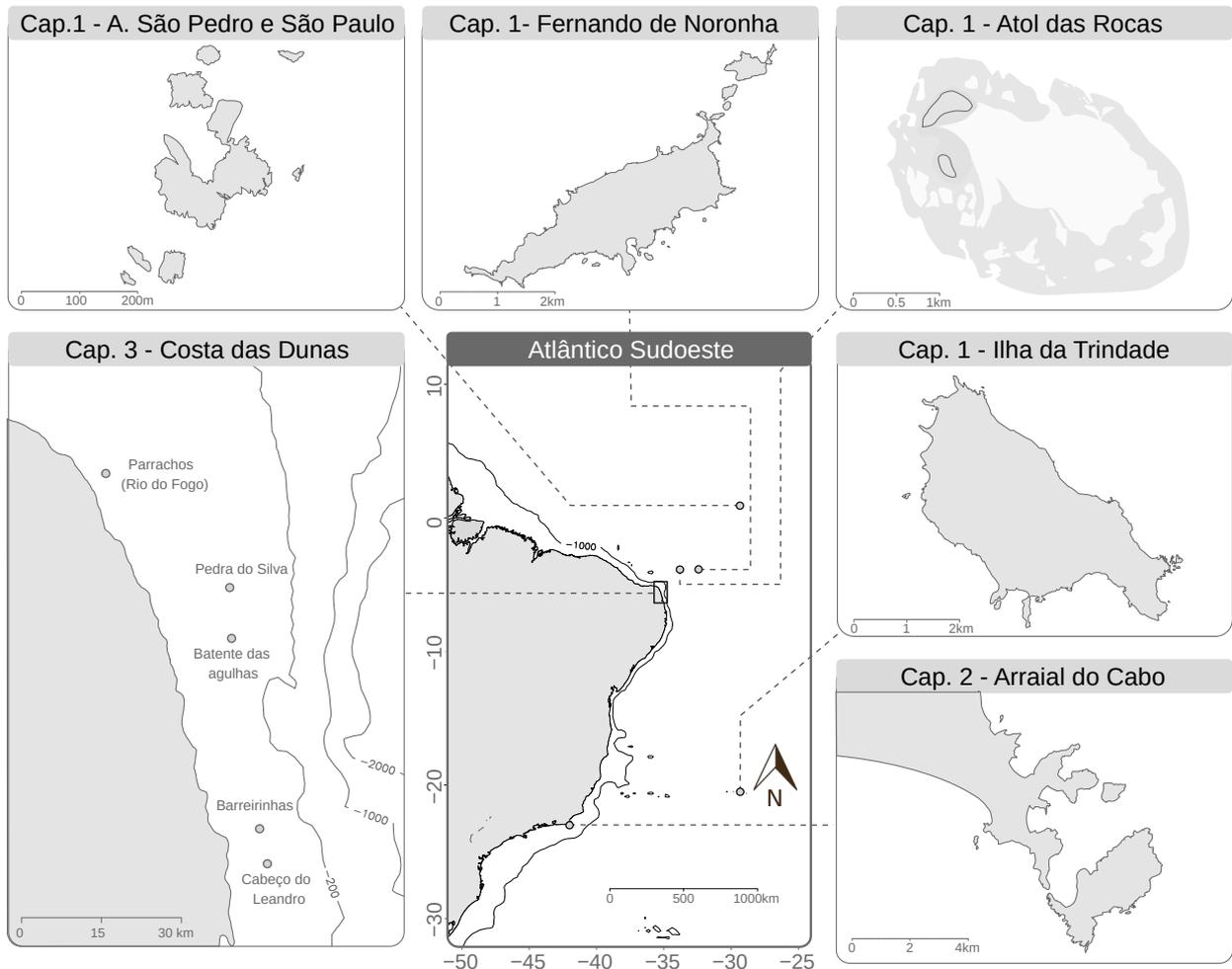
Uma boa parte do conhecimento existente sobre o impacto dos distúrbios climáticos e humanos veio de programas de monitoramento de longo prazo. Por exemplo, as redes de monitoramento de recifes de corais do Caribe, Índico e Pacífico mostraram um padrão recorrente de mudanças nas últimas décadas, perdendo cobertura de corais em resposta a ondas de calor (HUGHES et al., 2018). Ao mesmo tempo, o monitoramento revelou que a sobrepesca e a mortalidade em massa de corais afetaram essas comunidades em diferentes escalas de tempo, trazendo efeitos imediatos e tardios (KEITH et al., 2018; STUART-SMITH et al., 2018; SULLY et al., 2019). A longo prazo, a sobrepesca gradualmente remove predadores de topo, o que reestrutura as comunidades locais e muda suas interações tróficas em poucas décadas (PADDACK et al., 2009). Já as ondas de calor causam perda de cobertura de corais, alterando a fisionomia dessas comunidades em poucos dias, mas com impactos na complexidade estrutural dos recifes que duram anos (ALVAREZ-FILIP et al., 2009).

Redes de monitoramento

Tendo em vista o efeito que o tempo tem sobre as comunidades biológicas, meu objetivo foi avaliar comunidades recifais sob uma perspectiva temporal, usando peixes como organismos modelo. Essa escolha foi baseada na facilidade de amostragem, diversidade de interações e riqueza relativamente alta de espécies (PARRAVICINI et al., 2013). Serão três abordagens, cada uma em um capítulo, explorando como o tempo afeta a amostragem, o modo como as espécies interagem e a estrutura das comunidades. Todas ocorreram em recifes rasos no Atlântico sudoeste (Figura 1). Cerca de 730 espécies de peixes são associadas a recifes nessa província, das quais 405 são exclusivamente recifais e 102 são endêmicas (PINHEIRO et al., 2018).

Grupo alvo

Sítios Amostrais



70 Figura 1. Sítios amostrais no Atlântico Sudoeste abordados nesta dissertação. O primeiro capítulo
usa cinco sítios na Costa das Dunas, litoral leste do Rio Grande do Norte para avaliar estratégias de
amostragem de espécies com filmagens remotas. As amostragens do segundo capítulo aconteceram
na Baía do Forno em Arraial do Cabo, no Rio de Janeiro, avaliando como interações de limpeza
mudam no tempo. O terceiro capítulo envolve quatro das cinco ilhas oceânicas brasileiras,
mostrando a dinâmica de comunidades ao longo da última década.

75 *Introdução ao capítulo 1 – Comunidades no Tempo*

Diferente da maioria dos recifes do Caribe e Indopacífico, os recifes tropicais do Atlântico
Sul contam com uma baixa cobertura de corais (AUED et al., 2018) e um conjunto de espécies que
toleram condições ambientais adversas (MIES et al., 2020), o que os deve tornar resistentes aos
distúrbios climáticos que vêm assolando recifes de coral no mundo todo. O Atlântico Sul tropical é
80 bastante isolado das demais províncias recifais do mundo (FLOETER et al., 2008) e possui
plataformas continentais estreitas (Figura 2), com águas turvas e aporte de nutrientes constantes.
Essas condições empobreceram a região em termos de quantidade de espécies, mas selecionaram

linhagens capazes de tolerar uma frequência alta de distúrbios, que vem a ser uma característica vantajosa no contexto atual de mudanças globais (MIES et al., 2020). Dessa forma, a simplicidade aliada à resistência tornam os recifes da costa brasileira ótimos modelos para estudos temporais.

Plataformas Continentais Submersas

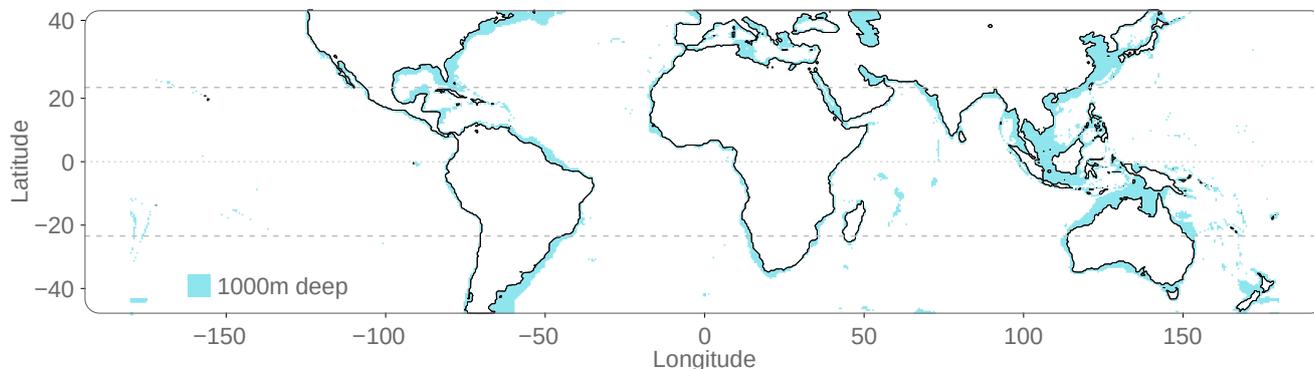


Figura 2. Isóbatas de 1000m, mostrando a plataforma continental nas regiões tropicais do globo. Notar como a plataforma continental no nordeste brasileiro é estreita se comparada ao Caribe, Sudeste Asiático e Oceania.

Em comparação com a costa continental, o isolamento das ilhas oceânicas cria condições ótimas para estudar padrões ecológicos ao simplificar dinâmicas populacionais e filtrar impactos comuns no continente (WARREN et al., 2015; WHITTAKER et al., 2017). Do ponto de vista dos peixes recifais, o isolamento reduz os efeitos dos impactos humanos e climáticos, notadamente sobrepesca e estresse térmico, criando condições ótimas para perceber e descrever variações naturais das comunidades ao longo do tempo (QUIMBAYO et al., 2019; SANDIN et al., 2008; WILLIAMS et al., 2015). O Brasil conta com cinco ilhas oceânicas, das quais quatro são alvo de monitoramento a longo prazo. Cada ilha está sujeita a diferentes níveis de proteção, partindo da restrição total ao uso, caso do Atol das Rocas, até o turismo massivo com pesca regulamentada de Fernando de Noronha. As demais ilhas contêm bases navais que contam com estações de pesquisas associadas, caso dos penedos de São Pedro e São Paulo e da ilha da Trindade. Em ambas ocorre atividade pesqueira não regulamentada, embora em São Pedro e São Paulo essa atividade seja direcionada a espécies pelágicas, sem atividades em ambientes recifais (VIANA et al., 2015). Os recifes de todas essas ilhas possuem biota e condições ambientais semelhantes à costa brasileira, como fundo bentônico dominado por algas e baixa cobertura de corais (menor que 10%) (AUED et al., 2018; MAGALHÃES et al., 2015).

A maioria dos peixes recifais colonizou as ilhas do Atlântico Sudoeste a partir da costa sulamericana, com algumas linhagens vindas do Atlântico Leste (como *Prognathodes* em São Pedro e São Paulo) e Caribe (caso do *Haelichoeres radiatus*) (FLOETER et al., 2008). Cerca de 10% das

espécies de peixes das ilhas oceânicas são endêmicas, com predomínio de colonizações recentes durante o Quaternário (PINHEIRO et al., 2017, 2018). As espécies de pequeno porte constituem a maior parte dos endêmismos, que aparecem em abundância nas poças de maré (ANDRADES et al., 2018). O restante das espécies, no entanto é amplamente distribuída pelo Atlântico Sudoeste, com perfil de grupos tróficos semelhantes aos encontrados nos recifes continentais (FERREIRA et al., 2004; MORAIS; FERREIRA; FLOETER, 2017). Mesopredadores de porte médio (por volta de 15 cm) contribuem para a maior parte da biomassa total, seguidos de herbívoros de grande porte (> 20cm) (MORAIS; FERREIRA; FLOETER, 2017). Uma diferença considerável entre as ilhas oceânicas e o continente está na quantidade de grandes predadores de topo, muito mais abundantes nas ilhas devido à menor pressão pesqueira (MORAIS; FERREIRA; FLOETER, 2017).

O programa ecológico de longa duração em ilhas oceânicas (PELD-ILOC) monitora recifes das ilhas oceânicas desde 2013, amostrando as assembleias de quatro ilhas oceânicas anualmente (PELD-ILOC, 2021). Embora todas as ilhas contem com descrições das assembleias de peixes locais (KRAJEWSKI; FLOETER, 2011; LONGO et al., 2015; LUIZ et al., 2015; PEREIRA-FILHO et al., 2011; PINHEIRO et al., 2011), apenas Trindade conta com análises temporais de longo prazo, embora focadas no impacto da pesca não regulamentada (GUABIROBA et al., 2020; PINHEIRO; MARTINS; GASPARINI, 2010). Trabalhos explorando diferenças em intervalos de tempo de alguns meses estão disponíveis para Fernando de Noronha, mostrando que as assembleias bentônicas e de peixes recifais não necessariamente mudam em sincronia (MEDEIROS; ROSA; FRANCINI-FILHO, 2011). Descrições detalhando o histórico de mudanças das comunidades recifais são raras na costa brasileira, com informações até então disponíveis apenas para o banco dos abrolhos (AMADO-FILHO et al., 2018; FRANCINI-FILHO et al., 2013; FRANCINI-FILHO; DE MOURA, 2008) e os recifes subtropicais de Santa Catarina (ANDERSON; JOYEUX; FLOETER, 2020). No intuito de contribuir com o conhecimento sobre a dinâmica temporal de peixes recifais no Atlântico sul, no primeiro capítulo descrevi como as assembleias de peixes recifais em quatro ilhas oceânicas brasileiras mudaram na última década, propondo mecanismos e explicações para os mudanças observados.

135 ***Introdução ao capítulo 2 – Redes de Interação no Tempo***

Peixes recifais possuem um repertório amplo de comportamentos que lhes permitem executar interações do mutualismo ao agonismo e da herbivoria à predação (FERREIRA et al., 2004; SAZIMA, 1986; VAUGHAN et al., 2017). Sabemos que algumas interações, em especial as tróficas, têm um potencial alto de mudar ao longo do tempo, respondendo às mudanças na abundância das espécies (USHIO et al., 2018). Outras interações, particularmente as mutualísticas,

contam com bem menos informações sobre dinâmicas temporais. Tendo essa lacuna em mente, no capítulo 2, meu foco foi investigar como mudanças na assembleia de peixes podem afetar interações de limpeza, usando um recife rochoso do sudeste brasileiro como área amostral (Arraial do Cabo - RJ).

145 Interações de limpeza acontecem quando um animal (limpador) remove ectoparasitas, pele morta ou muco da pele de outro animal (cliente), geralmente um peixe (VAUGHAN et al., 2017). Tanto limpador quanto clientes se beneficiam da interação, reduzindo níveis de estresse do cliente enquanto o limpador ganha uma fonte de alimento nutritiva e energética (ARNAL; CÔTÉ; MORAND, 2001; ECKES et al., 2015). Várias espécies de peixes e crustáceos atuam como
150 limpadoras nos recifes com diferentes graus de especialização (BALIGA; MEHTA, 2019). As mais especializadas, chamadas de dedicadas, foram selecionadas para convergir a cores, comportamentos e morfologias que otimizam sua atuação como limpadores (BALIGA; MEHTA, 2019; CHENEY et al., 2009). A maioria dos limpadores, no entanto, não é especializada e atua oportunisticamente, principalmente quando juvenis. Os chamados limpadores facultativos coexistem com os limpadores
155 dedicados e atuam nas redes de limpeza de modo complementar.

As redes de interação de limpeza em Arraial do Cabo contam com espécies dedicadas e facultativas. *Elacatinus figaro* consiste na única espécie dedicada na região, mas divide habitat com outros limpadores facultativos, como *Pomacanthus paru*, *Haemulon atlanticus* e *Haemulon aurolineatum*. Uma vez que limpadores facultativos se envolvem em interações apenas quando
160 juvenis, sua importância na limpeza está suscetível a variar de acordo com pulsos de recrutamento. Espécies com recrutamento contínuo ao longo do ano, como *P. paru* (FEITOSA et al., 2016), devem então estar continuamente participando de interações de limpeza. Por outro lado, aquelas com recrutamento de juvenis mais errático, caso dos hemulídeos (OGDEN; EHRLICH, 1977; SHULMAN; OGDEN, 1987), devem limpar de modo mais errático no tempo de acordo com os
165 momentos onde a sobrevivência larval é maior ou menor. Dessa forma, esperamos que as interações de limpezas variem ao longo do tempo, com maior parte das mudanças causadas por flutuações nas populações de limpadores facultativos (notadamente juvenis). Também esperamos que os limpadores facultativos de recrutamento mais errático variem mais no tempo (caso dos hemulídeos) que aqueles cujo número de juvenis varia pouco (caso do *P. paru*).

170 **Introdução ao capítulo 3 – Amostragens no Tempo**

Técnicas de amostragem baseadas em observação costumam ser estratégias eficientes para amostrar a composição de peixes recifais, com custo baixo e execução rápida (BOSCH et al., 2017). Essas técnicas possuem algumas falhas e vieses bem conhecidas, como imprecisões em contagens e

175 falha na detecção de espécies de pequeno porte, que frequentemente se camuflam com o fundo (MURPHY; JENKINS, 2010; PAIS; CABRAL, 2017; THANOPOULOU et al., 2018). Como alternativa, o uso de amostragem por filmagens aumentou consideravelmente nas últimas décadas por possibilitar checar os registros com mais calma e atenção após o trabalho de campo, dando uma certeza maior às estimativas de abundância (MALLET; PELLETIER, 2014).

180 Nas amostragens por vídeo, o esforço amostral costuma ser dividido entre tempo de análise e quantidade de réplicas espaciais. Não existe um consenso de um esforço amostral mínimo, o que faz a literatura publicada variar de alguns poucos vídeos durando horas até dezenas de vídeos com 10 minutos de duração (LONGO; FLOETER, 2012; VERGÉS; BENNETT; BELLWOOD, 2012). Cada estratégia parece ter uma vantagem. Amostragem vários vídeos curtos permite cobrir uma área maior, enquanto que ter poucos vídeos muito longos garante uma certeza maior sobre a riqueza e a
185 estrutura da assembleia em cada unidade amostral. Porém, não há trabalhos investigando qual estratégia é mais eficiente ou mesmo indicando qual seria um esforço amostral mínimo para melhor detectar a composição da fauna recifal. Assim, no terceiro capítulo tenho como objetivo estimar esse mínimo, considerando tanto o número mínimo de réplicas espaciais quanto o tempo de filmagem dos vídeos, e buscando determinar qual estratégia é mais eficiente para detectar mais
190 eficientemente a riqueza e a composição de espécies (muitos vídeos curtos ou poucos vídeos mais longos).

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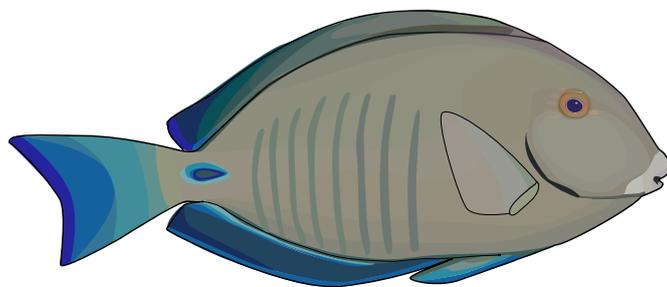
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Capítulo 1
Temporal dynamics of reef fish
assemblages in oceanic
islands of the Southwestern
Atlantic

A ser submetido para a Scientific Reports



Abstract

Long term monitoring offers an excellent opportunity to perceive and describe ecological patterns. Still, time assessments remain rare in the tropics, with even less efforts surveying the South Atlantic reef systems. Minding this gap, we provide over a decade of monitoring data on reef fish assemblages from four oceanic islands sampled in the Southwestern Atlantic in the first effort to temporally describe these systems. By tracking fish biomass over a decade we found the composition was quite stable in all islands. Time accounted for one third to half the variability on those assemblages, which presented significant but non-directional changes through time. A different mechanism appears to explain observed patterns within each island, ranging from a dynamic stability to a trophic cascade effect and a disturbance-recover scenario. Fish biomass fluctuated quite erratically in all island, though the frequency and magnitude of those changes seems to be related with length. We gathered evidences indicating these assemblages changed little over the last decade, posing they acquired a relatively strong stability that indicates resistance to recent environmental disturbances.

Keywords: Long-Term, Monitoring, Stability, Time Series

Introduction

Biological communities often change in response to environmental pressures^{1,2}. The frequency and magnitude of disturbances restructure species composition by causing generalized or selective mortality. The ability of biological systems to resist or recover from disturbs defines the stability concept, which encapsulate the complexity of a changing composition into a simpler time-comparative framework. Long term stability represent a rare feature among biological communities, where stochastic fluctuations and changes in environmental conditions often lead to rearrangements in species composition. For instance, disturbances in the form of climatic extremes or human impacts have recently reshaped reef communities worldwide within a few decades, transitioning towards more stress-tolerant arrangements by losing sensitive species, notably branching corals³⁻⁵.

Periodical monitoring offers a key tool to understand the dynamic of the assemblages and the causes behind changes in composition^{4,6}. Most of the monitoring efforts in tropical reefs in the Atlantic Ocean are concentrated in the Caribbean, where a notable network of monitored sites revealed how human impacts can affect reef ecosystems⁷. Among its results, It was shown how unmanaged fisheries caused a region-wide decline on the abundance of large fishes⁸, provided empirical evidence on the pathway invasive lionfishes took to spread across the entire Caribbean⁹ and pointed how the loss of branching corals caused widespread reef homogenization¹⁰.

400 Apart from the Caribbean, most tropical reefs in the tropical Atlantic currently lack monitoring efforts. In the Southwestern Atlantic (SWA), long term data is scarce, scattered across few sites and often including just a single species¹¹⁻¹³. Information on the temporal dynamics of reef communities is also rare (but see ¹⁴), meaning that our current knowledge is mostly based on quick snapshots^{15,16}. Despite providing essential information on community functioning, these surveys provide few clues
405 on how recent events unfold to shape the current community state. Thus a time series approach could improve our current understanding about reef ecology in the SWA by adding a temporal perspective.

A series of biogeographic barriers have kept the SWA isolated from other reef provinces^{17,18}, reducing the total richness but providing an expressive endemism among native species^{19,20}. For
410 instance, one third of all reef fish and zooxanthelate cnidarians are endemic to the province^{20,21}. In contrast to most monitored tropical reefs, biogenic reefs in the SWA are rare^{19,22}, with most reef bottoms dominated by macroalgae and naturally lacking high coral cover¹⁶. These conditions likely make the SWA reefs resistant to climatic extremes as several sites present little to no coral loss after massive bleaching events²³. Hence, a time series perspective on these systems could provide info on
415 how reef communities change on the absence of major phase shifts while providing community dynamics data to other types of tropical reefs.

Island systems provide good models to decipher ecological patterns due to their isolation, filtering several impacts found in the mainland^{24,25}. Most continental reefs across the Southwestern Atlantic show signs of human related disturbances, as a low top predators biomass and high
420 biomass of herbivore fishes¹⁵. SWA Oceanic islands on the other hand show fewer signs of pollution or overfishing²⁶, making their community dynamics the closest feasible scenario to a natural system in the region and thus attaining unique ecological value for reef community dynamics. The insular isolation could also favor temporal assays by simplifying demographic changes, reducing fluctuations in population size due to migration and thus facilitating tracking changes.

425 Given the paucity of available information on reef fish temporal dynamics in the SWA and particularly in its oceanic islands, we provide results from over 10 years of monitoring spanning four of the five oceanic islands in the province. As reefs on this region naturally harbor a low coral cover^{16,27} whose species possess traits associated with higher resistance to climatic stress, we expect to observe an ecosystem stability scenario that presented few changes in composition through time.
430 Due to their high prevalence within the reef community and consistent reaction to major changes²⁸⁻
³⁰, we used reef fishes as focal group. Our goal here was to observe how the reef fish assemblages

fluctuated over time, highlighting yearly and long term trends in their biomass in both a community and a population perspective while discussing possible causes for any emergent patterns.

Methods

435 *Sampling Localities*

The long term data covers four islands and archipelagos scattered across Atlantic ocean at about 150 and 900 km from the closest mainland in the Brazilian coast. Their fish fauna consist of a subset of the continental species pool with about one third of species as endemics^{20,31,32}. Still, each island encompasses a different set of local environmental conditions, as temperature, isolation and
440 shallow platform, that allow for a comprehensive understanding of temporal dynamics at different ecosystems within a same province.

The northernmost oceanic Islands comprise the remote and rather small rocky outcrops of São Pedro e São Paulo Archipelago (hereafter referred as St. Paul's Rocks). This near equatorial reef system lies in the mid-Atlantic ridge, isolated more than 900 km from the main coast and over
445 400 km from the closest island (Fernando de Noronha). Local reef systems contains mostly rocky shores in a steep relief heavily exposed to wave action. Algal turfs and macroalgae composes the dominant benthic cover, with a considerable encrusting of coralline algae²⁷. The intense isolation of these systems led to a unique fish composition and several endemic species^{20,33}. Reef fish fauna in the archipelago is deprived from a substantial number of lineages found at other nearby oceanic
450 islands^{20,34}. Surgeonfishes and parrotfishes are absent from St. Pauls' Rocks and the triggerfish *Melichthys niger* filled the niche of large scrapping herbivores, what likely boosted them to attain the largest single-species standing biomass within the islets³⁵.

The less remote Fernando de Noronha Archipelago lies southwestern from St. Paul's Rocks and harbors the widest shallow platform among the assessed islands, allowing for a diverser set of
455 reef environments and species³⁶. As usual in the SW Atlantic, macroalgae and algal turfs dominate most of the benthic cover, but there is a considerable presence of massive corals (mainly *Montastrea cavernosa*) and sponges in some deeper sites³⁷. Noronha contains the richest fish assemblages among Brazilian islands, including the main lineages also found at the continental shelf. Most fish species in Fernando de Noronha also inhabits the biogenic systems of the Rocas
460 Atoll²⁰, just a few kilometers west. Together, those two islands have about 10% of their fishes as endemics, with the higher endemism rates among tide pools species³².

Reefs in Rocas Atoll are biogenic constructions predominantly of crustose coralline algae, mostly the genus *Porolithon*, and relatively low coral cover³⁸. Erosion and localized

bioconstructions create a wide system of pools (about 2 to 5m deep), where the monitoring efforts
 465 have been performed. The wave exposure structure the reefs within the pool systems, creating pools
 protected from the wave surge and with no connection with the external area of the atoll ring during
 low tides (closed pools)³⁹. When those pools get eroded, they connect with the external area even
 during low tides, receiving constant influence of wave surge (open pools)³⁹. This creates distinct
 fish and benthic compositions between wave exposed and wave protected sites, with a substantial
 470 turnover of species across these two environmental types. In the macro level, however, algal turfs
 and macroalgae still spread upon most of the benthic cover, though the species composition and
 biomass differ between pool systems^{16,39}.

Over two thousand kilometers South lies the Trindade Island. Trindade, alongside the rocky
 Islets of Martin Vaz, belongs to a mountain chain stretching over a thousand kilometers from the
 475 coast towards the Atlantic. Sandy bottoms dominates the benthic cover in most reefs, followed by
 algal turfs, fleshy macroalgae and crustose coralline algae⁴⁰. The island contains a considerable
 diversity of reef fishes, most of which colonized Trindade island coming from the Brazilian coast
 using the seamounts chain as stepping stones⁴¹. This gave rise to a considerable number of both
 recent and ancient endemic species that combined with high immigration of continental species
 480 filled most trophic niches found in the coast, despite its extreme isolation.

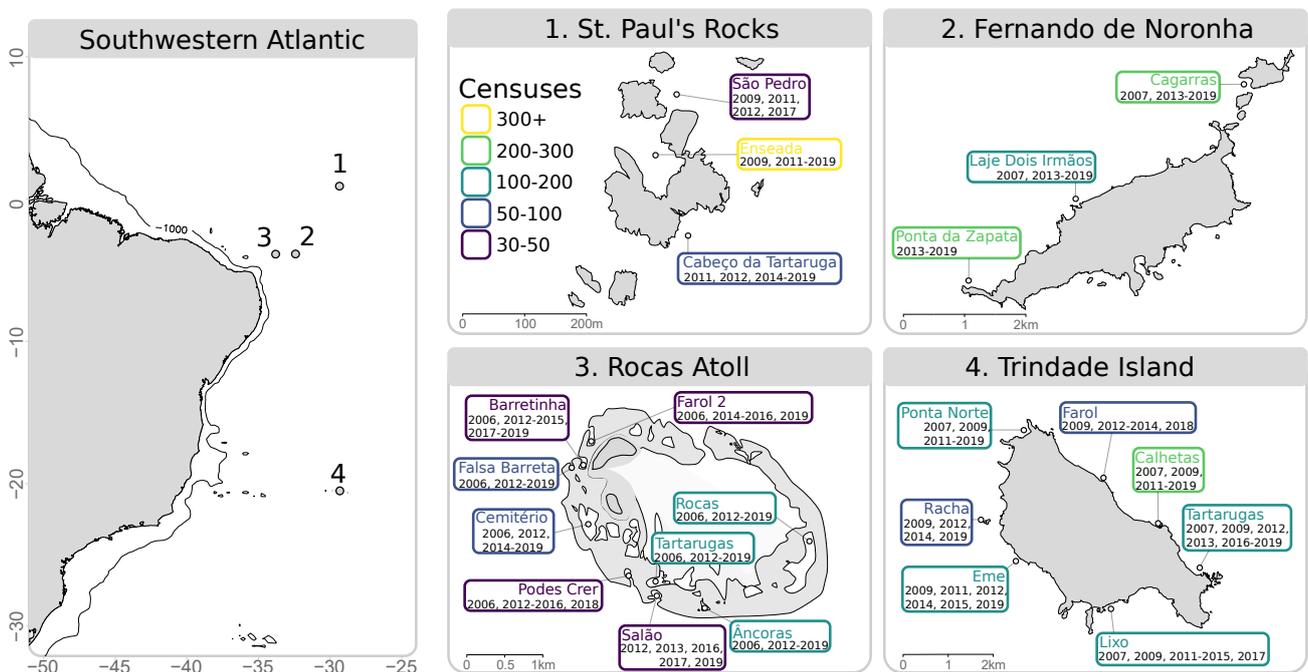


Figure 1. Details on the location of monitored islands relative to the South American Coast and the sampling sites within each island. The boxes display the years with available data as numbers and

the boxes colors indicate the total number of visual censuses performed within each site through the entire series.

485 Currently, Trindade is the only Brazilian oceanic island subject to an unmanaged fishing activity on reef systems⁴², with most fishing efforts focused in one grouper species (*Cephalopholis fulva*)⁴³. Besides Trindade, fishing activities directed to reef fishes also occurs in Fernando de Noronha, though catches follow a legislation restricting the fishing area and size of catches. Meanwhile, all monitored sites at this island locates within a no-take reserve, such that influences of
490 fishing activities should be minimal. Among the remaining two islands, Rocas Atoll comprise a no-take no-entry reserve with a ban in fishing activities reaching 40 years. Reefs in St. Paul's Rocks on the other hand have only recently (and partially) got included within a marine protected area⁴⁶. Fishing activities on pelagic species target at least one species (*Caranx lugubris*) frequently seen on shallower reefs⁴⁴, though its captures represents only about 2% of total catches⁴⁵. As no fishing
495 industry target reef fishes in the island and the standing biomass show no signs of depletion¹⁵, we found reasonable to assume reefs in St. Pau'ls Rocks suffer little impacts from fishing.

Sampling design

Biomass of fishes was estimated in each island through a hierarchical design, with underwater visual census as the sampling units performed within sites continuously revisited
500 through the series. In each census, a diver recorded the abundance, size and species of fishes in a fixed area (20 x 2m, sensu ¹⁵). Then, the fish biomass was obtained by applying length-weight relationships using allometric constants available in FishBase⁴⁷. Each sampling site had between 13 to 70 censuses per year, according to the range set of environmental conditions (sites with broad depth ranges had more censuses to cover the differences in composition related to depth). The exact
505 number of sites differed between islands due to environmental and financial constrains (as difficult access due to remoteness and expensive field campaigns), with Trindade and Rocas attaining 13 and 9 sites, respectively and St. Paul's Rocks and Fernando de Noronha featuring 3 sites each.

Time Series and Methodological Decisions

The long-term program (Programa Ecológico de Longa Duração – Ilhas Oceânicas⁴⁸) has
510 been carried in the four islands since 2013, providing 7 years of continuous data. By gathering visual censuses performed by other associated researchers, we managed to expand the total series in five to six years backwards. Their sampling procedure matched that performed in the long-term monitoring, enhancing the understanding of the main time series. Still we acknowledge that some differences in detected composition could be driven by the taxonomic progress in describing new

515 and endemic species. For instance, a taxonomic review on *Kyphosus* in 2014 revealed that individuals referred as *Kyphosus sectatrix* included other four species within the Atlantic, lacking the actual *K. sectatrix*⁴⁹. In Trindade Island, the descriptions of the endemics *Sparisoma rocha* and *Halichoeres rubrovirens* were published only in 2010^{50,51} and their first records on the census date from 2012, meaning these individuals might have been mistaken with the co-occurring *Sparisoma*
520 *frondosum* and *Halichoeres poeyi*, respectively. We contoured this by merging species likely to be confounded into a single operational taxonomic unit, reducing the total richness but also the probabilities of detecting changes coming from different taxonomic backgrounds. Those three comprise the only cases where these measures have been applied.

Sightings of rare species in censuses were not constant within years, creating gaps in the
525 record not driven by changes in abundance, but rather by false negatives⁵². To overcome this potential bias, we trimmed the total dataset to deal with a core set of better detected species. As a cut off criteria, we kept all species that either (1) were detected in all years or (2) appeared in at least five census of at least 50% of the total years or (3) attained an mean abundance larger than 0.5 individuals per square meter per year. This included common species that presented a low
530 abundance (as Chaetodontids does) as well as the highly abundant and yet erratic species at the scale of the censuses (as most Haemulids). The total analyzed set of species contained 19 out of the 45 species detected in St. Pauls' Rocks fishes, 34 of 76 in Fernando de Noronha, 26 of 72 in Rocas and 34 of a 92 in Trindade, thus keeping about 40% of the recorded richness in each island.

We first analyzed the time series at the assemblage level, then down-scaled into group of
535 species to finally analyze changes at the species level. The group level combined several species by summing their biomass within a same visual censuses, dividing the fish assemblages based on mean size and trophic level. By using biomass instead of abundance, we filter for differences in size between individuals of the same species, which also allows to combine species with different sizes but similar feeding habits into groups. We used the records in our base to estimate the mean size,
540 whereas the trophic level was obtained from FishBase⁴⁷. Regarding size, 'Small' species reached less than 15 cm long (snot-tail) on average, whereas 'Large' species were above this threshold. When dealing with trophic level, we split fishes into herbivores, mesopredators and top predators based on the fishbase trophic level score (ranging from 2 to above 4, representing first, second and third consumers). The combination of those two categories generated six groups (small herbivores,
545 small mesopredators, small top predators, large herbivores, large mesopredators and large top predators). However, as no species fit in the category of small top predators, we ended with five groups.

Analysis regarding species and groups of species all considered the visual censuses as sampling unit as this scale allow to use depth and sites as predictors affecting the standing biomass. For a community approach however the census level contained a substantial source of variability resulting from false absences⁵², which inflate the residual variance of multivariate analysis. We contoured this by averaging censuses within sites, thus considering the sites mean composition within a given year as sampling units for multivariate analysis. To account for differences in depth profiles between sites, we split each site into three depth categories before averaging, namely shallow (<5m), mid (5-10m) and deep sites(>10m). In the case of Rocas Atoll, where all monitored sites comprise shallow pools of about the same depth, the sites were sorted according to their wave exposure into open or closed pools, following previous information published in the literature³⁹. Finally, before any multivariate analysis we applied the hellinger transformation (square root of the relative mean biomass) in the data, a procedure useful to normalize biological data and make it suitable for most multivariate analyses^{53,54}.

Trends at the community level

To test whether time could explain variation in reef fish composition, we applied a permutational multivariate analysis of variance (PERMANOVA) in each island, taking the years as a categorical predictor. As other constrains could also cause variation in species composition, we added the sampling sites and the categorical environmental conditions (depth in most islands and wave exposure in Rocas) as predictors to account for such variability in our statistical models. By providing an intercept to each site we allowed the model to include differences in standing biomass related to distinct local conditions, such that the variance explained by the years predictor would be related only to changes in standing biomass.

To test for changes in composition along the series, we compared groups of years in each island, representing the expeditions set previously to the monitoring program (before 2011), at its begin (2011 to 2013), mid (2014-2016) and last years (2017-2019). This time windows filters single years in favor of long term trends, highlighting possible major changes in species composition. Each comparison used a PERMANOVA to test for differences in composition through time, taking the same predictors of the first analysis (time, sites and environmental conditions). A non-metric multidimensional scaling (NMDS) provided a graphical view on how composition changed through the years, displaying the years centroids (Figure 2).

Trends at the group and species level

To observe main changes in biomass through time we used smoothed trends provided by
580 generalized additive models (GAM). Two models were produced per island using the same
procedures for both species and groups. Each model had a gamma family with a log plus one link,
taking as response variable the biomass recorded by visual censuses and including as predictors four
fixed-effect terms, namely the groups/species (as a factor), the smoothed tensor products of years
and depths (both split by groups and with four splines), and the factor-smoothed sampling sites
585 (also split by groups). By limiting the number of splines of years in both models to four, we assured
the model would provide a smoother relation, approaching a long term trend. To provide an idea on
the actual observed biomass at each year, we fitted an extra model using the same predictors, but
increasing the number of splines for years (matching a spline for each year). The combination of
those four models revealed both major and minor changes in fish groups and species biomass over
590 the years.

Net changes in biomass were assessed by comparing the biomass (of either species or
groups) recorded by first and last four years of the series. We built a multiple linear model for
groups and another for species, taking the log-transformed biomass ($\log_{10}[x+1]$) as response and the
time (after and before) as predictor. We also accounted for effects of depth and sampling sites
595 effects by adding them as predictors to the models. Then, by applying t tests on the time parameter
estimates we tested the null hypothesis of no changes on biomass estimates after vs before. A
Bonferroni correction was applied to those p values to consider the multiple comparisons being
performed.

Results

600 Changes in fish composition through time were consistent, small and mostly non-sequential
in all islands (Figure 2). Time as sampling years explained most of the variation in fish composition
(Table 1), particularly in St Paul's Rocks and Trindade Island (about 35%), attaining a smaller
importance in Fernando de Noronha and in Rocas Atoll (at about 20%). In these last two islands,
local environmental conditions (represented by sampling sites and depth) had a higher importance,
605 explaining up to 30% of the differences in standing biomass (Table 1). However, a substantial
portion of the total variance (46% on average) remained unexplained in all islands.

Table 1. The effect of assessed predictors on fish assemblages at each oceanic Islands based on a PERMANOVA.

Island	Predictors	D.F.	Model. F	R ²	P
St Paul's Rocks	Categorical Depth	2	6.7	0.19	< 0.001
	Sampling sites	2	2.2	0.06	0.027
	Sampling year	9	2.4	0.31	< 0.001
	Residuals	29	-	0.42	-
Fernando de Noronha	Categorical Depth	2	4.7	0.12	< 0.001
	Sampling sites	2	7.7	0.19	< 0.001
	Sampling year	7	2.4	0.21	< 0.001
	Residuals	37	-	0.47	-
Rocas Atoll	Wave Exposure	1	6.6	0.06	< 0.001
	Sampling sites	7	4.1	0.26	< 0.001
	Sampling year	8	3.2	0.23	< 0.001
	Residuals	51	-	0.45	-
Trindade Island	Categorical Depth	2	4.5	0.04	< 0.001
	Sampling sites	6	2.3	0.07	< 0.001
	Sampling year	10	7.2	0.36	< 0.001
	Residuals	104	-	0.52	-

610 The fish composition changed in each island in different ways, varying through distinct, but somewhat similar arrangements. The fish assemblage in St Pauls' Rocks were the only to keep a stable species composition through time. The biomass of large top predators in this island, however, faced a seven-fold increase in about four years (2013-2016, Figure 3), followed by a sudden decline by the end of the series (2019). Those changes were mostly related to a single genus, *Caranx*,
615 whose species *Caranx lugubris* and *Caranx crysos* had net gains of about 50% their initial biomass over time (Supporting Figure S1). Large mesopredators went through similar fluctuations almost simultaneously, tripling their biomass from 2012 to 2014 before returning to their initial values by 2018. Within this group, *Canthidermis maculata* increased about 17% in their biomass, whereas *Canthidermis sufflamen*, *Halichoeres radiatus* and *Myripristis jacobus* decreased in about 20%.
620 Interestingly, net changes at the species level did not implied in changes at the group level, such as the case of the large herbivore *Melichthys niger*, which faced net biomass declines (-20%, Supporting Figure S1) while the total biomass of large herbivores remained unchanged (Figure 3). Biomass of small herbivores and small mesopredators remained stable through time, with

oscillations every two to three years when peaks and valleys coincided with year clusters in the
 625 multivariate space (Figure 2 and 3).

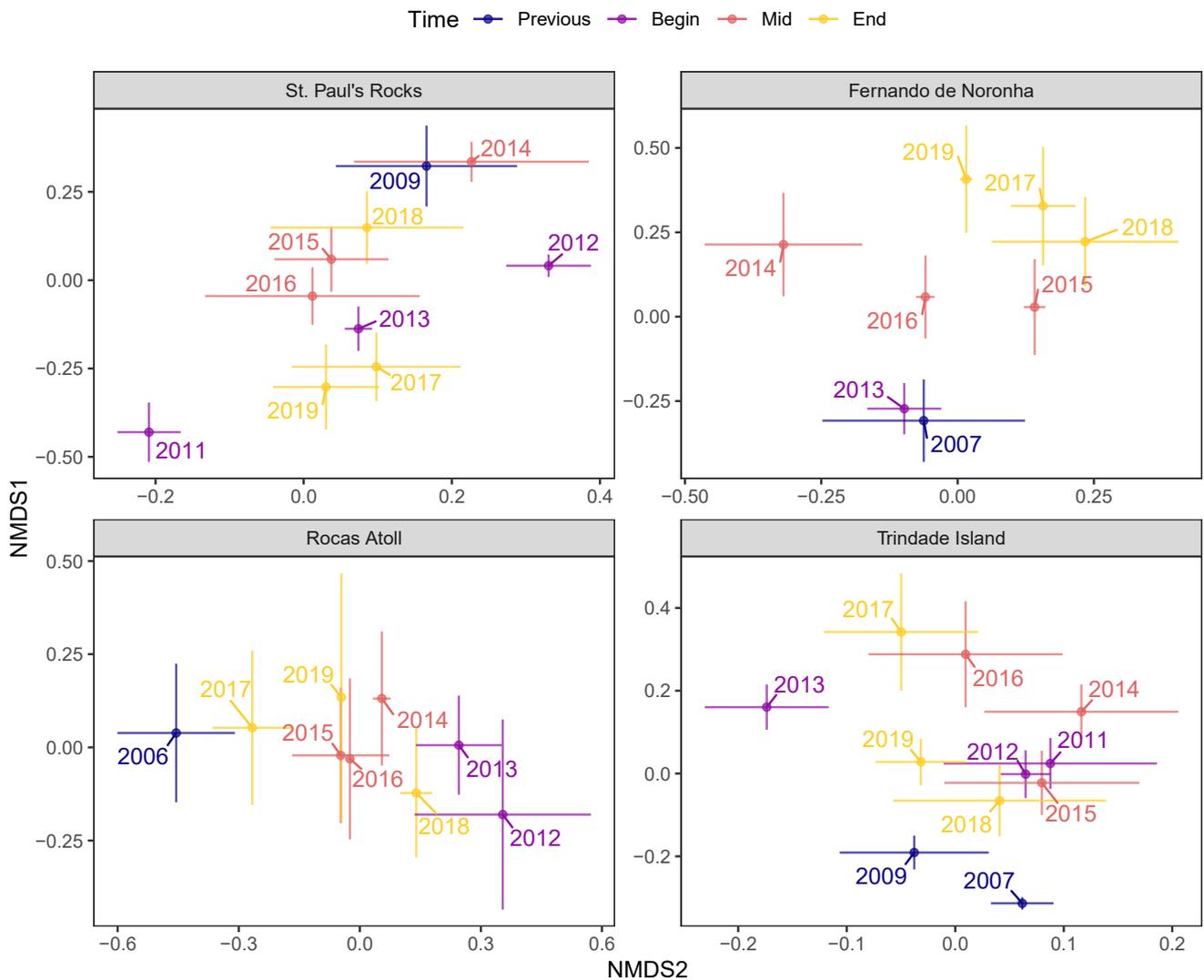


Figure 2. Changes in mean fish composition through time summarized by non-metric
 multidimensional scalings (NMDS) with two axes. Mean fish composition based on biomass data in
 the multidimensional space is represented by the position of years (crosses represent the standard
 deviation in both dimensions). Colors represent the four periods (previous, begin, mid and end) of
 630 the monitoring.

In Fernando de Noronha, there were no differences in fish assemblage between the period
 previous to the monitoring program (2007) and the remaining series (2013-2019, Fig 2). Although a
 directional trend was captured in the NMDS, the only significant differences regarded the series
 begin (2013), differing from both mid (2014-2016) and end periods (2017-2019), though these last
 635 two periods did not differ between them (Table 2). Interestingly, only small-sized fishes suffered

consistent changes in biomass, declining over time while oscillating constantly every three to four years. Similar fluctuations also affected large top predators, though within shorter periods, of about 2 to 3 years. This group also had the only species with a net biomass increase, *Cephalopholis fulva*, which gained 22% of their initial biomass over time, peaking by 2017. At least five species of large fish faced significant net biomass declines through time, following more erratic patterns. Standing biomass of barracudas (*Sphyraena barracuda*) repeatedly increased and decreased by a three-fold magnitude through the series, reaching their lowest level by the end of the series (2017-2019, Supporting Figure S2). Among species on other groups, two mesopredators (*Paranthias furcifer* and *Anisotremus surinamensis*) and two large herbivores (*Sparisoma frondosum* and *Sparisoma axillare*) ended the series with significantly less biomass, losing between 7 and 17% of their initial biomass (Supporting Figure S1). Particularly within large herbivores, as the biomass of *Sparisoma* and *Kyphosus* declined, the biomass of *Acanthurus chirurgus* increased, with significant net losses only for parrotfishes (Supporting Figure S2).

Table 2. Pairwise comparisons of assemblage composition based on fish biomass between four time periods. Each comparison consist of a PERMANOVA containing the composition as response variables and time as predictor plus depth and sampling sites as covariates (not shown here). Periods represent four moments in time series, representing the data collected previously to the monitoring program (<2011), the beginning (2011-2013), mid (2014-2016) and the end (2017-2019) of monitoring program. Note that the length of the available time series differed among islands.

Island	Comparisons	Total D.F.	Residual D.F.	Model. F	Model. R ²	Residual R ²	P
St. Paul's Rocks	Previous vs Begin	25	20	2.76	0.09	0.66	0.116
	Previous vs Mid	23	18	1.63	0.06	0.62	0.989
	Previous vs End	22	17	1.89	0.07	0.66	0.715
	Begin vs Mid	19	14	3.16	0.12	0.55	0.089
	Begin vs End	18	14	3.59	0.14	0.53	0.032
	Mid vs End	16	11	1.90	0.09	0.50	0.683
Fernando de Noronha	Previous vs Begin	16	11	1.72	0.08	0.51	0.554
	Previous vs Mid	16	11	2.87	0.13	0.48	0.066
	Previous vs End	22	17	1.89	0.06	0.55	0.353
	Begin vs Mid	25	20	3.09	0.09	0.55	0.017
	Begin vs End	31	26	3.05	0.07	0.56	0.017
	Mid vs End	31	26	2.26	0.05	0.55	0.156
Rocas Atoll	Previous vs Begin	29	20	4.11	0.10	0.48	0.001
	Previous vs Mid	29	20	3.66	0.08	0.45	0.001

	Previous vs End	21	12	3.93	0.11	0.33	0.002
	Begin vs Mid	45	36	1.48	0.02	0.59	0.863
	Begin vs End	37	28	4.5	0.09	0.54	<0.001
	Mid vs End	37	28	5.08	0.09	0.49	<0.001
	Previous vs Begin	59	50	3.14	0.05	0.74	0.019
	Previous vs Mid	59	50	5.13	0.07	0.70	0.002
Trindade Island	Previous vs End	54	45	23.92	0.28	0.53	<0.001
	Begin vs Mid	67	58	1.57	0.02	0.81	0.815
	Begin vs End	62	53	12.77	0.17	0.69	<0.001
	Mid vs End	62	53	6.44	0.09	0.71	<0.001

655 In Rocas Atoll, the previous and the end periods were significantly different from the series
begin and mid, whereas the begin and mid periods showed no differences in species composition
among them (Table 2). We also detected changes through time in biomass of most groups. Large
predators and mesopredators increased in biomass from the begin (2012) to mid years (2016),
decreasing below their initial value by the end of the series (2018). Small herbivores and
660 mesopredators showed a similar trend, but the peak in their biomass occurred four to five years
earlier (2012-13). By the end of the series, only one species, the large herbivore *Acanthurus*
chirurgus showed net declines in biomass through time (15% of decline), with all the others
remaining unchanged (Supporting Figure S1).

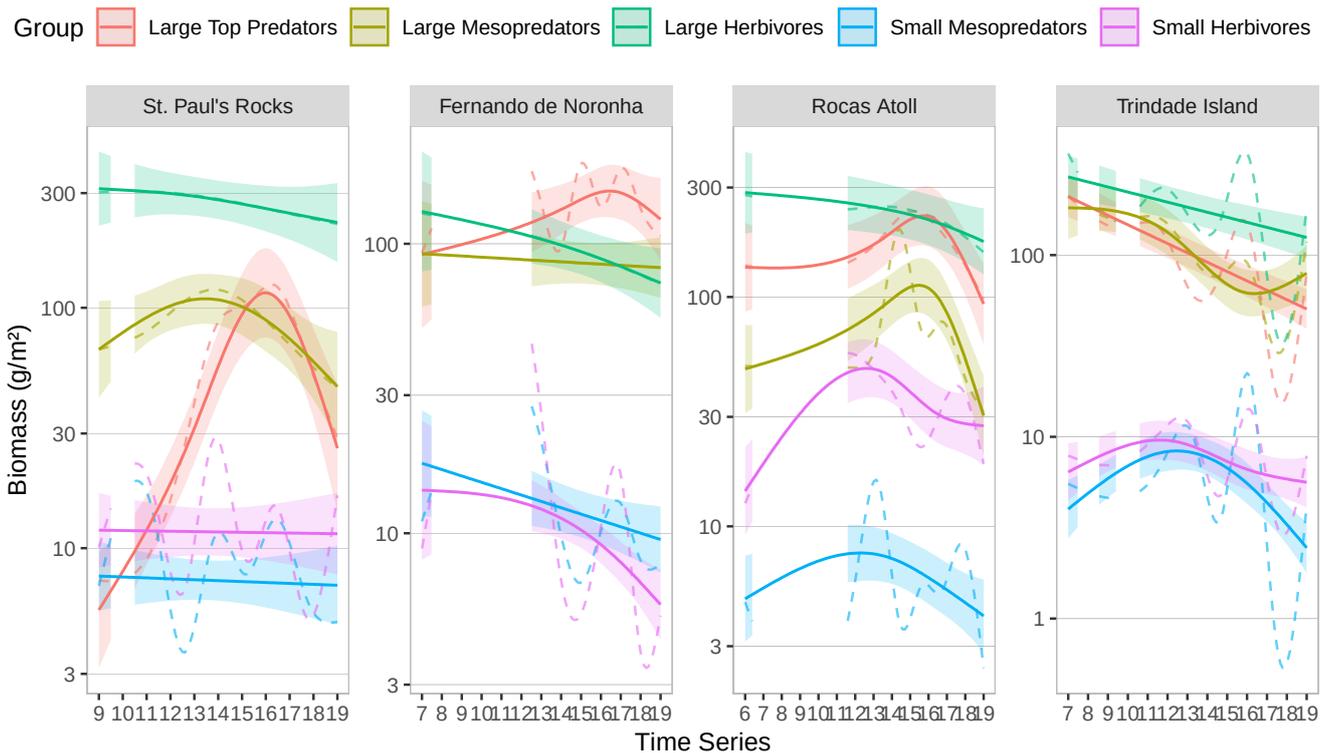


Figure 3. Fluctuations in groups biomass through time. The thick line display long term changes in biomass (GAMs with only four knots), whereas the broken lines show the actual biomass observed (GAMs with a knot for each year). Groups were chosen based on a combination of size (smaller or larger than 15cm) and Fishbase's trophic level (2-3: herbivores, 3-4: mesopredators and 4<: top predators).

The fish composition of Trindade island in the period previous (2007-2009) the implementation of the monitoring program was significantly distinct from all the other following periods (Table 2). The begin and mid periods showed no differences among each other, but did differed from the other periods of the series. The end was the most distinct period, and the decreasing importance of time ($R^2_{\text{Previous vs End}} = 0.28$, $R^2_{\text{Begin vs End}} = 0.17$, $R^2_{\text{Mid vs End}} = 0.09$, Table 2) in explaining biomass of fish assemblage indicate consistent changes through time. Net differences in fish biomass showed most large-bodied species faced declines regardless of their trophic levels, except for *Rypticus saponaceous* and *Balistes vetula* whose biomass remained unchanged through time. Small mesopredators showed high oscillation in biomass, whereas small herbivores showed no significant long term trend, even though their biomass fluctuated with an increasing amplitude over time. Two small mesopredators (*Halichoeres penrosei* and *Chromis multilineata*) and a small herbivore, *Microspathodon chrysurus*, faced net biomass decline, whereas no net increase was recorded in this island. Interestingly, all groups presented synchronized periodic fluctuations of

about four to five years (Fig 2). The amplitude of those fluctuations increased substantially throughout the series, containing the highest peaks in 2015-16 and the lowest valleys by 2017-18.

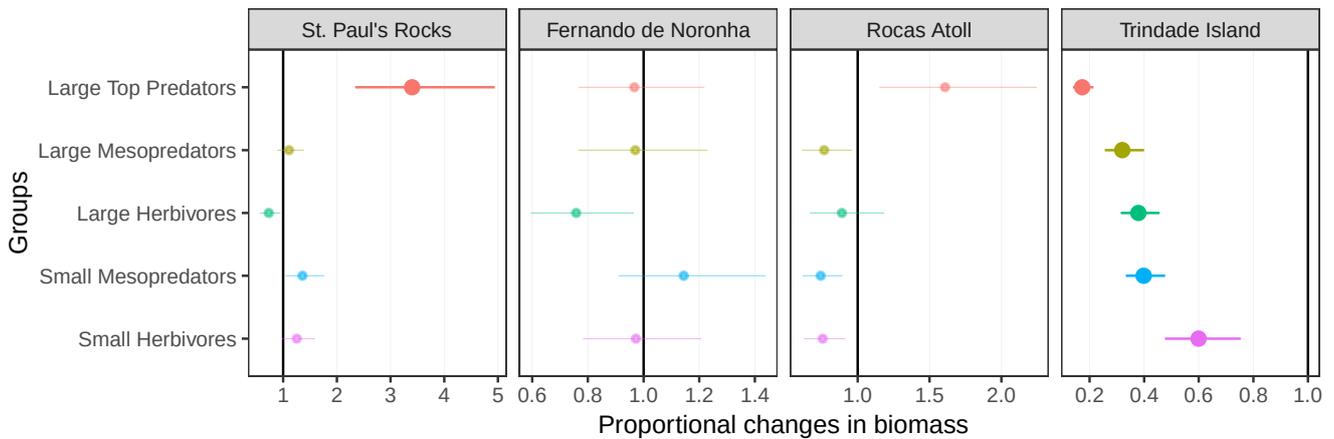


Figure 4. Net changes in fish groups biomass observed in over ten years of monitoring in the four Brazilian oceanic islands. The horizontal axis represent the ratio between the biomass at the end and beginning of the series (the mean first and last four sampling years were considered within each of these periods). Significant changes were represented with bolder dots.

Discussion

Our results point the temporal stability of fish assemblages varied according to events taking place locally, leading either towards a stable arrangement of composition (*e.g.* Fernando de Noronha and St. Paul's Rocks) or towards a high species temporal turnover (*e.g.* Rocas Atoll and Trindade Island). In the Brazilian oceanic islands, time (as years) accounted for one third of the measured variability in reef fish composition. The importance attributed to time matched the importance of other environmental constrains, revealing the temporal component indeed structured local reef fish assemblages. Still, a significant time predictor did not imply in constant or sequential composition changes through time, as some reef assemblages which heavily depended on time to explain their variance presented little to no composition changes (as in St. Paul's Rocks).

In all islands, most fish groups underwent cycles of biomass changes, whose magnitude and duration varied slightly between islands. The cycles however presented a feasible correlation with group size, with smaller fishes oscillating faster, though in a smaller amplitude than longer ones. Similar patterns have been observed in other island systems on the eastern pacific, as the Uva, Galapagos and Gorgona islands, usually following Niño events^{6,55,56}. Direct effects of climatic oscillations on local assemblage still remain unclear, though several other fish communities are influenced by those events in the Atlantic^{57,58}.

705 We found evidence for a stability scenario in two of the monitored Islands (St Paul's Rocks
and Fernando de Noronha), in which individual population fluctuations imply in minor to no effects
on the total composition. The lack of population depletion support this idea, though the population
stability of rare species might be questionable since we had not enough data to confidently track
their population size (and thus they were not considered here). A handful of species still presented
710 net changes, indicating a natural background turnover might continuously affect those communities.

The biomass of large fish groups in Fernando de Noronha remained stable. Still, the species
composition and some individual species did changed, indicating a within group temporal turnover.
Signs of these changes were high particularly among large herbivores (Supporting Figure S2). For
instance, increases on the abundance of *Acanthurus chirurgus* followed decreases on the abundance
715 of other large herbivores, as *Kyphosus* and *Sparisoma*, though their summed biomass showed no
significant changes. Those patterns were not exclusive among herbivores, affecting large top
predators as well. Only large mesopredators seems to lack turnover patterns, with most species
populations behaving quite erratically through time. As no causes seems to explain this pattern, we
assume it might be related to a neutral process in which the fluctuations on biomass are attributed to
720 natural turnovers.

Fish composition in Rocas Atoll kept changing throughout the series, pointing towards a
high temporal turnover scenario. The changes in composition were followed by changes in groups,
though each group fluctuated in its particular way. Still, some patterns did emerged. For example, as
the biomass of large predatory fishes grew, the biomass of smaller fishes shrank, indicating a
725 negative effect of one in the other. Given the predatory behaviors of both large groups, we found a
trophic cascade effect could be regulating these communities, in which the increase in number of
top predators limit the growth of smaller fishes. The three years delay between biomass peaks of
small and large predatory fishes also indicates a lagged response, posing that the effect of one
trophic level on the other occurs indirectly, possibly through increased survival of large predatory
730 fishes as seen for North Atlantic Cod population⁵⁷. Large mesopredators however often do not
include small fishes in their diet, indicating the peak in their biomass might be following increases
of other small benthic animals, as arthropods, mollusks and annelids, from which we currently lack
data. A community-wide time series in Galapagos Islands found similar results, where oscillations
in sea surface temperature triggered effects throughout the trophic chain⁵⁶. If that is the case, it is
735 likely that the entire local ecosystem might present an oscillating pattern of changes, with the
effects of trophic cascades extending much beyond reef fish biomass.

Trindade Island counted with the most erratic fish assemblages among Brazilian oceanic Islands, presenting a higher temporal turnover. The sampling occasions set previously to the monitoring program (2007 and 2009) attained the most differences from the remaining series, 740 indicating a shift in composition likely took place at the beginning of the monitoring program. These changes at the assemblage level were matched by peaks and valleys on the biomass of all groups, starting after 2009 and increasing in amplitude towards the end of the series. The series end also recorded dramatic declines in biomass of all fishes (between 2017 and 2018), making most species finish the series with significant net biomass losses (Supporting Figure S1). Recent 745 investigations attributed population declines of some predatory species to a local fishery^{43,59}, which could explain the long term decline of large sized targeted taxa, namely the grouper *Cephalopholis fulva*. However, all groups and most analyzed species presented net losses, the majority of which were not targeted by fishing, as the small but highly abundant *Chromis multilineata*. Common effects of fishing activities on reef systems includes a continuous decline on top predators 750 abundance, usually followed by an increase in abundance of their preys, neither of which were detected in Trindade. As the fishing efforts in the island have been highly selective towards large predators⁵⁹, we find fishing alone as not enough to explain the extreme synchronization on biomass fluctuations of seemingly unrelated groups. Thus, other causes could stand behind the periodical and generalized biomass declines.

755 Massive fish mortality events have been reported at least two times (1975 and 2007) in Trindade^{60,61}. These events seem to follow the arrival of unusually cold waters, postulated to trigger blooms of toxin-producing cyanobacteria⁶⁰. The trigger mechanism still remains unclear, though several species involved in synchronized biomass oscillations in our dataset went through massive die-offs in 2007, as *Cephalopholis fulva*, most *Kyphosus* species, *Melichthys niger* and *Myripristis* 760 *jacobus*. Therefore algal blooms *could* represent an alternative explanation to the generalized mortality, capable of causing a community-wide mortality.

The lack of directional changes in all islands suggests reef fish assemblages have remained somewhat stable within the last decade. Meanwhile, the

Conclusions

765 We did not found a unique cause of changes in reef fish compositions that applied to all four islands. Instead, each case seems to be island-specific. Two of the four monitored assemblages (Noronha and St. Paul's Rocks) exhibit stable arrangements, showing a background species turnover. The remaining two islands deployed a more erratic set of responses. In one of these (Rocas Atoll), the changes in fish assemblages seemingly approach a dynamic stability, likely

770 mediated by trophic cascades. In the other (Trindade), reef fishes are facing repeated biomass losses, constantly changing between an high and low biomass states, though in general showing resilience to changes. Despite the particularities of each islands, a core set of species seems to dominate each system, indicating the overall assemblages structure looks consistent over time.

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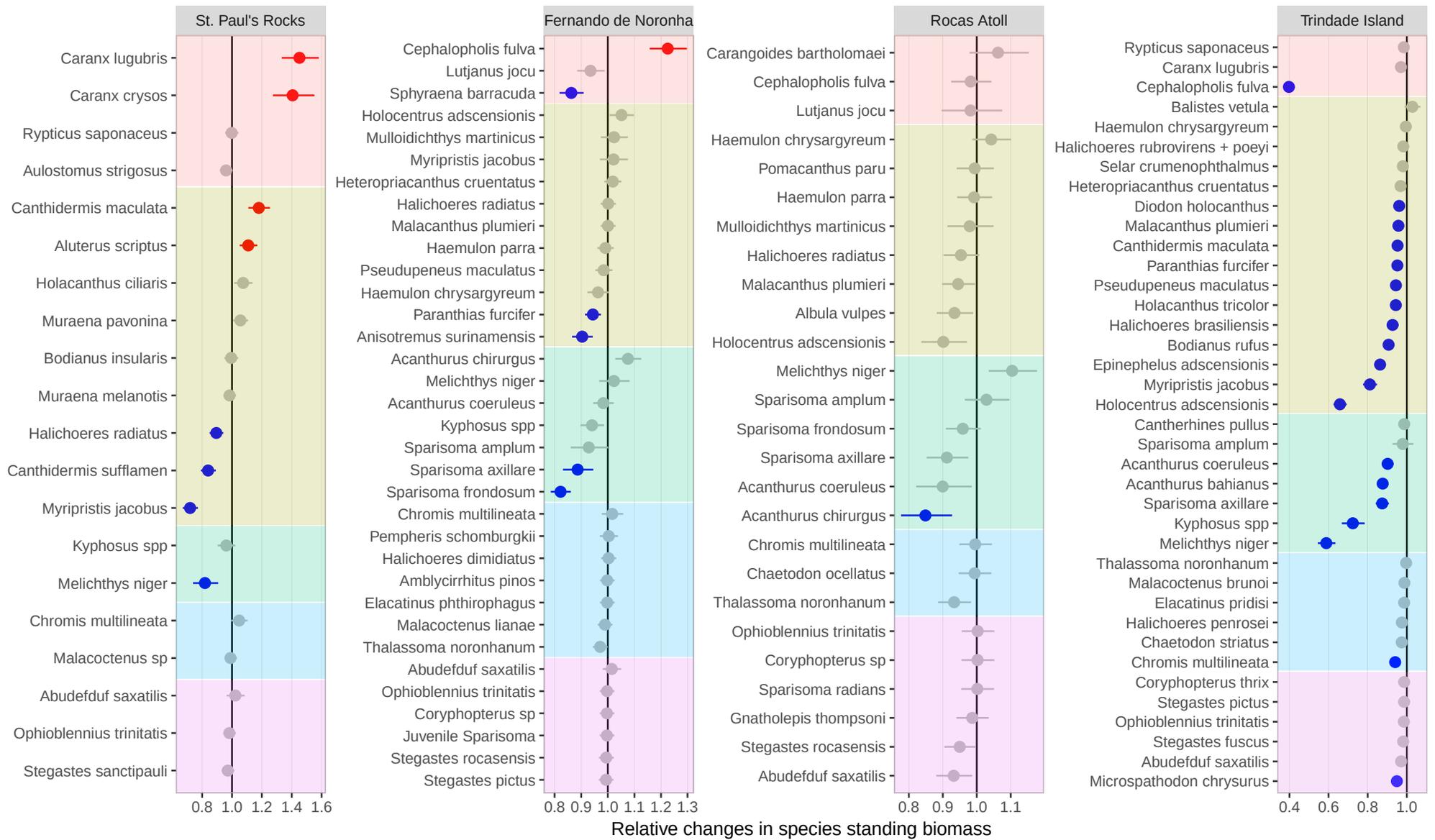
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Supporting Information

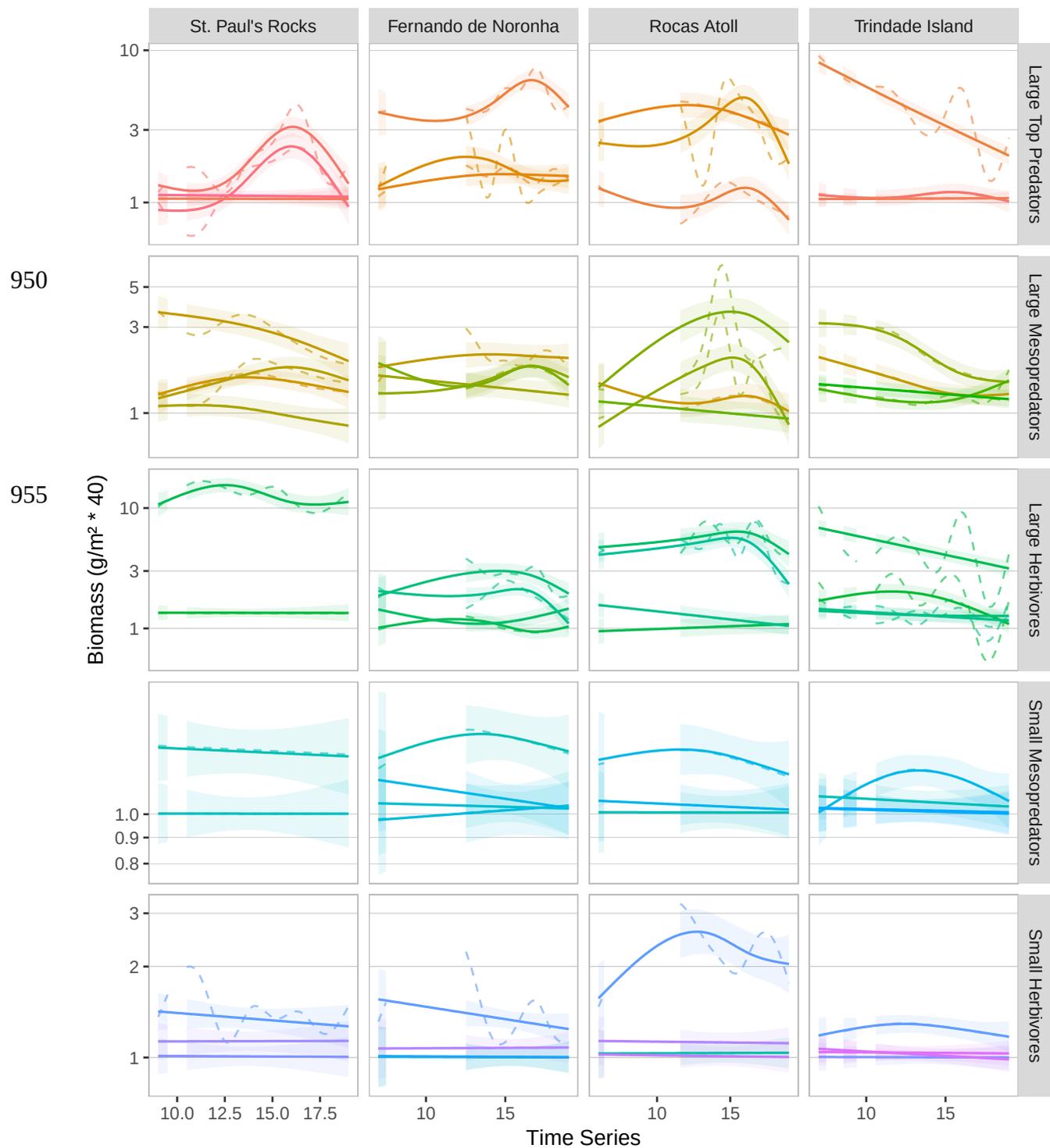
Temporal dynamics of reef fish assemblages in oceanic islands of the Southwestern Atlantic

Large top predators Large mesopredators Large herbivores Small mesopredators Small herbivores

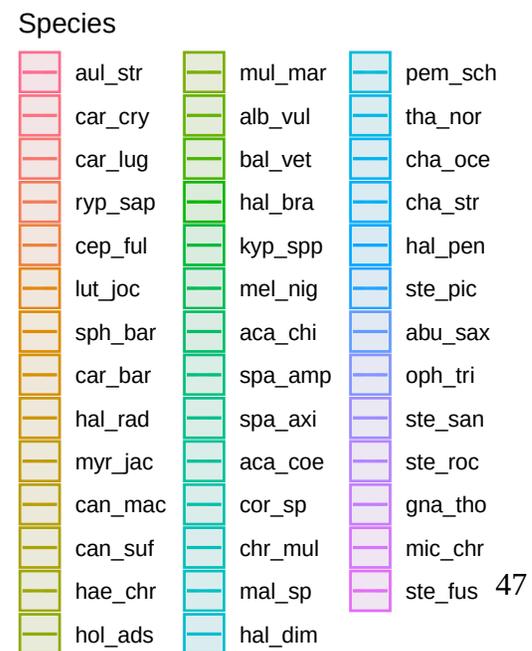


Supporting Figure S1. Net changes in species biomass. Each point show the ratio between the mean biomass of the first and last 4 years. Red color indicate significant increases in biomass, while blue indicate significant decreases. Background colors match the groups to which each species was assigned according to their size and trophic level.

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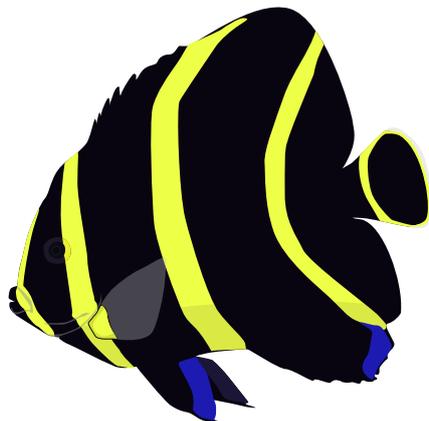
Supporting Figure S2. Trends in biomass of individual species, sorted by groups (lines) and Islands (columns). A maximum of four species are displayed per group, selected by decreasing biomass. The legend on the right represent abbreviated codes for species, showing the first three letters of the genus and species epithets. The codes match the complete species names provided in Figure S1.



Capítulo 2

Temporal variability on cleaning interactions in a rocky reef in the Southwestern Atlantic

A ser submetido para a Plos One



960 **Abstract**

Cleaning interactions occur when one animal, called cleaner, feed upon parasites, mucus or dead skin from another, called client. Over 250 reef species, mostly fishes, engage as cleaners, each with different degrees of specialization to cleaning. Dedicated cleaners comprise the most specialized and perform cleaning behaviors through their lives, while facultative cleaners engage into cleaning mostly as juveniles, transitioning to other feeding strategies as they age. Facultative cleaners make the majority of cleaners. Still, as they clean only as juveniles, their presence on cleaning networks might be unstable. We report and describe how cleaning interactions changed along two years in a rocky reef in Southwestern Brazil, where local fish cleaners comprise the dedicated *Elacatinus figaro* and the facultatives *Pomacanthus paru* and juvenile schools of *Haemulon*. Between 970 occasions, the number of juvenile hemulids decreased dramatically, and so did their cleaning activities, dropping from one third of total to a single cleaning event. Meanwhile *E. figaro* and *P. paru* remained important on both occasions, with an increase in interacting strength after the juvenile haemulid schools vanished. Haemulid schools likely provided a faster cleaning alternative to its main client, *Pseudupeneus maculatus*, such that when the schools were gone *P. maculatus* 975 relied upon other cleaners, increasing their importance. Also, we detected a slight partitioning in clients attended by *E. figaro* and *P. paru*, in which *P. paru* interacted with more sand dwellers while *E. figaro* had more predatory fishes as clients. Crustaceans also took part as cleaners, whose main clients were nocturnal fishes hidden among lodges and crevices on the reef. In a nutshell, we find the structure of cleaning interactions are stable, but changes a little in the presence of facultative 980 juvenile cleaners.

Keywords: Arraial do Cabo, Facultative cleaners, Time series

Introduction

Cleaning associations involve a broad set of marine fish species and happens when one individual (referred as cleaner) removes parasites, dead skin, or mucus from another (referred as 985 client) [1,2]. These interactions are essentially mutualistic, with cleaner species freeing clients from undesired skin items while gaining an energetic food source in exchange [2,3]. Over 260 species of fish and crustaceans have been reported acting as cleaner species with different levels of specialization[1]. Cleaners may be divided into two categories according to their life stage and dependence on the cleaning behavior [1,4]. Facultative cleaners are the most abundant type, 990 represented by fishes that only clean at the juvenile stage or sporadically across their ontogeny [5],

whereas dedicated cleaners have specialized to engage on cleaning interactions and depend on this interaction through their life [6].

995 Dedicated cleaners often present a characteristic set of colors and behaviors made to call clients attention [4]. They possess mouth parts adapted to selectively pick items on the clients' skin while their slender maneuverable bodies allows them avoid predators and seek for clients on the water column [6–8]. Despite attaining a considerable species diversity worldwide, the only dedicated cleaners in the Atlantic Ocean are cleaning gobies of the genus *Elacatinus* [8]. Only one species (*Elacatinus figaro*) is found along the Southwestern (SW) Atlantic coast [9], making it the only local dedicated cleaner species in those reefs [10–12].

1000 Despite sharing habitat with dedicated cleaners, most species in the SW Atlantic engage into cleaning as facultative [13–15]. Of those, the majority interact only as juveniles, among which *Pomacanthus* species often attain a substantial importance on local interactions [16,17]. Juvenile *Pomacanthus* in the Atlantic possess several traits that qualify them as effective cleaners, as showy yellow-in-black striped coloration and a specialized oral morphology that allows for selective
1005 feeding [8,18,19]. In the Atlantic ocean, the genus is represented by the co-occurring *Pomacanthus paru* and its sister species *Pomacanthus arcuatus*, of which *P. paru* account for most cleaning reports in the SW Atlantic [16,17,20]. Additionally, other species lacking proper cleaning adaptations may opportunistically engage in cleaning interactions, as some hemulids do so [13]. Their suction-feeding apparatus however limits their cleaning abilities to early life stages [21],
1010 making adult individuals of these species unable or discouraged to perform cleaning behaviors.

Both dedicated and facultative cleaners coexist throughout the SW Atlantic, occurring either alone or more often sharing the same habitat [12]. Client species often prefer services from dedicated cleaners and their presence reshape the structure of local cleaning networks by lowering the importance of facultative ones [15]. Even so, dedicated cleaners rarely hold all attention as their
1015 abundances are quite low, leaving cleaning opportunities open for facultative cleaners. So most reefs in SW Atlantic contain mixed sets of cleaners [13,14,20]. The presence of facultative cleaners might not be constant through the year as nearly all perform cleaning only as juveniles, so that their importance should vary depending on the reproducing timing of each species. Species spawning constantly through the year, as *Pomacanthus paru* [22], should have a near constant importance on
1020 local cleaning interactions, while species that spawn seasonally, as many hemulids does [23,24], should attain an oscillating presence on the cleaning networks.

To understand how the importance of cleaners might change in time, we report cleaning interactions recorded in a rocky reef at the SW Atlantic in two occasions spaced by a year. Given

the erratic influx of juvenile *Haemulon* species [23,24], we expect to observe changes in age
1025 structure of hemulids that affect their role on cleaning interactions. Meanwhile, juveniles of the
facultative cleaner *Pomacanthus paru* have been reported to appear continuously throughout the
year [22], suggesting less variability on cleaning activities due to a potentially similar size structure.
As *P. paru* would thus constantly share cleaning activity with the dedicated cleaner *Elacatinus*
figaro, we should likely observe a competition between those two species, expressed by selecting or
1030 avoiding the same clients, possibly followed by some partitioning among attended clientele.

Methods

Study area

The fieldwork took place in the Forno Bay within Arraial do Cabo (22°58'S 42°01'W, Figure
1), in southeastern Brazil. Local reefs are rocky, immerse in clear waters and covered by
1035 macroalgae and algal turfs, with little presence of bioconstructors in general, including corals [25].
Despite its subtropical location, the oceanographical conditions of Arraial do Cabo create an inner
warmer bay (~25°C) isolated from outer colder waters (~18°C) by a cape of rocky shores [26]. So,
local fishes share both a tropical and temperate affinity, with temperate-affinity fishes prevailing on
the outer waters while tropical fishes dominates the inner warmer bay [27].

1040 *Sampling Cleaning interactions*

Observation sessions of cleaning interactions took place between 13-15 January 2019 (102
observed interactions) and 4-6 February 2020 (107). We find this effort suitable as the individual-
based accumulation curve on species number approached an asymptote, such that doubling the total
effort (209 to 418 interactions) would detect only more 5 client species (Supporting Figure S1). All
1045 samplings occurred during the morning (7:00am to 11:00am), sampling at both sides of the Forno
Bay (Figure 1). Within each day, four to five snorkelers swam through the rocky shores actively
searching for cleaning interactions at depths from 1 to 5m. Upon finding, the divers identified both
the client and cleaner species and annotated their sizes. To increase odds of detecting a greater
variety of cleaners, the divers were instructed not to stay longer than 5 minutes on a single cleaning
1050 station. We considered an interaction event the moment when a diver spotted physical contact
between cleaner and client species, usually starting when the client species assumed an immobile
position and ending when one of the fishes withdrew or the cleaner changed clients.

Sampling fish size and abundance

Reef fish abundance and size structures were estimated using underwater visual censuses
1055 (UVC). During each UVC, a diver swam through the reef stretching a 20m line and recording large

mobile fishes within a meter on either side (total 40m², sensu [28]). Then, at the 20m mark the same diver returned recording small or cryptic fishes that might have gone unnoticed in the first passage. In this process the diver visually identified the fishes to the lowest taxonomic level possible, recording their abundances while assigning sizes (in cm). A total of 29 censuses were performed in the two occasions (13 censuses in 2019 and 16 censuses in 2020), each lasting for about 10 minutes. This total provided a rough description of the local fish assemblages, suitable for providing estimates on fish abundance and size profile as it recorded all species observed in cleaning interactions.

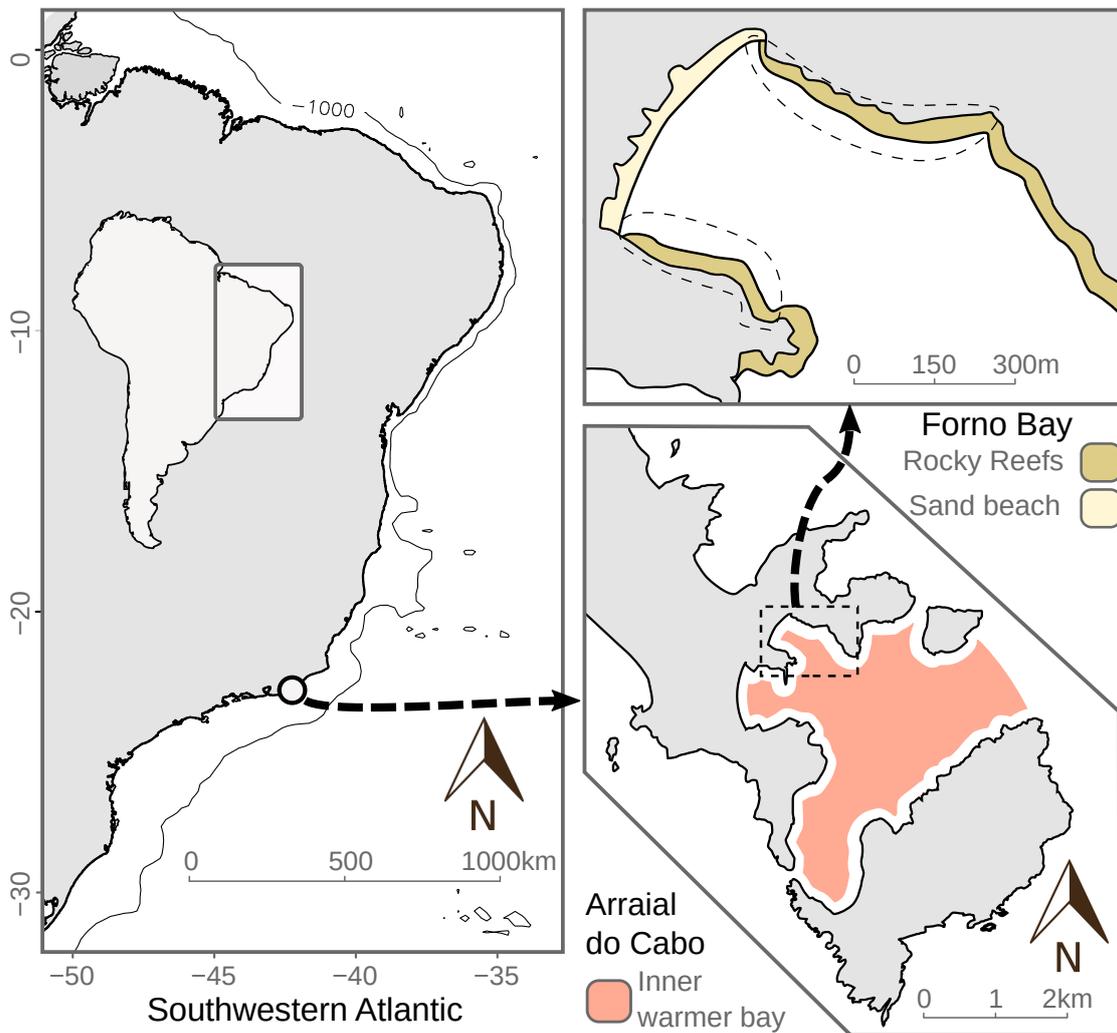


Figure 1. Location of Arraial do Cabo within South America, detailing sampling sites in the Forno Bay. Dashed lines indicated where observation sessions took place.

Changes in Cleaner Size

As facultative cleaners interact only as juveniles, any changes in age structure (detected through changes in size distribution) should also affect the cleaning engagement. To test whether

the size of facultative species, particularly *Haemulon* species changed between years, we compared
1070 the size distribution recorded on visual censuses, taking the size of each individual as sampling unit.
A permutational analysis of variance (P-ANOVA) was used to test for changes in size as the
residuals lack normality [29]. Histograms of cleaner size distributions are provided in Supporting
Figure S2. To assure changes in cleaning were driven by changes in size profile and not fluctuations
on fish composition, we performed a permutational multivariate analysis of variance
1075 (PERMANOVA) on the censuses, testing for differences in composition between years while
including other predictors of potential importance, namely: the distance to the shore, depth and side
of the bay. Details on predictors significance are provided in Supporting Table S1 and a non-metric
multidimensional scaling on the species composition is provided in Supporting Figure S3.

Species strength

1080 The importance of each interacting species was estimated within the cleaning network using
the species strength metric. This metric estimate the importance of a species within the network by
summing its relative dependencies [30]. In a cleaning perspective, the metric sums the proportion of
client interactions performed by a given cleaner and vice-versa, such that this metric could be
calculated for both cleaners (high level) and clients (low level). Here, our focus regarded the cleaner
1085 species, though we eventually accessed the clients metrics to provide a complete picture of
interactions. In order to compare species between years, we estimated standard error by
bootstrapping the matrix of interactions, selecting 80% of the records on each randomization. Then,
we used these intervals to test for changes using a t-test.

Species selectivity

1090 We used Krebs selectivity index (also called as Ivlev electivity) to determine which clients
are preferred by *E. figaro* and *P. paru* based on the clients relative abundance and in their proportion
of the interactions total. The index value species in a -1 to 1 scale, indicating positive selection
close to 1 and negative selection or avoidance by -1. In a competition scenario, we would expect to
observe a high correlation on selection, such that both *E. figaro* and *P. paru* prefer and avoid the
1095 same clients. In a partitioning scenario. We searched for a potential competition between those two
species by relating their selectivity index with a linear model, such that we tested whether
selectivity of *E. figaro* could be explained by the selectivity of *P. paru*. To account for some
partitioning in clientele, we added a categorical predictor indicating which clients were exclusive of
each species and which were shared. This test used data recorded on both years, combining the
1100 interactions records while averaging the mean abundances recorded on each year. Parameters

estimate of this model are provided in Supporting table 1 and a graph relating selectivity by both species is provided in the Supporting figure S4, showing the relation in total and for each year.

No fish was captured nor harmed during field observation sessions. As the area consist of a extractivist reserve, no permit for conducting non-invasive field reasearch was required. The
1105 Brazilian constitution guarantees continental and coastal oceanic waters as public, so no privately owned land was invaded while conducting this survey.

Results

Cleaning interactions

In total, 102 cleaning interactions were recorded in 2019 and 107 in 2020. Four fishes and
1110 two crustaceans species were identified as cleaners in the Forno Bay. Combining both years, the cleaning goby *Elacatinus figaro* accounted for most cleaning interactions (~50%), also attending the largest number of species (19, Figure 2). *Pomacanthus paru* contributed to one-third of interactions (35%) but attended almost the same number of clients (18 species). Juvenile individuals of
1115 *Haemulon aurolineatum* and *Haemulon atlanticus* also took part as cleaners but accounted for a much smaller proportion of observed interactions (14% and less than 1% of interactions, respectively). These two species interacted opportunistically with two client species (*Pseudupeneus maculatus* and *Epinephelus marginatus*), in which a single client was cleaned by several juvenile *Haemulon*. In addition to fishes, the cleaning shrimp *Stenopus hispidus* (detected only in 2019) and the spider crab *Stenorhynchus seticornis* (only in 2020) were spotted cleaning, but comprised rare
1120 sightings together accounting for only 5 interactions (1 by *S. hispidus* and 4 for *S. seticornis*).

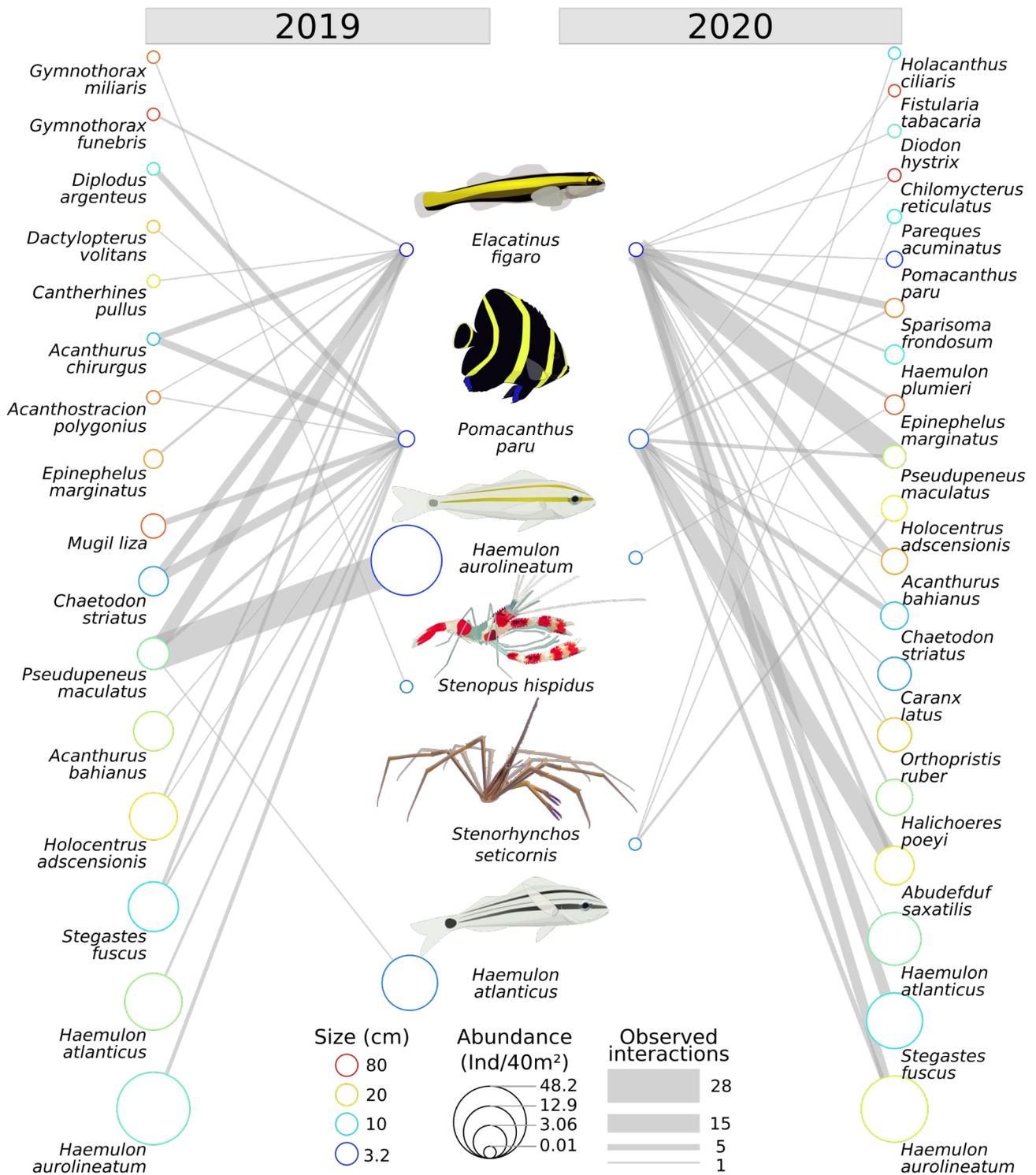


Figure 2. Network of cleaning interactions recorded in 2019 and 2020. Line thickness displays number of observed interactions. Dot size indicate recorded abundance on visual censuses and circle contour color indicate the mean observed size (snout-tail).

Changes in Cleaner Size

1125 The size of *Haemulon* species significantly increased from 2019 to 2020, gaining about 7cm
in length (P-ANOVA, for *H. aurolineatum*, $F_{1, 1132} = 1815.0$, $R^2 = 0.62$, $p < 10^{-16}$, for *H. atlanticus*,
1130 $F_{1, 426} = 680.1$, $R^2 = 0.61$, $p < 10^{-16}$; Supporting Figure S1). This increase in size was followed by a
sharp reduction in the number of juveniles (< 10cm) and a depletion of cleaning activities by 2020,
dropping from 30% of the total in 2019 to a single cleaning event (Figure 2). Meanwhile, the
species composition did not changed between years (PERMANOVA, pseudo- $F_{1, 24} = 1.31$, $R^2 =$
0.04, $p = 0.214$; Supporting Table S1 and Figure S3), posing the differences in size as the cause for
the changes in cleaning activities by hemulids.

Species Strength

Combining years, *E. figaro* attained the highest species strength values (13.4), surpassing *P.*
1135 *paru* by a 2.5 score margin (10.9, Figure 3). In 2019 both cleaners had a lower strength, with *P.*
paru reaching a slightly greater importance than *E. figaro* (8.4 against 5.9, respectively). By 2020,
E. figaro regained its status of stronger interacting species, with an increase in the interacting
strength of both species (10.3 for *E. figaro* and 6.4 for *P. paru*). Even when combining years,
Haemulon species had a disproportionately small strength in comparison to other cleaners (Figure
1140 3), with *H. aurolineatum* attaining a greater importance than *H. atlanticus* (0.58 against 0.01,
respectively). The importance of *H. aurolineatum* dropped by half from 2019 to 2020 as it dropped
from one third of the total of interactions in 2019 to only a single interaction in 2020 (0.65 against
0.25). As we did not observed *H. atlanticus* interacting in 2020, its strength declined from 0.01 (in 1
interaction) to 0. Crustaceans were rarely spotted in cleaning in comparison to fishes, which made
1145 their strength lower than *E. figaro* or *P. paru* (Figure 2). Even so, they attained a larger importance
than both *Haemulon*, likely as they serviced an exclusive set of rare species (Figure 3).

Among clients, almost all species had a low importance to the network. When combining
records from both years, *Pseudopeneus maculatus* figured as the most important client species in
the network, accounting for 67 of the 209 total interactions (species strength of 2.4; Figure 3). 42%
1150 of those interactions were recorded in 2019, when this species was the most important client (2.4,
Figure 3). By 2020 though, *P. maculatus* had its strength reduced substantially (0.39) contributed to
a much smaller proportion of the total interactions (22%), leading to more homogeneous strength
values among clients (Figure 3).

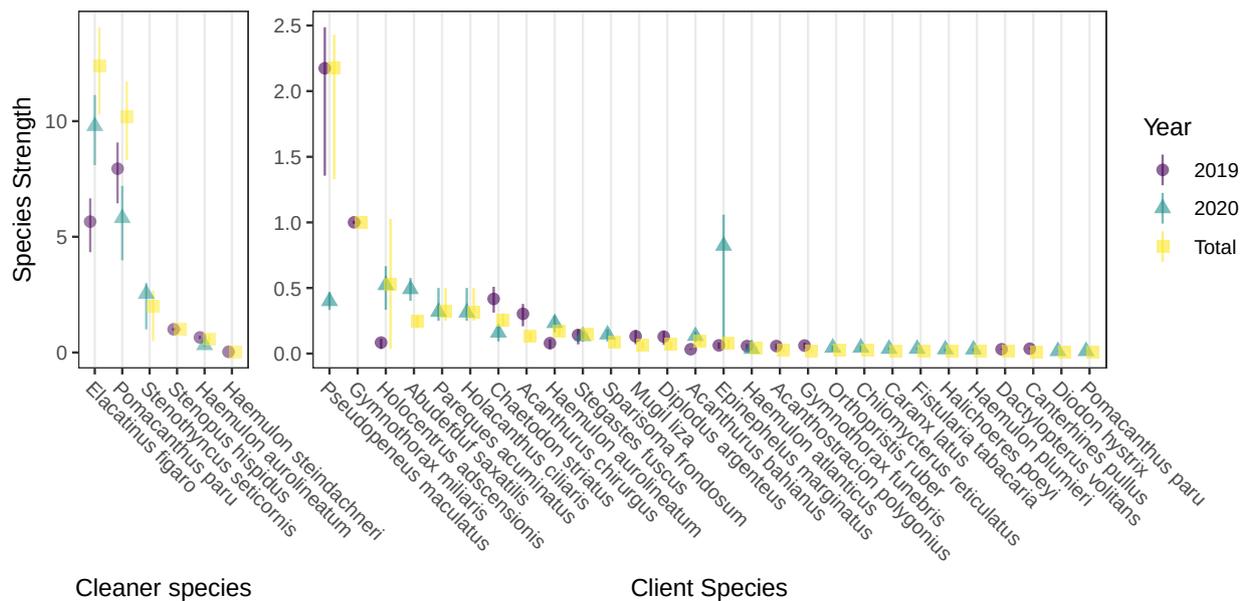


Figure 3. Species strength metric recorded in 2019, 2020 and combining both years (Total). Error bars show confidence intervals obtained by bootstrapping 80% of total.

Cleaner selectivity

We found a positive relation on selectivity for clients between *E. figaro* and *P. paru* ($p < 0.001$, Supporting Table 2). So these species share most their clients, but they also showed significant signs of clientele partitioning (Supporting Table S2, Supporting Figure S4). 8 species interacted exclusively with *E. figaro*, whereas 6 species interacted only with *P. paru*. No clear qualitative differences in selectivity for a particular species arose between years, such that both cleaners likely selected for the same clients on both occasions. Interestingly though, all exclusive clients of *P. paru* comprised sand dwellers as *Mugil liza*, *Diplodus argenteus* and *Dactylopterus volitans*, whereas exclusive clients of *E. figaro* included predatory fishes, as *Epinephelus marginatus* and *Gymnothorax funebris*.

Discussion

Effect of intermittent cleaners

Cleaning interactions in Arraial do Cabo mostly relied upon two cleaner species (*Elacatinus figaro* and *Pomacanthus paru*) that achieved a similar importance in the local cleaning network. Juvenile hemulids acted as second party cleaners particularly in 2019, when they attained a greater abundance. By 2020 the juvenile *Haemulon* population reduced sharply, also depleting their cleaning activities. Meanwhile, the interacting strength of *E. figaro* and *P. paru* increased, with *E. figaro* figuring as the strongest cleaner on the network. So, the intermittent flux of juvenile

hemulids have little impact on the overall structure of the local cleaning network, affecting mostly a
1175 single client species, *Pseudupeneus maculatus*.

Cleaning activity performed by juvenile haemulid is reported in other sites of the SW Atlantic, particularly where dedicated cleaners are missing [13]. In Arraial do Cabo, we observed juveniles individuals of at least five haemulid species (*Anisotremus virginicus*, *H. atlanticus*, *H. aurolineatum*, *Haemulon plumieri* and *Orthopristis ruber*) aggregating into large schools, of which
1180 at least two species (*H. atlanticus* and *H. aurolineatum*) were observed acting as opportunistic cleaners. These schools were frequently joined by juveniles of *Diplodus argenteus* and *Caranx latus*, from which at least *D. argenteus* have been reported to engage in cleaning interactions [31]. Given the generalist profile of facultative cleaners, cleaning behaviors should represent a common feature of those schools, not restricted to two species observed here. Therefore, the schools presence
1185 might temporarily increase the amount of cleaning interactions, though the drivers for preferences towards non-dedicated cleaner remain unclear.

When the schools were present, we observed several individuals simultaneously attending a same client, providing a much faster cleaning service in comparison to other dedicated, but solitary cleaners. At first instance this indicates the preference of *P. maculatus* for *Haemulon* cleaners could
1190 be linked to a quicker service, faster in comparison to what less abundant *E. figaro* and *P. paru* could provide. The schools thus represent a temporary alternative route for quickly getting parasites removed. Still, a greater client diversity should be expected if availability was the only reason behind the observed patterns. Instead, we observed only one species, *P. maculatus*, consistently relying upon juvenile *Haemulon* for cleaning

1195 *Selectivity on cleaning*

Adult hemulids and most other schooling fishes were cleaned much less than expected by their abundance, indicating a cleaners preference for solitary clients. During fieldwork this negative selection was observed as a clear avoidance of *E. figaro* and *P. paru* towards approaching *Haemulon* clients, even after those individuals assumed cleaning positions (as displaying flanks
1200 with full pelvic extension or adopting a vertical body alignment). As those schools often include a mixed set of species, this avoidance might be linked to a self-preservation behavior, as potential predators may hide among the school, increasing predation risk. Most attended clients were in fact solitary. Some notable exceptions regarded some exclusive clients of *P. paru*, which comprised schooling sand dwellers, as the mullet *Mugil liza*. Exclusive clients of *E. figaro* were all solitary and
1205 included two piscivorous species that turn into potential predators, the moray *Gymnothorax moringa* and juveniles of the grouper *Epinephelus marginatus*.

Elacatinus species have frequently been reported to service potential predators throughout the Atlantic, species which facultative cleaners often avoided interaction [32,33]. During our field observations, chasing events of groupers towards cleaners were recorded, though cleaning *E. figaro* always managed to dodge the attacks and resume interacting shortly after (usually with other species). Juvenile *P. paru*, on the other hand, rarely interacted with predatory species. This avoidance could be learned through similar chasing events seen for *E. figaro*, though innate responses shall not be discharged. These findings differs from cleaning reports on other SW Atlantic reefs where *P. paru* frequently interacts with large predatory fishes [12,17], pointing towards local heterogeneity on cleaning activities. As a curiosity, only *E. figaro* cleaned *P. paru*, revealing an intraspecific cleaning avoidance possibly resulting from their territorial behavior [22].

Quite few surveys investigated the importance of cleaning crustaceans on local cleaning networks [1]. In our survey those represented rare sightings, accounting for only 5 interactions, all of which hiding in lodges or crevices among the reef. The cleaning shrimp *Stenopus hispidus* was spotted only once, cleaning a spotted moray (*Gymnothorax miliaris*), whereas three yellowline arrow crabs (*Stenorhynchus seticornis*) were detected, interacting with two squirrel fishes (*Holocentrus adscensionis*), a high-hat (*Pareques acuminatus*) and a queen angelfish (*Holacanthus ciliaris*). With the exception of *H. ciliaris*, all observed crustacean's clients comprise nocturnal species that seeks shelter within the reef during the day [34,35]. Both *S. hispidus* and *S. seticornis* lack surveys dedicated to detail its cleaning behaviors in the SW Atlantic. A collection of interaction reports of *S. seticornis* cite only nocturnal clients [36], suggesting those species either comprise nocturnal cleaners or are daytime cleaners that interact with species hiding within the reef.

Conclusions

We observed that changes on the abundance of juvenile schooling fishes could provide a periodical influx of opportunistic facultative cleaners in the rocky reefs of Arraial do Cabo. The presence of hemulid schools partially rearranged the structure of local cleaning networks mostly by absorbing one important client, *P. maculatus*. Still, other cleaners with constant presence on the reef as *E. figaro* and *P. paru* suffered little changes in their importance or cleaning behavior, indicating the cleaning networks to be overall stable over time. We noticed the dedicated *E. figaro* and *P. paru* shared most clients, preferring solitary benthic dwellers while avoiding schooling species likely due to a higher predation risk. In addition, we detected a slight partitioning among those two species, with *P. paru* cleaning more sand dwellers while *E. figaro* serviced more large predatory fishes. For now, fish species dominated the cleaning interactions in Arraial do Cabo, but we acknowledge that our sampling efforts occurred only during daytime, certainly underestimating the importance of

1240 shrimps and crabs on cleaning. Investigations on their local importance would represent an
important next step towards an complete ecosystemic understanding of cleaning interactions, as
well as assessing what clients they attend.

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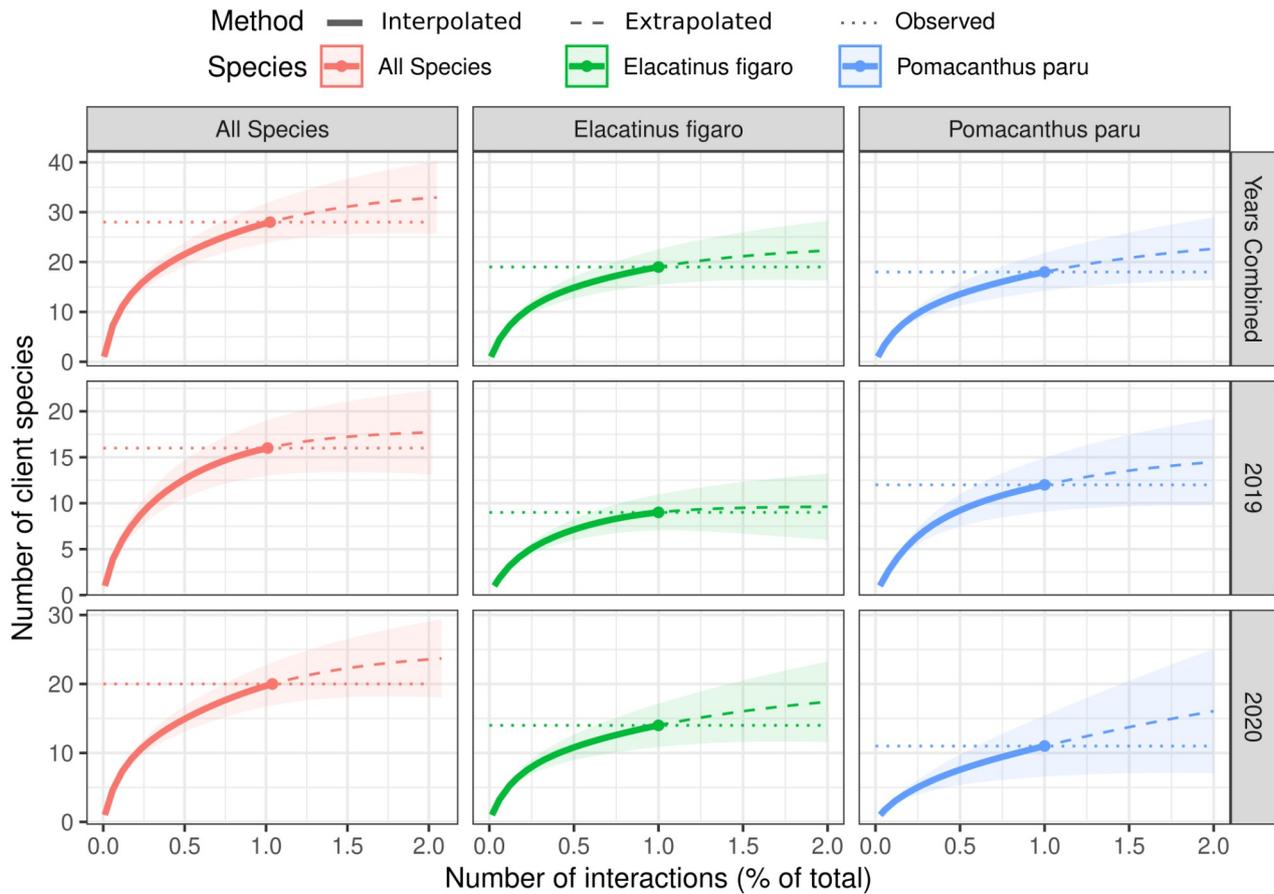
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Supporting material

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Figure S1. Individual based accumulation on number of client species. The thick line indicates the interpolated growth in species number. The points and horizontal dotted lines show the observed richness of client species, while the dashed lines indicates the extrapolated number of clients obtained by doubling the total of observed interactions. In total, the applied effort sufficed to record client richness, as only 4.9 species might have gone missing (in a total of 28 species on 209 interactions). Regarding years, 1.7 species might be missing in 2019 and about 3.7 others were possibly not recorded in 2020. Among cleaner species, the observed client richness of *Elacatinus figaro* deviated much less from the extrapolated value than *Pomacanthus paru*. In total, 3.3 clients of *E. figaro* might not be recorded, while 4.6 of *P. paru* might have gone missing. Less than a single client species of *E. figaro* might not be recorded in 2019, while 3.4 might have been missing in 2020. About 2.5 species were not recorded for *P. paru* in 2019, while 5.0 were not detected in 2020.

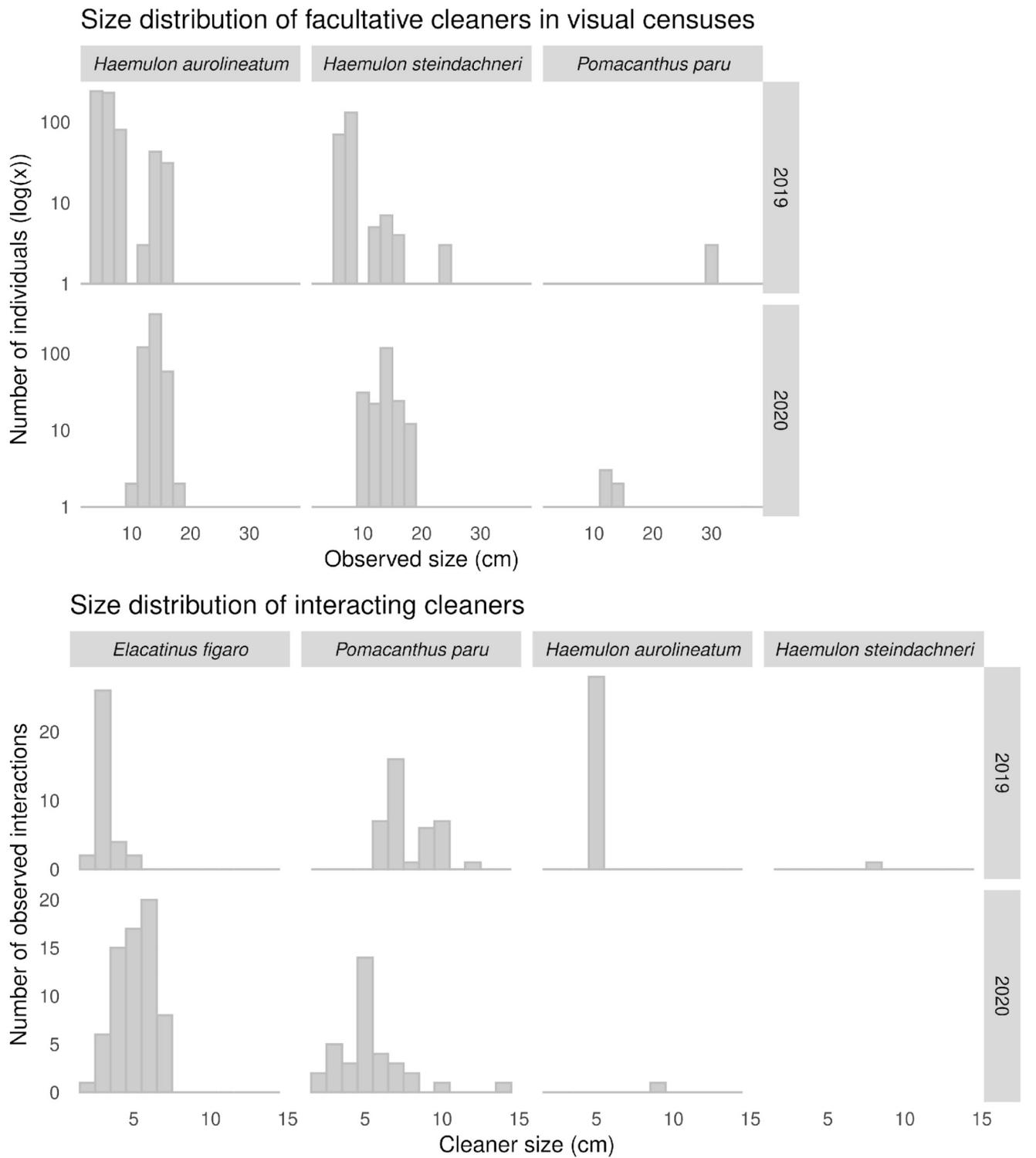
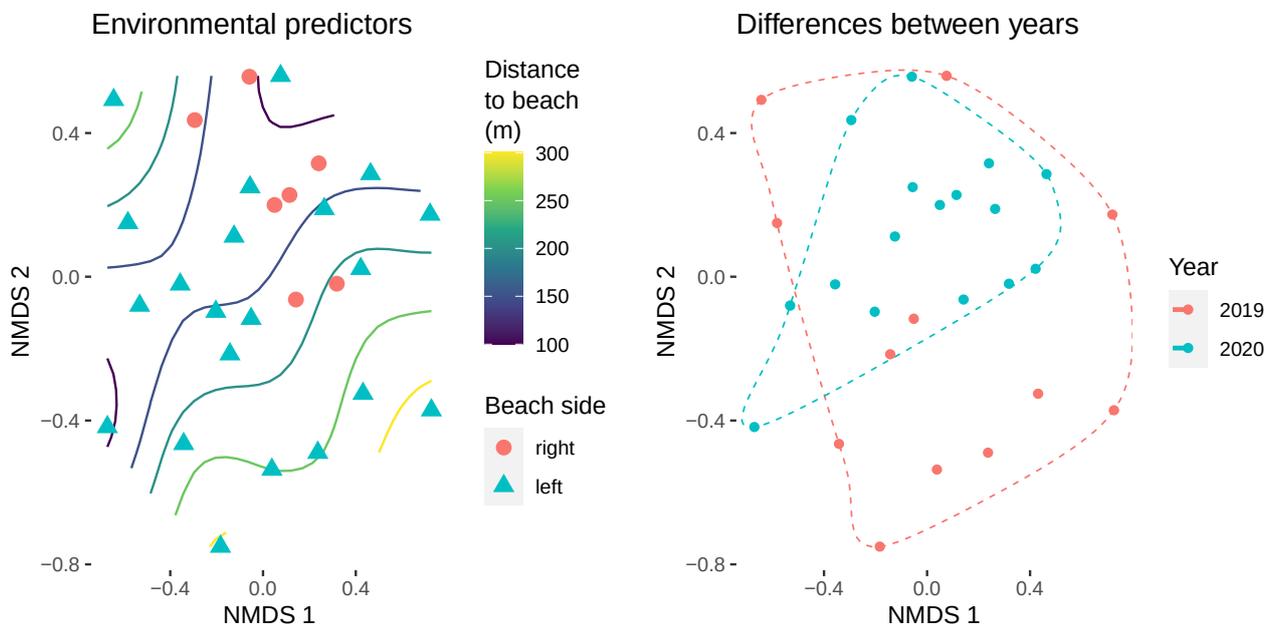


Figure S2. Size distribution of facultative cleaners obtained from underwater visual censuses and the size distribution of cleaners engaging in cleaning interactions.

1370 **Table S1. Parameters estimate derived from the PERMANOVA.** We used a permutational analysis of variance to test whether the species composition changed between years. Our main predictors consisted in the years, but we also added depth, distance from the sand shores and the side of the Forno Bay at which visual censuses were performed. We found no significant differences in composition between years. The composition seems to respond much better to the recorded environmental conditions, though three quarters of the total variation remain unexplained.

Predictor	Degrees of Freedom	F modelled	R ²	p
Side	1	2.86	0.09	0.002
Distance	1	2.57	0.08	0.004
Depth	1	0.73	0.02	0.687
Year	1	1.37	0.04	0.197
Residual	24	-	0.76	-



1375 **Figure S3. Non-metric multidimensional scaling of visual censuses showing available predictors.** The left panel shows the distance to the shore (contour lines) and the side of the forno bay where each visual census was performed, whereas the right panel shows the years.

Species selectivity index

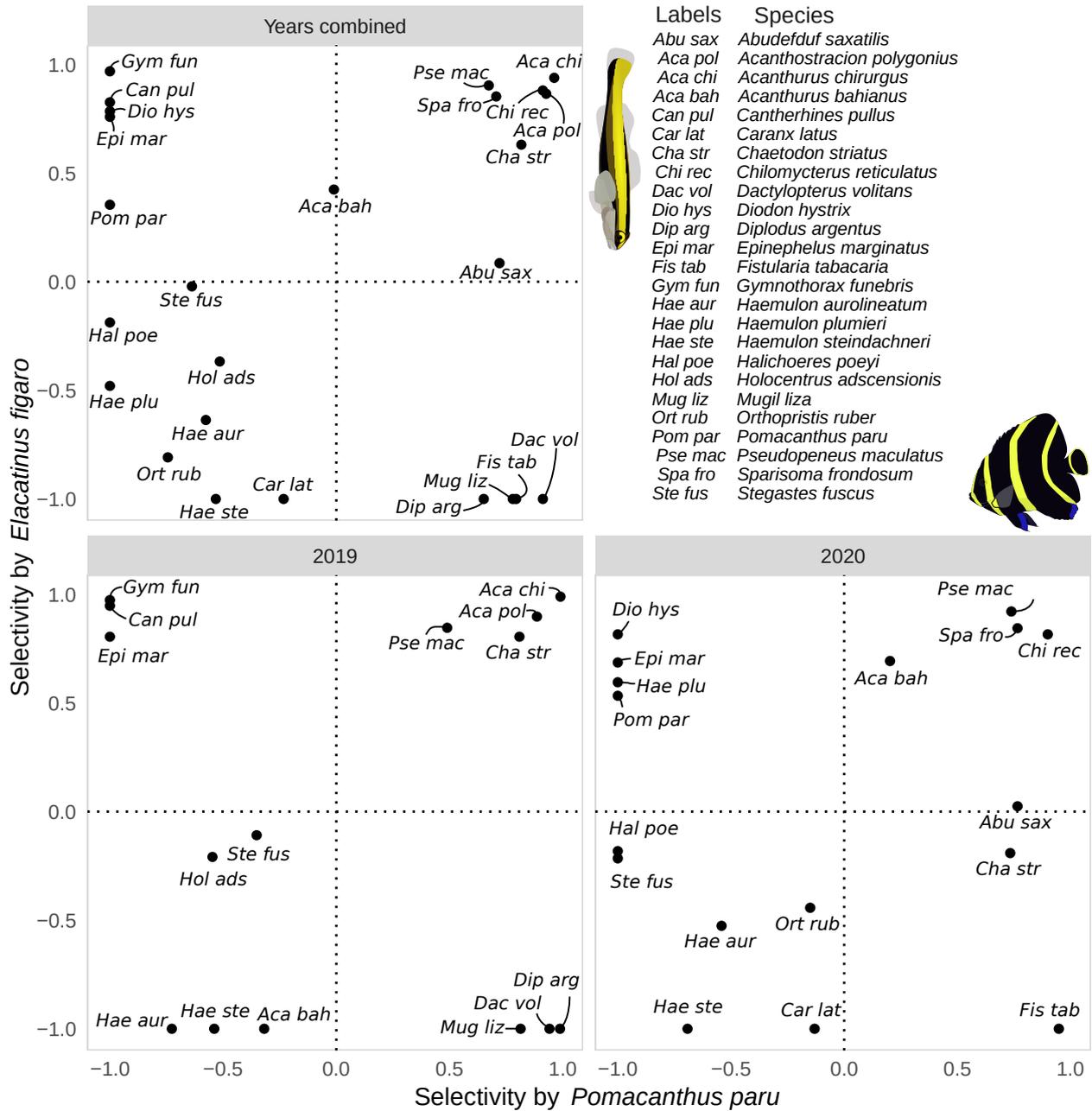


Figure S4. Comparison of client selectivity by *Elacatinus figaro* and *Pomacanthus paru*. The y axis displays selectivity by *E. figaro* and the x axis displays selectivity by *P. paru*. Positive values indicate preference while negative ones indicate avoidance. Species names are abbreviated according to the code displayed on the right.

1380 **Table S2. Parameter estimates on the linear model.** This model assessed whether *Elacatinus figaro* and *Pomacanthus paru* compete for clients, performed by testing whether client selectivity by *P. paru* could explain client selectivity by *E. figaro*. An additional predictor indicated shared and exclusive clients of those two species. T values on parameter estimates tests for differences from 0.

Model: Selec. by *E. figaro* ~ Selec. by *P. paru* + Exc. clients

Coefficients	Estimate	Std. Error	T	p
Intercept (Shared clients)	0.014	0.079	0.175	0.862
Selectivity by <i>P. paru</i>	0.851	0.103	8.344	1.49*10 ⁻⁸
Exclusive clients of <i>P. paru</i>	1.580	0.194	8.145	2.29*10 ⁻⁸
Exclusive clients of <i>E. figaro</i>	-1.682	0.211	-7.976	3.32*10 ⁻⁸

Residual Std. Error: 0.343 on 24 D.F.
Multiple R² = 0.841
F_{3, 24} = 42.34

Adjusted R² = 0.821
p = 9.64 * 10⁻¹⁰

Capítulo 3

Assessing cost-efficiency of remote underwater videos to record richness and composition of reef fish assemblages

Submetido para a *Journal of Fish Biology*



1385 **Abstract**

Remote underwater videos are widely employed to assess the structure of reef fish assemblages. Still, the sampling effort employed on each survey differs considerably, indicating that both the number of assessments and time of video analysis could be optimized. We searched for this optimal sampling effort in remote video samples to assess community composition and discussed
1390 the relation between number of replicates and video length, as well as how it impacts the method's ability to characterize fish assemblages. We used remote video recordings from tropical reefs in Northeastern Brazil as a model to investigate how fish species richness and composition builds across time and number of assays. We found videos as short as 5 min worked well for recording richness, with about 5 repetitions recording most species. Recording species composition required
1395 even less time, setting a minimum of 3 min with the same 5 videos for Southwestern Atlantic reefs. By comparing the detected richness per analyzed time unit, we found several shorter videos recorded more species than a few longer videos, indicating that increasing the sampling coverage in the reef area might be better than just extending video length.

Key words: Video Plots, Reef Fishes, Sampling Effort, Rapid Assessments, Accumulation curves

1400 **Introduction**

The biodiversity crisis highlights the need to assess natural communities (Cardinale *et al.*, 2012; Dornelas *et al.*, 2014). Because basic attributes such as local species richness and composition are rarely available, aquatic biologists constantly need to improve sampling techniques for optimizing sampling efforts (Legg & Nagy, 2006). Low-cost visual approaches are extensively
1405 used to estimate basic ecological data of fish assemblages as they tend to be less invasive and easily applicable on clear water environments (Bosch *et al.*, 2017). Such methods have been heavily used to estimate reef fish richness and composition, particularly through visual counts of individuals on fixed areas, known as underwater visual censuses (Murphy & Jenkins, 2010).

Although underwater visual censuses became the most common technique for surveying reef
1410 fish assemblages (Caldwell *et al.*, 2016), they are prone to biases regarding accuracy of fish detection (Pais & Cabral, 2017). Errors in counting have been linked to how the local biota reacted to a human observer (Emslie *et al.*, 2018; Tuytens *et al.*, 2014), as well as the ability and experience of the sampling diver (Dickens *et al.*, 2011; Pais & Cabral, 2017, 2018; Thompson & Mapstone, 1997). Even some non-obvious effects could affect samples, as fish fleeing responses
1415 due to scuba bubbles and juvenile fish avoiding divers (Lindfield *et al.*, 2014; Longo & Floeter, 2012). To avoid these biases, a considerable number of methods involving remote videos have

emerged in aquatic sciences in order to record fish abundance and composition on the absence of a human observer (Bicknell *et al.*, 2016; Ebner *et al.*, 2015).

1420 The use of techniques involving fixed or moving cameras have substantially increased over the past few decades (Mallet & Pelletier, 2014). Video assessments have proven useful for a wide array of issues. Some of them include estimating abundance of large predators, monitor human impacts on biodiversity and measuring fish feeding pressure on the benthic cover (Bicknell *et al.*, 2016; Cappo *et al.*, 1999; Harvey *et al.*, 2007; Longo & Floeter, 2012). Remote video techniques, either baited or not, appeared on aquatic sciences as a less invasive technique capable of avoiding
1425 several observer related biases (King *et al.*, 2018; Nanninga *et al.*, 2017; Pita *et al.*, 2014). In some areas, the absence of an observer allowed for a much deeper understanding of species difficult to spot, for instance revealing unprecedented fish diversity and biomass on seagrass beds (Zarco-Perello & Enríquez, 2019). The use of video analysis can also optimize field efforts by allowing for simultaneous samples of the reef assemblage, reducing sampling time. This turns particularly useful
1430 when diving is constrained by reduced funding or rush conditions, such as in deep or glacial habitats (Cappo *et al.*, 1999; Post *et al.*, 2011).

Despite being a well-established methodology, there appears to be no consensus on the total sampling effort regarding the number (related to the covered area) or the length of videos (Langlois *et al.*, 2010; Mallet & Pelletier, 2014). Each assessment often uses its own sampling strategy
1435 regarding time and video repetitions, leading to a high variation among published literature. For instance, the longer video assessments often occurred in herbivory assays, varying from one to several hours (Fox & Bellwood, 2008; Rasher *et al.*, 2013). Baited approaches reached between 30-60 min of video analysis (Bosch *et al.*, 2017; Ebner *et al.*, 2015; Langlois *et al.*, 2010; Post *et al.*, 2011). Shorter videos (about 10 min) were used to assess fish feeding pressure on the benthos in
1440 reefs and freshwater ecosystems (Canterle *et al.*, 2020; Longo *et al.*, 2014, 2015, 2019; Miranda *et al.*, 2018; Nunes *et al.*, 2020). This method prompted macroecological approaches in trophic interactions based on a large number of replicates per sampling site (Longo *et al.*, 2019; Fontoura *et al.*, 2020). The large variability in published sampling times and number of replicates indicate a possible trade-off between sampling more or sampling longer videos. Additionally, a considerable
1445 number of surveys found few differences on species richness and abundance as time increased (Gladstone *et al.*, 2012; Campbell *et al.*, 2015; Harasti *et al.*, 2015), indicating that video analysis could be improved by better defining repetitions and time.

Aiming to discuss the trade-offs between sampling more or longer videos, we used remote video recordings from tropical reefs in Northeastern Brazil as a model to investigate how ecological

1450 estimators of reef fish assemblages, species richness and composition, changed with an increasing
sampling effort. We chose stationary remote video as this methodology stands within the cheaper
and easier to deploy among video sampling techniques (Longo & Floeter, 2012; Mallet & Pelletier,
2014). Our analysis took three steps: (1) describe how time affected sampled richness and
composition; (2) list the effects of increasing video numbers with videos of different lengths; and
1455 (3) indicate which combination of video number and length record more species per analyzed
minute. Regarding time, we expected richness and similarity in species composition to grow more
steeply at the beginning of the video, approaching an asymptote under larger sampling efforts. A
similar trajectory would occur for the number of videos, with an expressive initial growth followed
by a plateau in the number of species recorded under a certain sampling size. In both cases we also
1460 estimated a minimum effort that could help direct field research. Finally, we argue that several
videos of a short length record more species per time unit than a few longer videos as they would
enable covering larger reef areas with more replicates.

Materials and Methods

Sampling design and video analysis

1465 We conducted remote video recordings in five reefs in the eastern coast of Rio Grande do
Norte state, in northeastern Brazil (between 05°14'S, 35°22'W and 6°00'S, 35°02'W). Reefs in this
area comprise past coastlines flooded when sea levels rose after the last glacial maxima (Leão *et al.*,
2016; Santos *et al.*, 2007). Macroalgae and algal turfs dominates most of the benthic cover, with
coral cover often representing less than 10% of the total (Aued *et al.*, 2018; Roos *et al.*, 2019).
1470 Local Reef fish assemblages compose the tropical southwestern Atlantic fauna, which harbors a
total of 730 species, of those 31% (240) are included within Northeastern Brazil (Pinheiro *et al.*,
2018).

We recorded 46 videos across five sampling sites ranging from 2 and 20 km away from the
shore and at depths varying between 1 and 25m (details on field work in the supporting material).
1475 None of the locations lie within no-take zones and a few surveys at local and broader scales reveal
signs of high fishing pressure on large predators and parrotfishes, some of them possibly being
already overfished (Morais *et al.*, 2017; Roos *et al.*, 2016, 2019). This scenario may affect the
detection of large species as their abundance declined over time but does not invalidate the video
analysis as this configure the current state of these communities and many species are not subject to
1480 fishing pressure. Also, we could detect several fishing targets that are rare sightings in other visual
approaches in the region (Morais *et al.*, 2017; Roos *et al.* 2016).

The video recordings occurred within a 10 days period in March 2013 to minimize temporal variations of fish assemblages (Thompson & Mapstone, 2002). While sampling, we placed the cameras within at least 10m apart from each other to reduce duplicate records of the same individuals. During each sampling occasion a diver operator placed a camera on the reef bottom, recording in video a 2m² area signalized with a tape during the first seconds. Each video lasted for about 15 minutes, of those we used the central 10 minutes (sensu Longo & Floeter, 2012). This provided a brief habituation period and prevented effects of spooking fauna when handling the cameras back. As we noticed only minor signs of changes in composition related to diver presence, we find the 3 to 5 min habituation period satisfactory for the study (Longo & Floeter, 2012).

During video analysis, our focus was to record the moment in which every fish first appeared on video, filling in a list of new species records on all videos. This created an in-video accumulation curve, saving the order in which the species first came into sight, as well as their identity. To simplify any analysis, instead of working in the scale of seconds we used minutes, creating 10 one-minute time steps matched by all videos. We then used several accumulation methods to perceive how increases in observed time and in the number of videos affected the total richness and the recorded species composition.

Statistical analysis of sampling time

Initially we drew attention to how the number of detected species increases as the analyzed time got longer. We expected the cumulative number of species to increase quickly at first but get steady towards longer observed times. To test this, we used a linear mixed effect model (LMM) containing the observed richness at each video (response variable) as a function of the observed time (predictor) in a log_e scale. To account for non-independence of time steps within each video, we added the videos as random factors, providing a random slope and intercept for each of the 46 analyzed videos. Our conclusions were based at first if the parameter estimate differs from 0 and then on the total explained variance, obtained through Nakagawa's marginal and conditional R² (Nakagawa & Schielzeth, 2013; Nakagawa *et al.*, 2017). Details on the model validation are provided in supporting information. We then searched for a minimum sampling time enough to capture a consistent richness. We did this by comparing the richness between each pair of time steps through Tukey's honestly significant differences tests (THSD), testing the hypothesis of two tailed differences on richness between each combination of minutes.

To address how an increasing observation time affected the recorded species composition we used a permutational multivariate analysis of variance (PERMANOVA) based on a Sorensen dissimilarity matrix. As predictor we added the log transformed time, expecting to observe the same

1515 steadying behavior predicted for richness, meaning changes became subtle towards longer times. To
assess the lack of independence within time steps from the same videos, we added the videos as a
categorical predictor in the model. We also used PERMANOVAs to perform pairwise comparisons
among minutes. A graphical view of those changes is presented in a non-metric multidimensional
scaling (NMDS) on 2 axis. Further details on model validation and parameters estimates are
1520 provided in the supporting information.

Statistical analysis of video number

To visualize how richness changed as the number of analyzed videos increased, we used a
random sample accumulation curve performed under a thousand randomizations (Gotelli &
Colwell, 2001). In order to create a graphical view on how both time and replicates interacted to
1525 build the observed richness, we constructed a curve for each of the 10 one-minute time steps
previously used. To estimate a minimum video number within each time, we used piecewise
regressions to split the accumulation trends in two pieces, representing the initial steeper growth
and the subsequent gentle trend. The break point between those two moments acted as an estimate
of the minimum number of videos enough to sample most of the local species richness.

1530 To inform how many videos would be required to sample the overall species composition,
we used a similarity accumulation approach, by randomly selecting a subset of videos and
calculating how similar (Sorensen index) the achieved composition was to the total species set. The
calculated similarity should increase as more replicates are added, accumulating until reaching an
asymptote towards one (100% similarity). As with richness, we built a curve for the each of the 10
1535 time-steps, providing a graphical comparison on how an increasing number of videos of different
lengths accumulate similarity on species composition. Also, we estimated a minimum sampling
number by fitting piecewise regressions to these curves, addressing the point when the trend started
approaching an asymptote.

Cost-efficiency between observed time and number of videos

1540 To assess the potential trade-off between the duration and the number of videos required to
estimate richness and composition of reef fish assemblages we used the breakpoints provided by the
piecewise regressions in our previous tests. We provided the breakpoint estimates of the 10 time-
steps as response variable to a linear model, with the numeric time of each step as predictor. A
separate model was constructed for break points estimates of richness and composition. As this
1545 decay could be non-linear, we tested the significance of both a linear and a quadratic term.

Finally, we aimed to determine the combination of video number and observed time that record more species under a same analyzing time. We used randomization designs to compare whether prioritizing more videos of short lengths yields more species than just observing entire videos sequentially. To assess this, we constructed two accumulation trends representing the total
1550 analyzed time in these two scenarios. The first curve prioritized the first minutes, permuting videos with a constrain on minutes. That is, all species detected within the first minute of all videos should be considered before adding the species found in the second minute, then all species in the second minute have to be considered before going to the third and so on. The second curve permuted video order but had no constrain in minutes except from preserving its original order within a video. It
1555 means that all the species found at the first video should be computed before going to the second, then all species found on the second video should be computed before going to the third and so on. The differences on mean richness recorded by each permutation design should indicate which combination of observed time and number of videos yields more species under a same time spent analyzing videos.

1560 All analyses were performed in the R software (R core Team, 2020). We used functions from several packages to perform statistical analysis, namely: lme4 (Bates *et al.*, 2015) for the LMM, the performance package to obtain Nakagawa's marginal and conditional R^2 (Lüdecke *et al.*, 2020), vegan for multivariate analysis (Oksanen *et al.*, 2008), segmented to estimate breakpoints in accumulation trends (Muggeo, 2008, 2017) and permute for the permutation designs (Simpson,
1565 2007). Data handling and plotting were done with tidyverse (Wickham *et al.*, 2019). A summary of statistical procedures is provided in Table 1.

Table 1. Summary of statistical procedures used to assess the effects of time, videos and both predictors on species richness and composition. We first assessed how richness and composition changed as a function the assessed predictor (time or replicates) and then looked for a minimum
1570 sampling effort by combining both time and video repetitions. * These analyses captured the relation between variables, but do not apply hypothesis test on them. ** These analyses estimated only the threshold at which no significant differences arise, not the full set of pairwise comparisons.

Metric	Test	Analyses		
		Time only	Videos only	Time + Videos
Richness	Priori	Mixed effects model	Accumulation on richness*	Linear model
	Post-hoc	Tukey test	Piecewise regression**	Permutations design*
Composition	Priori	PERMANOVA	Accumulation on composition similarity*	Linear model
	Post-hoc	Pairwise PERMANOVA	Piecewise regression**	-

Results

Sampling Time

1575 Overall, the combined 7h and 40min of the 46 video replicates recorded 56 species. The first
minutes uncovered most of the total richness, detecting fewer new species as the observed time
increased. As a result, there was a strong relationship between the log transformed time and the
observed richness (LME, estimate parameter for $\ln(\text{time}) = 3.5$, std. error = 0.24, $t = 14.52$, $p <$
0.001). Time (as minutes) alone explained about 26% of the within video changes in richness
1580 (marginal $R^2 = 0.26$), whereas the combination of time (as fixed effects) and videos (as random
effects) explained almost all the variance in the total dataset (conditional $R^2 = 0.97$). Besides, the
pairwise comparisons revealed that the minimum sampling time lies at about 5 min, after which no
significant differences to 10 minutes could be detected (Figure 1a, THSD pairwise contrasts, all $p <$
0.05).

1585 The species composition changed quite less with time in comparison to the richness. The
observed time explained a tiny but highly significant amount of variation in species records,
meaning the composition changed with time, only at a quite small rate (PERMANOVA, $R^2 = 0.02$,
modeled $F = 53.92$, $p < 0.001$). The videos themselves explained a much larger portion of the total
variation, posing that the order and identity of species detection varied substantially between
1590 samples (PERMANOVA, $R^2 = 0.82$, modeled $F = 46.61$, $p < 0.001$). The pairwise comparisons also
revealed no significant changes in composition after 3 minutes of video observation (pairwise
PERMANOVAs, all $p < 0.05$), posing most of the total species set was detected up to that time.

Number of Videos

An increasing number of samples affected both richness and composition (Figure 1c and
1595 1d). As expected, the number of detected species increased quickly with the first videos but

stabilized toward larger sampling efforts. Considering the complete 10-minute videos, almost all species were detected within 20 videos, missing only 7 species from the total of 56. However, the estimates of minimum sampling size were much lower than that, pointing to at least five videos as enough to sample most of the species richness (70%, see Figure 2). Videos of shorter lengths
1600 required just a few more repetitions to approach an asymptote (see Figure 1b), but in all cases using less than 10 repetitions to do so.

For all time-steps, the similarity on composition increased substantially with few videos (Figure 1). All video lengths accumulated similarity in a quite similar way, differing only in initial and final values. Greater time-steps had higher initial similarity values than shorter ones, reaching
1605 higher scores at the end too. So, the longer the observed time, the less replicates it would require to approach a consistent composition sample (see Figure 1d). Even so, videos of all lengths would require just about 5 replicates to approach an asymptote in similarity growth. Shorter video lengths required more repetition than longer ones, with one-minute videos reaching their breakpoints at 6 videos, whereas 10-minute videos used only 4. Thus, surprisingly small sampling sizes could thus
1610 detect suitable amounts of the local fish assemblages.

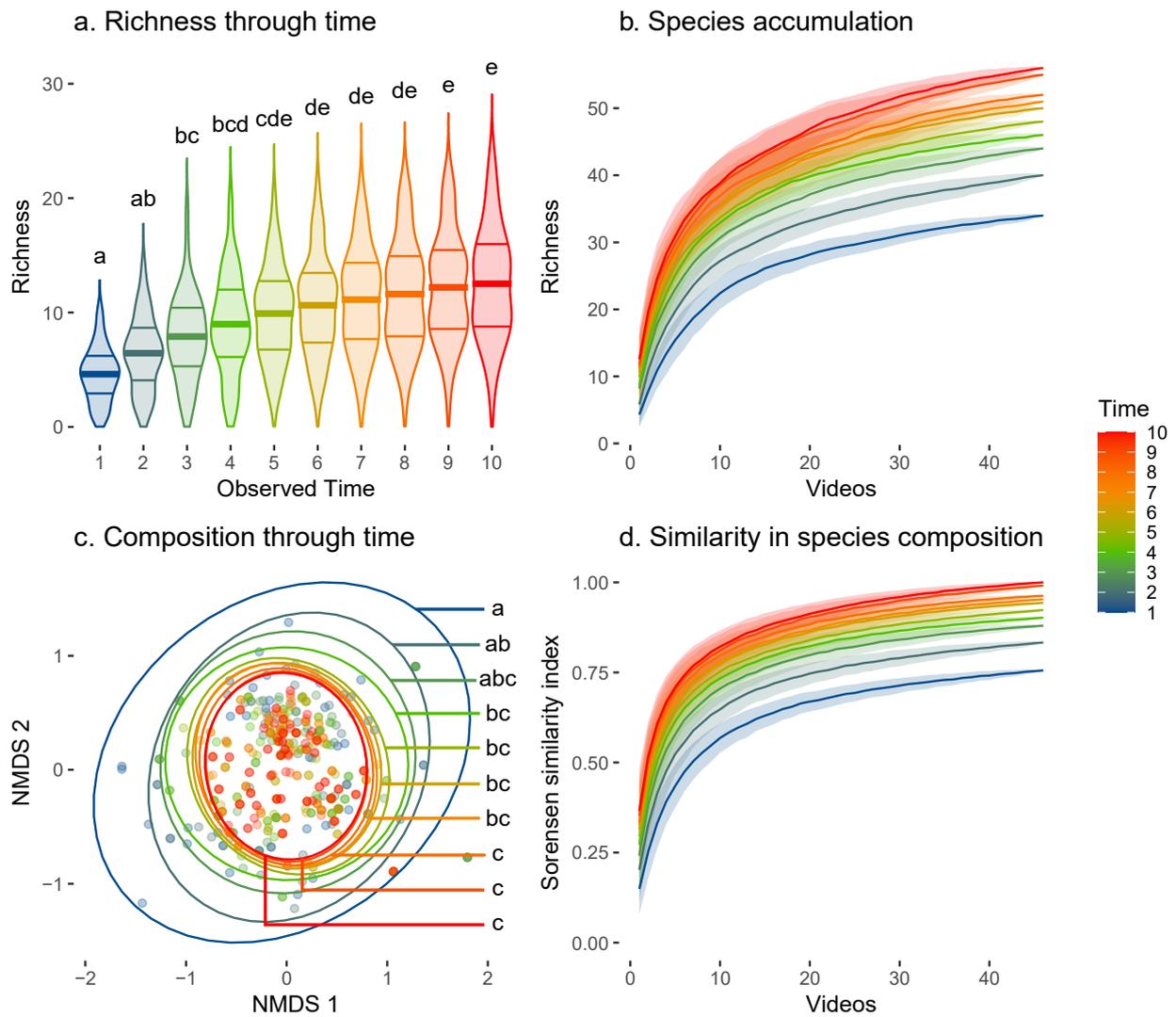
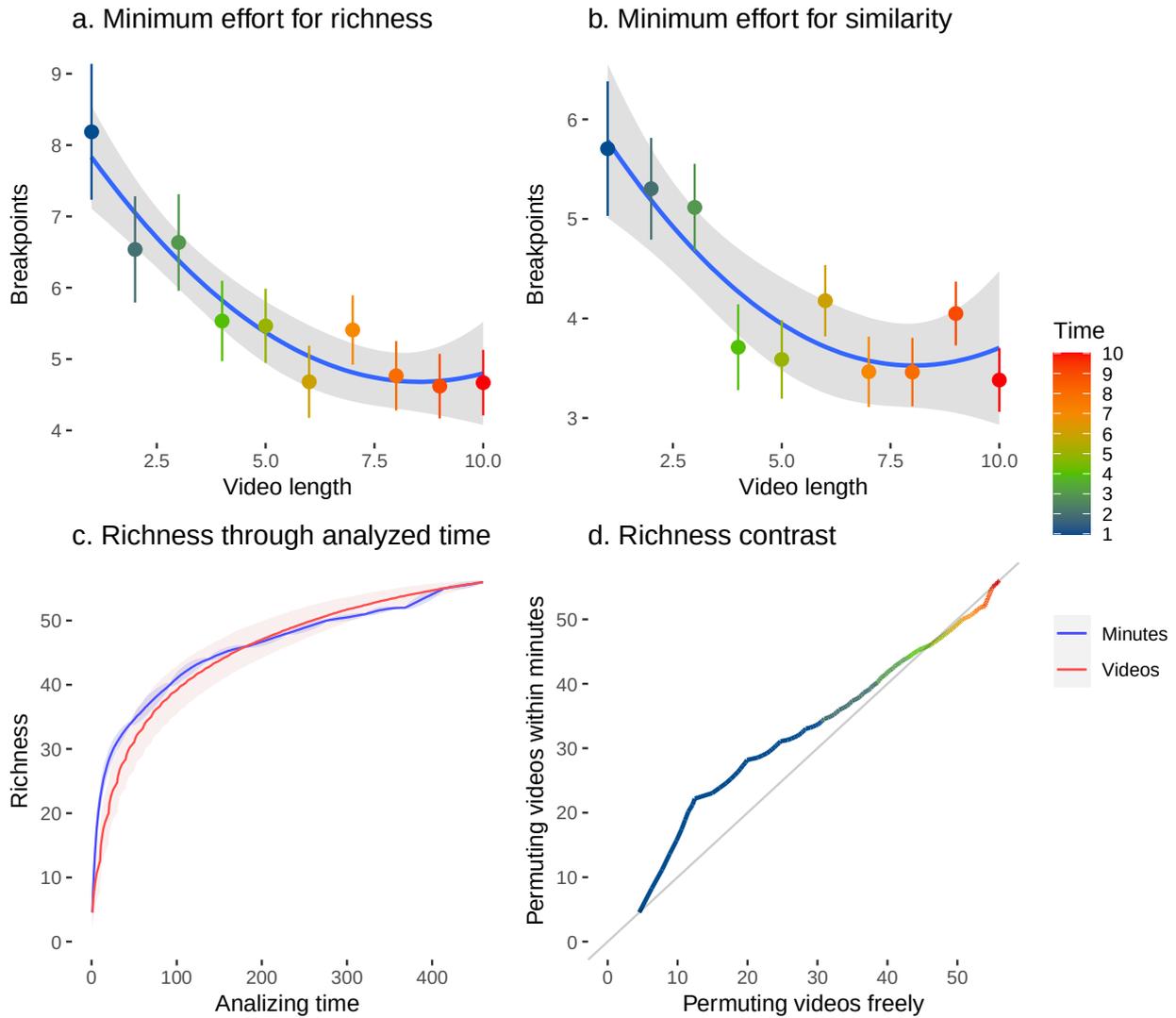


Figure 1. Relationship between richness (top) and main species composition (bottom) with number of videos (right) and their length (left). 10 time lengths (steps) are represented under the color scale at the left. a. Distribution of richness accumulated at each time step, showing mean and 25% of the data above and below it. Shared letters with different time steps indicate the absence of significant differences. b. Random sample accumulation curves of species richness. The mean richness trend is represented by the continuous line, while the shaded are represent the standard deviation. Each curve represents a different time step. c. Ordination representing the evolution of species composition with an increasing time. The ellipses represent 95% of the deviance between videos at each time step. Letters shared between time steps indicate the absence of significant differences. d. Random sample accumulation curve of species similarity. The mean similarity at each number of videos are represented by the continuous line, whereas the shaded area shows it standard deviation.

Cost-efficiency between number and length of videos

As we expected, longer videos required less replicates to reach suitable sampling efforts. We
1625 found a significant negative relation between the minimum number of videos (as break point
estimates) and video length (in minutes), implying that longer videos require less replicates to reach
consistent sampling sizes (Figure 2a and 2b). This held true for both richness (LM, $F_{2,7} = 36.43$,
adjusted $R^2 = 0.887$, $p < 0.001$) and similarity on composition (LM, $F_{2,7} = 15.9$, adj. $R^2 = 0.768$, p
< 0.001, further details on model validity in supporting information). Also, these relations had
1630 significant quadratic terms, posing that longer observing periods require progressively less
replicates to minimally sample fish assemblages.

Prioritizing the first minutes recorded more species than just watching entire videos
sequentially (Figure 2c and 2d). This held particularly true for the first minute, which returned
almost twice more species per analyzed time unit than the null strategy (21 vs 12 species). These
1635 differences started to fade away at the third minute, after which both curves became similar. Beyond
the fourth minute, there is almost no differences between the two strategies. So, under a same time
effort, several replicates of short videos record more species than few replicates of long videos,
increasing the rate at which new species are detected.



1640 Figure 2. Trade offs between sampling more or sampling longer videos (above) and the efficiency in
 each combination of number of samples and video length (below). a. Relation between the
 breakpoints in accumulation curves and the video length, representing the minimum number of
 1645 videos required to provide a consistent sample of species richness at each time step. b. Relation
 between the time steps and the breakpoints in the similarity accumulation curves (representing a
 minimum number of samples). In both a. and b. points represent the mean breakpoint estimate and
 the lines show its standard errors. c. Randomization trials permuting number of videos and their
 lengths. The null hypothesis of equal gain of species throughout the video length is represented by
 the red curve. The alternative hypothesis, that the video first minutes are more effective, is shown
 by the blue line. The differences between the two trials are shown in d., where the growth in
 1650 richness at both curves are plotted against each other. The colors represent the moment in time
 being evaluated, whereas the spikes can be traced to the number of videos.

Discussion

We assessed the cost-benefit between time and number of videos for detecting reef fish species with stationary remote videos using Brazilian tropical reefs as model system. The video tapes detected 54 of the 240 species reported regionally (Pinheiro *et al.*, 2018), a quite impressive finding given the sampled area (5 sites) and the brief field work window (10 days). By observing video duration, we noticed most species were detected within the first five minutes, with negligible gain of species thereafter. Regarding the number of videos, we found that at least five videos were enough to sample a substantial amount of the species total. In both cases, the minimum sampling size came from surprisingly small numbers, indicating brief analyzing efforts suffice for gathering basic ecological parameters. Also, longer videos required progressive less repetitions to record a consistent number of species, showing evidences for a trade-off between sampling more and longer videos. Interestingly, when supplied with enough replicates, shorter videos detected more species than longer ones per analyzed time unit, posing the most efficient sampling design may lie in scattering several but quick videos through the reef area.

The reason for a higher efficiency of several shorter videos may lie in the somewhat random distribution of fishes within the reef (Belmaker *et al.*, 2007). Reef communities comprise a large range of environmental conditions, as wide depth ranges and patches of distinct complexity, implying in an uneven distribution of species within the reef area (Oakley-Cogan *et al.*, 2020). By performing more replicates, the chances of detecting any given species could increase simply by covering a larger area, in a classic species-area relation. On the other hand, new species records driven by extending the video length would depend on some fish behaviors, particularly mobility as shown for baited approaches (Wines *et al.*, 2020). For instance, large predatory species could have their abundance overestimated by arriving quickly at the lure, which in turn, underestimate the abundance of smaller fishes by spooking them (Coghlan *et al.*, 2017; Dunlop *et al.*, 2015; Taylor *et al.*, 2013). Unbaited videos may not account for those biases, but it at least suggests some behaviors could influence video detection.

The role of reef fish traits in biasing samples is quite diverse. Species schooling behavior, size and their ability to blend in with the background comprise the best known of them (Cappo *et al.*, 1999; Willis, 2001; Thanopoulou *et al.*, 2018). In visual transects, abundant schooling species (in our database represented by *Thalassoma noronhanum*, *Chromis multilineata* and schooling haemulids) could have their population overestimated by imprecise or double countings (Tuytens *et al.*, 2014). Our video tapes often cover small areas, which could make them prone to miss site-attached species if not provided with enough replicates. When dealing with Brazilian reef fishes, those biases should be minimal as most species comprise habitat generalists (Araújo *et al.*, 2020).

1690 Sampling richer assemblages however might require a larger effort in both time and number of assays, particularly in reefs where site-attached species dominates. In our database, the group of site-attached species is restricted to territorial damselfishes within the genus *Stegastes*, detected in almost all videos. Still, previous assays in the brazilian coast identified cryptobenthic fishes might have their detectability reduced (Longo & Floeter, 2012), though changing the transect area could correct for biases (Zarco-Perello & Enríquez, 2019).

1695 In our assessments most species had a quite variable order and time of first detection. Detections of rare, fishery targeted species were scattered across the entire video. Therefore, the odd indicates longer videos have a higher chance of detecting a species but short videos could do better with equivalent numbers of repetitions. Still, caution should be taken when handling the cameras in and out of the reef, as the diver presence could affect local assemblages for a considerably long time (Emslie *et al.*, 2018). We could notice the detection of at least one species, *Scarus trispinosus*, was potentially biased by diver presence, as its rare detection did not match previous reports on their abundances (Roos *et al.*, 2019). Longer habituation periods (from half to one hour) before shooting could solve this issue, providing more reliable estimates for fishery targeted species. As the remaining species has little to no sign of biases, we indicate the total sampling effort of quick assessments could and should be adjusted according to the survey goals.

1705 Our assessments use fishes in Southwestern Atlantic to estimate the minimum sampling effort required to detect reef fishes using videos. We found evidence of a trade-off between sampling more or longer videos. That means the richness detected in a single long video could be matched by a few short ones. Yet, short videos often detect more species per analyzed minutes as they cover a larger area, so quick assessments would benefit from deploying several quick videos instead of a few longer ones. The total sampling effort should depend on the intended subject, adjusting time and repetitions to better suit the researcher's goals. By now, our findings represent more of a case study than an absolute recommendation, hence we encourage surveys in other ocean basins to determine their own sampling optimum. As thumb rule for researchers in Southwestern Atlantic, we recommend using at least 5 videos of about 5 minutes to describe communities at local scale. Still, it is up to the researcher to ponder about how to sample, considering their knowledge about expected conditions and target species.

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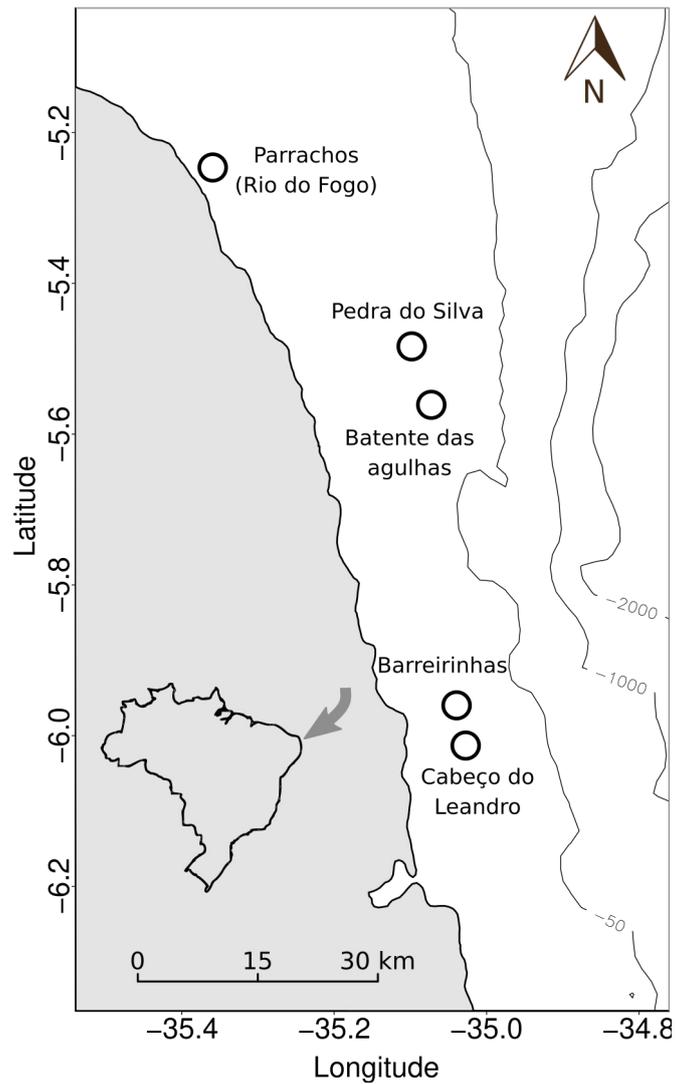
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Supporting Information



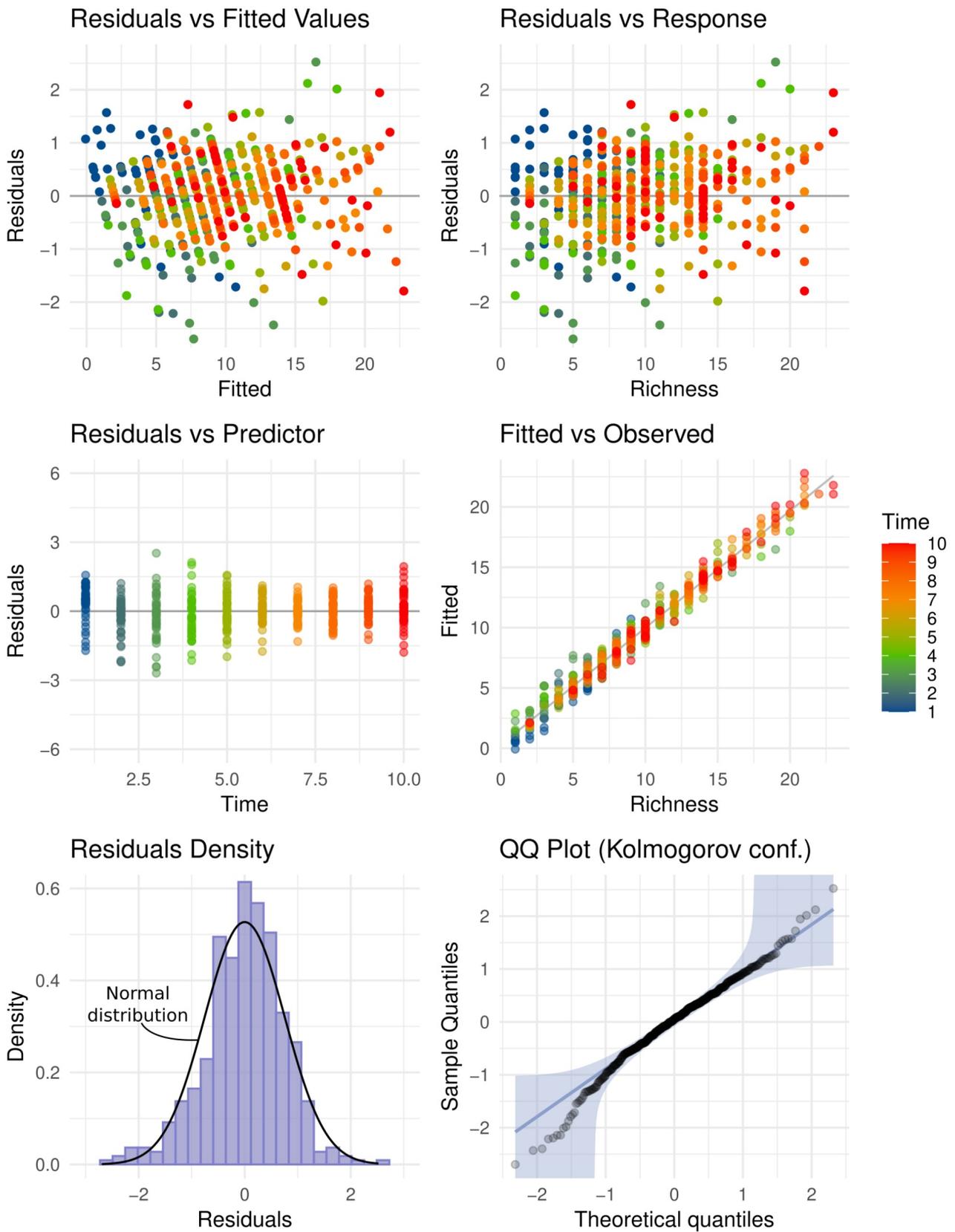
Supporting Figure S1. Map showing location of the five sampling sites relative to the coastline (grey area). Continuous lines show the isobaths of 50, 1000 and 2000m deep.

1895 Supporting Table S1. Details on physical parameters of each sampling localities.

Site	Date	Latitude	Longitude	Depth Range	Distance to shore (km)	Sampling Size	Detected Richness
Parrachos (Rio do Fogo)	2013/03/29	-5.245778	-35.359787	0-3m	2	10	18
Pedra do Silva	2013/03/25	-5.490422	-35.10500	15-25m	18	12	46
Batente das Agulhas	2013/03/26	-5.560972	-35.072500	20-24m	17	8	34
Barreirinhas	2013/03/23	-5.960083	-35.039306	8-22m	7	7	25
Cabeço do Leandro	2013/03/21	-6.013500	-35.027306	8-23m	6	9	27

Supporting Table S2. Linear mixed model parameters estimates on richness explained by time. Differences to 0 on parameter estimate were used to assess significance of fixed effects. Explained deviation was calculated through Nakagawa's marginal (fixed effects) and conditional R² (fixed + random effects)

Formula: Richness ~ log(Time) + (1 + log(Time) Videos)				
Random Effects				
Groups	Name	Variance	Std. Dev.	Correlation
Videos	(Intercept)	6.91	2.63	
	log(Time)	2.59	1.16	0.17
	Residuals	0.70	0.84	
Number of observations: 460. Number of groups: 46				
Fixed Effects				
	Estimate	Std. Error	T value	P value (based on t)
Intercept	4.24	0.40	10.63	< 0.001
log(time)	3.54	0.24	14.52	< 0.001
Scaled residuals				
Min	1st Quartile	Median	3 rd Quartile	Max
-3.22	-0.52	0.06	0.58	3.01
Nakagawa's R ²				
Marginal:	0.267		Conditional:	0.970



Supporting Figure S2. Residuals graphical analysis of linear mixed effects model.

1905 Supporting Table S3. Parameters and statistics estimated for the PERMANOVA used to test the relation between species composition (similarity on species presence) and time (expressed by 1 minute time steps)

Formula: Composition ~ Videos + log(Time)

Number of permutations: 1000

Permutation design: Free

	D.F.	F Model	R ²	P
Videos	45	46.61	0.82	< 0.001
log(Time)	1	53.92	0.02	< 0.001
Residuals	413	-	0.16	-

1910 Supplementary Table S4. Pairwise comparisons of composition between time steps (pairwise PERMANOVAs). On each comparison, the associated F statistic, explained deviation and significance are displayed.

Pair	F Model	R ²	p	Pair	F Model	R ²	p	Pair	F Model	R ²	p
1 vs 2	0.52	0.01	0.83	2 vs 9	2.73	0.03	0.009	5 vs 6	0.01	0	0.994
1 vs 3	1.36	0.01	0.22	2 vs 10	3	0.03	0.003	5 vs 7	0.2	0	0.967
1 vs 4	2	0.02	0.055	3 vs 4	0.14	0	0.983	5 vs 8	0.36	0	0.926
1 vs 5	3.03	0.03	0.004	3 vs 5	0.4	0	0.908	5 vs 9	0.47	0.01	0.843
1 vs 6	3.71	0.04	0.001	3 vs 6	0.62	0.01	0.748	5 vs 10	0.65	0.01	0.715
1 vs 7	4.22	0.04	0.001	3 vs 7	0.91	0.01	0.518	6 vs 7	0.05	0	0.993
1 vs 8	4.78	0.05	0.001	3 vs 8	1.14	0.01	0.308	6 vs 8	0.13	0	0.991
1 vs 9	5.34	0.06	0.001	3 vs 9	1.43	0.02	0.193	6 vs 9	0.2	0	0.974
1 vs 10	5.65	0.06	0.001	3 vs 10	1.62	0.02	0.107	6 vs 10	0.34	0	0.93
2 vs 3	0.21	0	0.979	4 vs 5	0.13	0	0.983	7 vs 8	0.04	0	0.995
2 vs 4	0.66	0.01	0.703	4 vs 6	0.24	0	0.965	7 vs 9	0.11	0	0.984
2 vs 5	1.21	0.01	0.308	4 vs 7	0.48	0.01	0.857	7 vs 10	0.15	0	0.979
2 vs 6	1.62	0.02	0.109	4 vs 8	0.72	0.01	0.667	8 vs 9	0	0	0.995
2 vs 7	2.01	0.02	0.03	4 vs 9	0.94	0.01	0.499	8 vs 10	0.03	0	0.993
2 vs 8	2.34	0.03	0.023	4 vs 10	1.12	0.01	0.349	9 vs 10	0.03	0	0.992

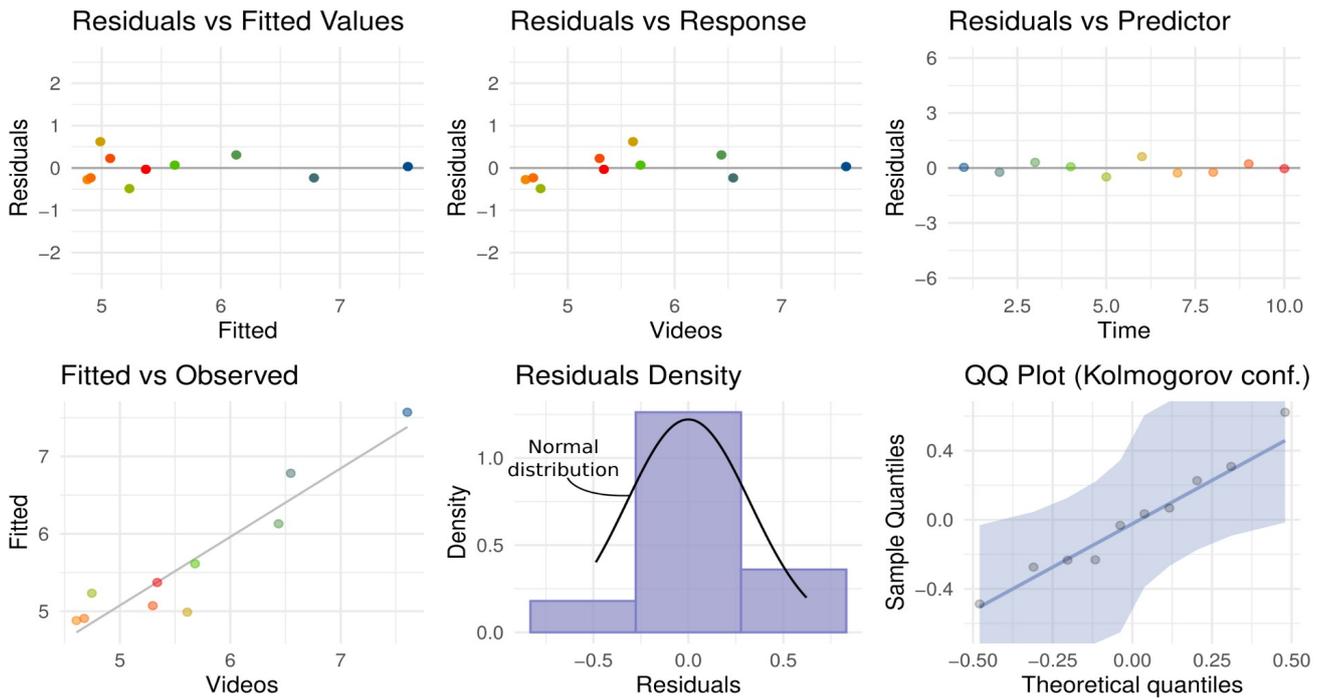
1915 Supplementary Table S5. Break-Point estimates for richness and composition similarity and its respective confidence intervals

Richness				Composition similarity			
Time (min)	Estimate	C.I. low (95%)	C.I. up (95%)	Time (min)	Estimate	C.I. low (95%)	C.I. up (95%)
1	7.60	6.65	8.56	1	6.31	5.67	6.94
2	6.55	5.82	7.27	2	4.68	4.16	5.20
3	6.44	5.81	7.06	3	4.47	4.04	4.91
4	5.68	5.10	6.26	4	3.68	3.27	4.10
5	4.75	4.21	5.28	5	3.57	3.19	3.94
6	5.61	5.09	6.13	6	3.53	3.17	3.89
7	4.61	4.13	5.08	7	3.46	3.12	3.80
8	4.68	4.21	5.15	8	3.44	3.11	3.77
9	5.30	4.86	5.73	9	3.40	3.08	3.72
10	5.34	4.91	5.77	10	3.38	3.07	3.69

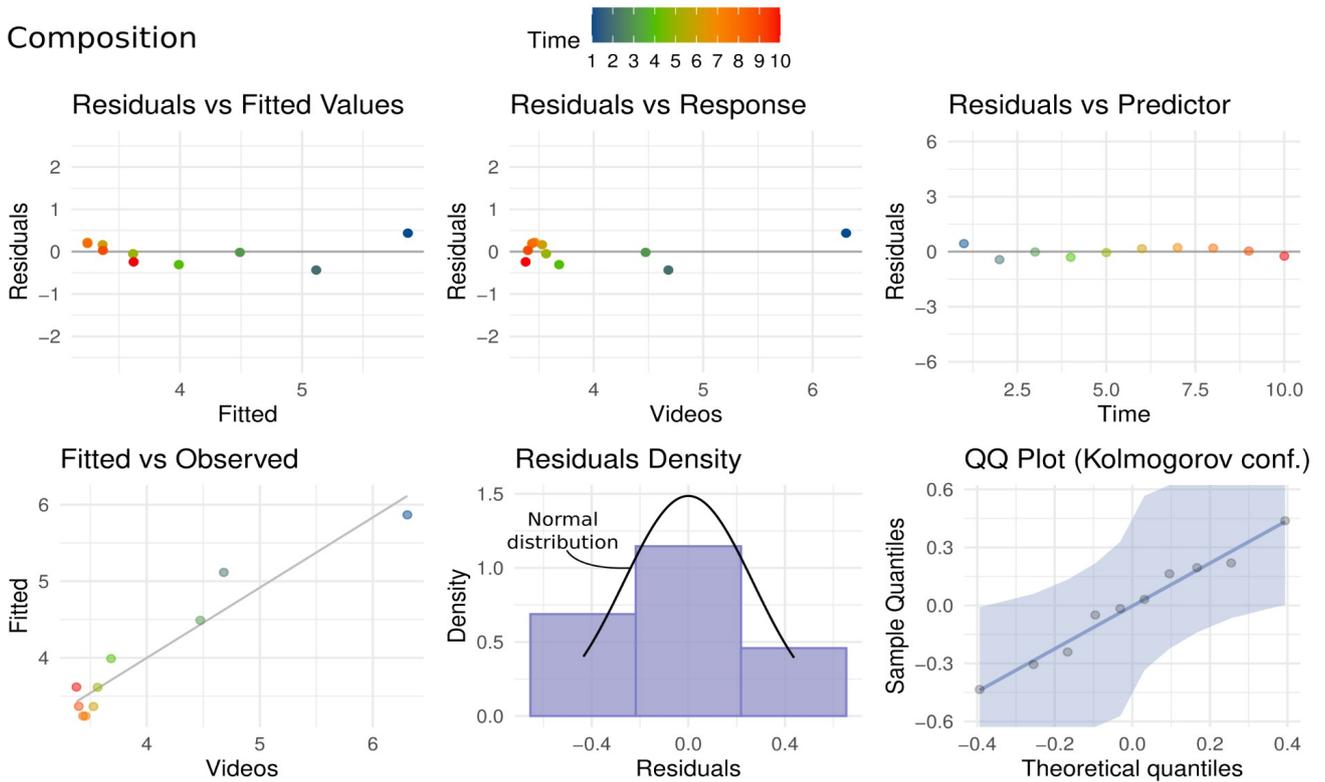
Supporting Table S6. Parameter estimates provided by the linear model relating minimum number of replicates (as breakpoints) and video length (in minutes).

Linear model on richness					Linear model on composition similarity				
Formula: BreakPoints ~ Time ² + Time					Formula: BreakPoints ~ Time ² + Time				
Coefficients					Coefficients				
Parameters	Estimate	Std. Error	T value	p	Parameters	Estimate	Std. Error	T value	p
Intercept	5.655	0.117	48.267	<0.001	Intercept	3.992	0.096	41.4670	<0.001
Time	-2.219	0.370	-5.990	<0.001	Time	-2.268	0.304	-7.453	<0.001
Time ²	1.562	0.370	4.216	0.004	Time ²	1.440	0.304	4.730	0.002
Residuals standard error: 0.371 on 7 degrees of freedom					Residuals standard error: 0.304 on 7 degrees of freedom				
Multiple R ² : 0.885 Adjusted R ² :0.852					Multiple R ² : 0.918 Adjusted R ² :0.894				
F statistic: 26.83 on 2 and 7 degrees of freedom P: <0.001					F statistic: 26.83 on 2 and 7 degrees of freedom P: <0.001				

Richness



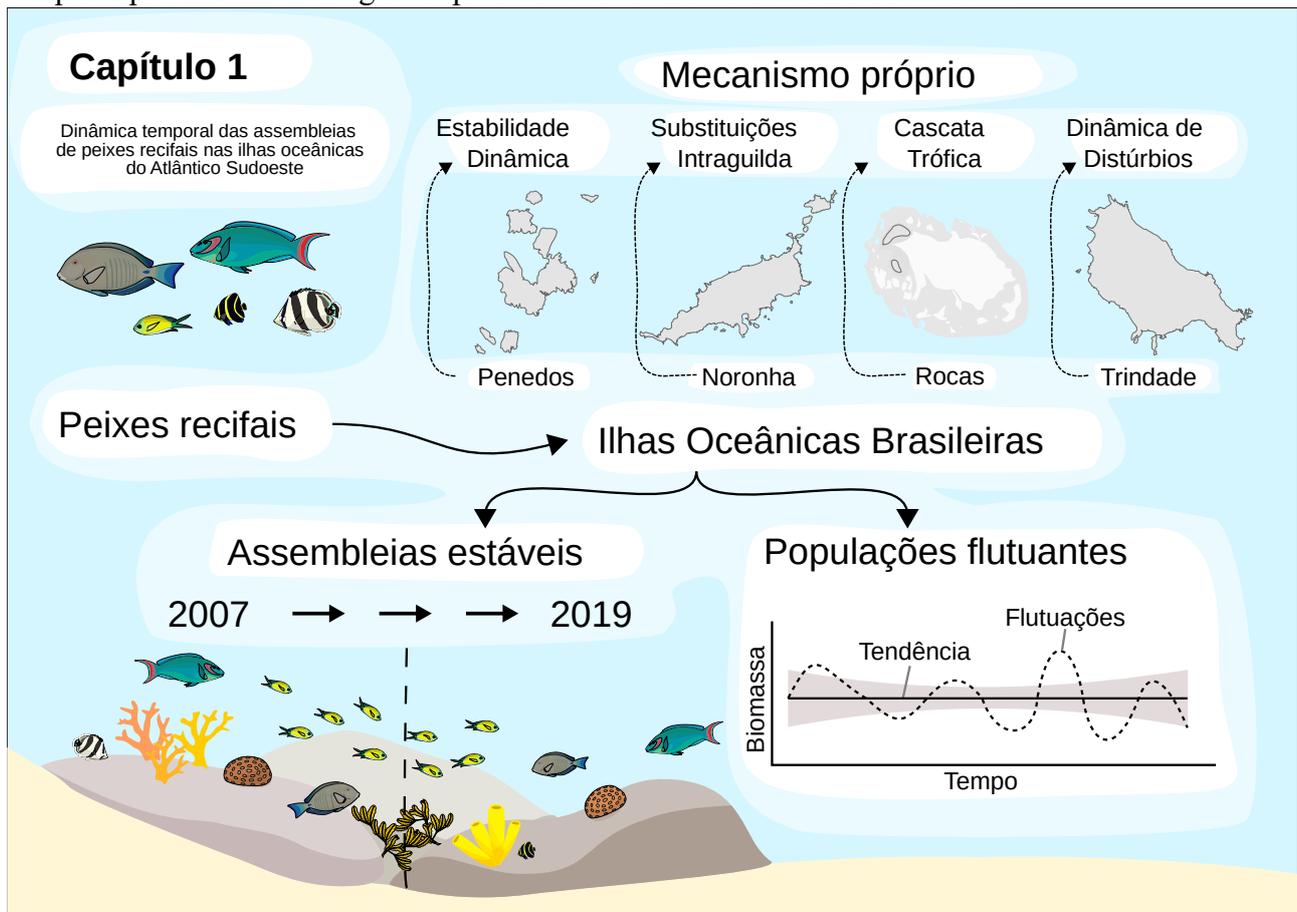
Composition



Supporting Figure S3. Graphical residual analysis of linear models used to test trade-offs between video number and length for detecting richness and composition.

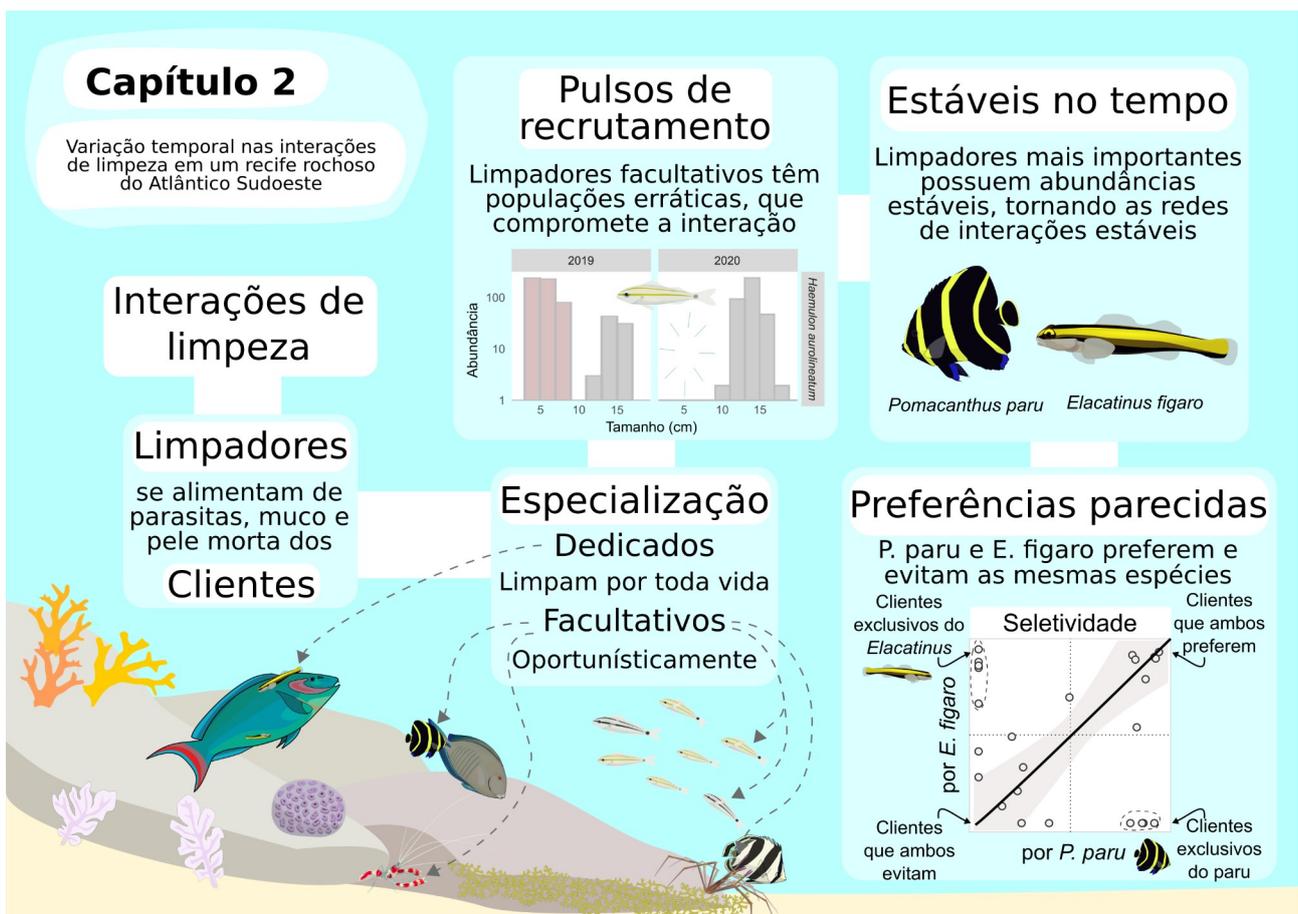
Conclusão geral

1925 Tendo como objetivo detalhar a dinâmica temporal, no capítulo 1 eu descrevi o histórico de
mudanças dos peixes recifais nas ilhas oceânicas brasileiras. Como resultado principal, encontrei
que essas comunidades mudaram constantemente na última década. No entanto, a maioria dessas
1930 mudanças não foram direcionais, mas sim flutuações específicas de cada espécie, o que sugere que
as comunidades estão estáveis. Cada ilha possuiu um histórico próprio de mudanças que sugere a
atuação de um processo ecológico distinto (Figura 1). A biomassa dos peixes recifais de São Pedro e
São Paulo flutuou bastante no tempo, mas sem apresentar mudanças significativas na composição
de espécies, indicando uma estabilidade dinâmica. Já em Fernando de Noronha, a biomassa dos
grupos tróficos permaneceu constante, mas a biomassa das espécies individuais variou
consideravelmente, mostrando indícios de competição intragrupo. As flutuações na biomassa dos
1935 grupos no Atol das Rocas são bastante erráticas, mas a ordem dos picos na biomassa é relacionada
ao tamanho das espécies, o que sugere um efeito de cascata trófica. Por fim, os peixes recifais de
Trindade passaram por dois eventos de mortalidade em massa, em 2013 e 2016, com uma dinâmica
temporal potencialmente regulada por distúrbios de causa ainda desconhecida.



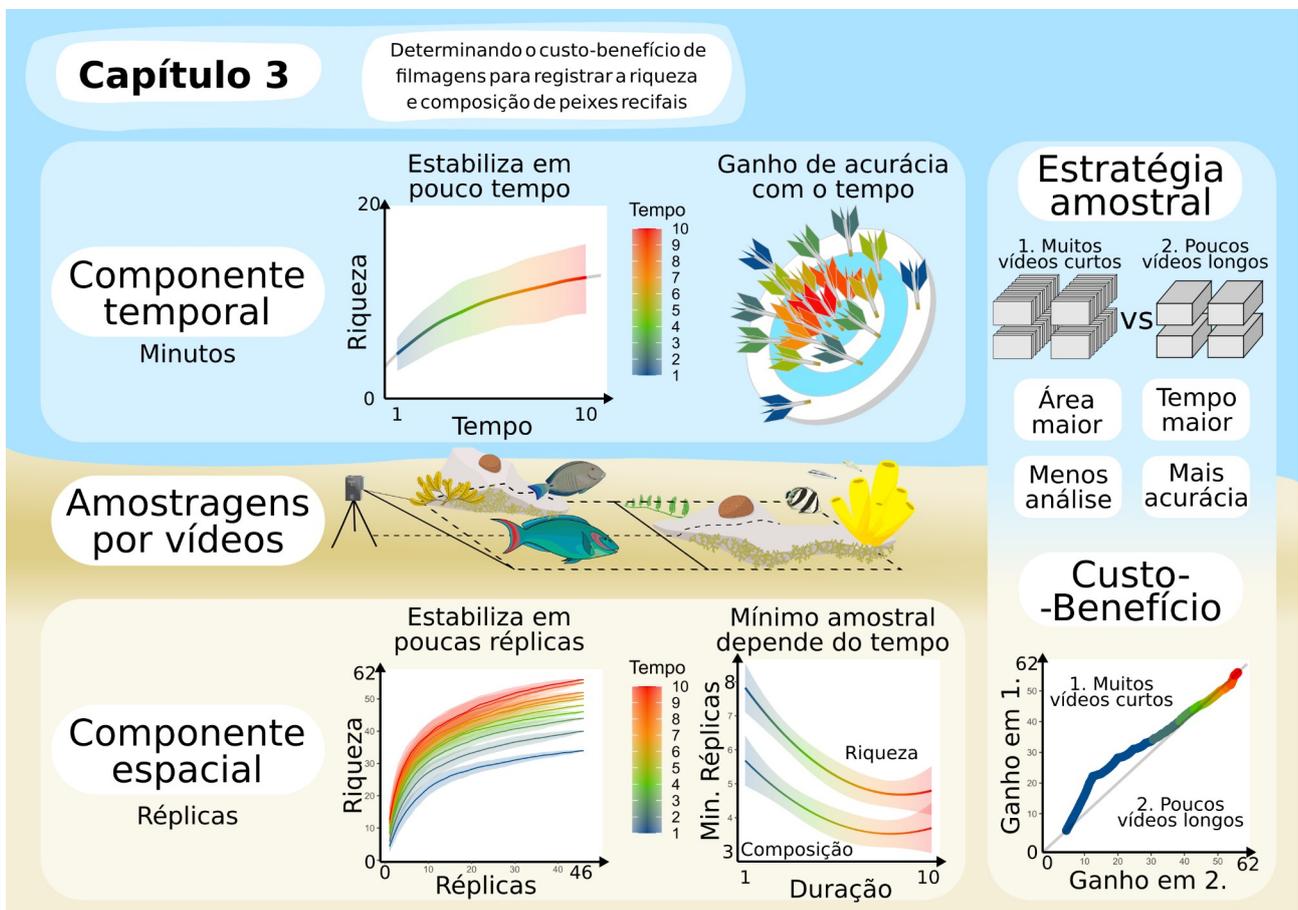
1940 Figura 1. Resumo gráfico do primeiro capítulo. Explicações estão disponíveis ao longo do texto principal (vide parágrafo anterior).

1945 Nosso objetivo no capítulo 2 foi descrever as interações de limpeza em uma Baía de Arraial do Cabo, detalhando como a rede mudou entre duas amostragens espaçadas por um ano. Encontramos que as redes de limpeza em Arraial permaneceram relativamente constantes de 2019 para 2020. Os limpadores com maior variabilidade foram hemulídeos juvenis, que passaram de abundantes em um ano para praticamente ausentes no ano seguinte. Isso reduziu sua importância na rede de limpeza ao diminuir a quantidade de interações observadas, que passou de um terço do total a apenas uma. No entanto, por interagir somente com uma espécie (*Pseudupeneus maculatus*), a interrupção da limpeza por hemulídeos afetou pouco a rede de interações. Grande parte disso se deve à atividade de limpeza de *Elacatinus figaro* e *Pomacanthus paru* ter permanecido constante, mostrando que as redes são estáveis desde que as espécies centrais não sejam afetadas (Figura 2). Por fim, detectamos uma ligeira partição na preferência de clientes dessas espécies, onde *E. figaro* atendeu mais predadores potenciais e *P. paru* interagiu com mais espécies associadas a bancos de areias. Mesmo assim, ambas as espécies preferem e evitam os mesmos clientes, compartilhando a maior parte das espécies atendidas.



1955 Figura 2. Resumo gráfico do segundo capítulo. Explicações estão disponíveis ao longo do texto principal (vide parágrafo anterior).

No capítulo 3, tivemos como objetivo encontrar qual o mínimo amostral pra registrar a riqueza local e a composição de peixes, buscando determinar qual a melhor estratégia de amostragem. Vimos que cerca de 5 vídeos de 5 minutos são suficientes para descrever a riqueza local de peixes, com um mínimo de 5 vídeos de 3 minutos para descrever a composição de espécies (via similaridade de presenças e ausências). Existe uma relação negativa entre tempo e número de vídeos, de modo que vídeos mais curtos precisam de mais réplicas para detectar um mesmo número de espécies que vídeos mais longos detectariam. Porém, essa relação não é linear, de modo que, mesmo usando mais réplicas, os vídeos mais curtos podem ser mais eficientes em termos de tempo total de análise. Por exemplo, 10 vídeos de 10 minutos (1h e 40min) detectaram 37 espécies, enquanto 10 vídeos de 5 minutos (50 min) detectaram 34 espécies. O mesmo número de vídeos de 5 e 10 minutos registram uma riqueza parecida, mas vídeos de 5 min usaram metade do tempo total de análise dos vídeos de 10 min (50 contra 100 min, respectivamente). Isso sugere que analisar vários vídeos de poucos minutos é uma estratégia mais eficiente para detectar mais espécies em menos tempo de análise, provavelmente por cobrir uma área maior (Figura 3). A comparação de estratégias de amostragens reafirma isso ao mostrar que mais espécies são detectadas nos primeiros minutos de cada vídeo, reafirmando que vários vídeos curtos são mais eficientes em registrar a riqueza local que alguns vídeos mais longos.



1975 Figura 3. Resumo gráfico do terceiro capítulo. Explicações estão disponíveis ao longo do texto principal (vide parágrafo anterior).

1980 Cada capítulo explorou uma faceta diferente de como o tempo pode afetar as inferências ecológicas em nível de comunidades. Seja na escala de amostragem, redes de interações ou estrutura de comunidades, ter uma perspectiva temporal possibilitou um entendimento mais profundo sobre os padrões observados (Figura 4). Nesses 3 casos, a perspectiva temporal trouxe avanços que dificilmente poderiam ser observados fora da esfera temporal. Assim, espero nesta dissertação ter demonstrado como abordar o tempo pode enriquecer as conclusões de um estudo, além de estimular futuros pesquisadores a se estender no tempo para explicar os padrões observados.



1985 Figura 4. Esquema resumindo o conteúdo dos três capítulos. Todos os capítulos foram baseados em aplicar perspectivas temporais em temáticas comuns na ecologia de comunidades e cada abordagem contou com uma escala de tempo diferente que melhor se adequou a cada sistema.

“E no final, assim calado, eu sei que
vou ser coroado rei de mim”.

De onde vem a calma,
Los Hermanos, 2003