UNIVERSIDADE FEDERAL DE SANTA CATARINA
CAMPUS REITOR JOÃO DAVID FERREIRA LIMA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

LUCAS NUNES TEIXEIRA

ECOLOGIA TRÓFICA DE PEIXES RECIFAIS COMO CONECTORA ENTRE DIFERENTES ESCALAS ECOLÓGICAS

Florianópolis
2020

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

Orientador: Prof. Sergio R. Floeter, Dr.

Florianópolis
2020

Ficha de identificação da obra elaborada pelo autor,
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Teixeira, Lucas Nunes
Ecologia trófica de peixes recifais como conectora entre diferentes escalas ecológicas / Lucas Nunes Teixeira ; orientador, Sergio Ricardo Floeter, 2020.
134 p.

Tese (doutorado) - Universidade Federal de Santa Catarina, Centro de Ciências Biológicas, Programa de Pós Graduação em Ecologia, Florianópolis, 2020.

Inclui referências.

1. Ecologia. 2. Ecologia trófica. 3. Peixes recifais. 4. Dieta. I. Floeter, Sergio Ricardo . II. Universidade Federal de Santa Catarina. Programa de Pós-Graduação em Ecologia. III. Título.

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O presente trabalho em nível de doutorado foi avaliado e aprovado por banca examinadora composta pelos seguintes membros:

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Certificamos que esta é a **versão original e final** do trabalho de conclusão que foi julgado adequado para obtenção do título de doutor em Ecologia.

Documento assinado digitalmente
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CPF: 844.565.237-00

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CPF: 883.819.517-04

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Florianópolis, 2020.

AGRADECIMENTOS

Agradeço a minha família pelo apoio e carinho durante os 10 longos anos dentro da academia. Agradeço ao meu orientador pelas oportunidades, apoios e conselhos profissionais e pessoais valorosos. Agradeço a todos os meus amigos por todo apoio, carinho e diversão que tivemos juntos durante todos esses anos. Agradeço aos meus co-autores, que me auxiliaram no desenvolvimetno de artigos que constituem essa tese. Agradeço aos professores e revisores que ajudaram de diversas formas a melhorar os capítulos dessa tese. Agradeço, também, a todas pessoas que estiveram envolvidas de alguma forma nessa tese, seja pela ajuda na coleta de dados, conselhos ou ideias. Agradeço a CAPES e ao Programa de Pós-Graduação em Ecologia pela bolsa de estudos que me permitiu permanecer na academia e, assim como tantos outros estudantes, me permitiu fazer ciência no Brasil. Agradeço também a todos os projetos e orgãos que financiaram os artigos que compõe essa tese.

"...Try not. Do or do not. There is no try."

Master Yoda

RESUMO

A ecologia trófica pode ser definida como o estudo das relações alimentares que acarretam a troca de energia e nutrientes entre diferentes organismos. Nessa tese eu proponho utilizar a ecologia trófica como forma de integrar diferentes subdivisões de conhecimento da ecologia. Historicamente, a Ecologia adota uma visão reducionista para estudar as relações entre os organismos e o ambiente em que vivem, porém, nas últimas décadas vem se intensificando estudos que utilizam uma visão mais holística para entender essas relações. Essa tese é composta por três capítulos, nos quais eu utilizo a ecologia trófica de duas famílias de peixes recifais com objetivo de demonstrar a importância de ambas as visões para a ciência. No primeiro capítulo eu estudei a ecologia trófica e distribuição vertical de uma espécie endêmica de um dos menores e mais isolados arquipélagos do oceano Atlântico. No segundo capítulo, eu estudei a co-ocorrência de peixes-borboleta em diferentes ambientes recifais do mundo, focado em como características tróficas e evolutivas podem influenciar na co-ocorrência das espécies em um habitat. No terceiro capítulo, estudei como temperatura da água, tamanho corporal individual e dieta influenciam a taxa de consumo de peixes recifais criptobênticos. Através desses três capítulos eu demonstro como uma abordagem mais completa, ou seja, tanto reducionista quanto holística, pode ser utilizada para melhor compreender padrões ecológicos tanto na escala local quanto macroecológica.

Palavras-chave: Blenniidae. Chaetodontidae. Ecologia alimentar. Evolução. Metabolismo. Oceano Atlântico.

ABSTRACT

Trophic ecology can be defined as the study of food relationships causing the exchange of energy and nutrients between different organisms. In my thesis, I propose to use trophic ecology as a way to integrate different ecological subdivisions. Historically, Ecology adopts a reductionist view to study the relationships between organisms and the environment in which they live, however, in the last decade, scientists have intensified the use of a holistic way-of-view to understand these relations. This thesis consists of three chapters, in which I use the trophic ecology of two reef fish families to demonstrate the importance of both visions for science. In the first chapter, I studied the trophic ecology and vertical distribution of an endemic species from one of the smallest and most isolated archipelagos in the Atlantic Ocean. In the second chapter, I studied the co-occurrence of butterflyfishes in different reef environments around the world, focusing on how trophic characteristics and species relatedness can influence the co-occurrence of species in the habitat scale. In the third chapter, I studied how water temperature, individual body size, and diet influence the consumption rate of cryptobenthic reef fishes. Through these three chapters, I demonstrate how a comprehensive approach, including both holistic and reductionist points-of-view, can be used to better understand ecological patterns at local and macroecological scales.

Keywords: Atlantic Ocean. Blenniidae. Chaetodontidae. Evolution. Feeding ecology. Metabolism.

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INTRODUÇÃO GERAL

Definição da ecologia trófica

A ecologia pode ser definida como o estudo das relações entre os organismos e o ambiente em que vivem (BEGON et al., 2005). Essas relações ocorrem em diferentes escalas espaciais e temporais, sendo a ecologia historicamente dividida em diferentes níveis de organização que caracterizam os níveis de estudo (e.g. indivíduos, populações, comunidades). Essa divisão da ecologia é motivada pela visão reducionista, adotada pela ciência a partir do século XVI, que tem como estratégia fragmentar o conhecimento para entender o "todo" através do estudo de cada parte (CARNEIRO; CARNEIRO, 1996). Cada uma desses níveis trabalha com perguntas e hipóteses específicas, o que facilita estudos isolados, porém, torna escassos trabalhos que mesclam ou testam hipóteses que se aplicam a dois ou mais níveis de organização.

Apesar dessa compartimentalização, algo comum a todos os níveis é o estudo da alimentação dos organismos, ou seja, sua ecologia trófica. Por exemplo, ecólogos que trabalham a nível de indivíduo testam variação individual no consumo; ecólogos populacionais investigam a distribuição das populações de uma espécie frente ao seu recurso alimentar; ecólogos que trabalham com comunidades verificam o efeito do predador na população de presas. Assim, a ecologia trófica pode ser definida como o estudo das relações alimentares que acarretam a troca de energia e nutrientes entre diferentes organismos (GERKING, 1994; GASALLA; SOARES, 2001; GARVEY; WHILLES, 2016). A palavra "trófico" vem do termo *trophe*, ou *trophus*, cujo significado remete a nutrição. No inglês a palavra *trophy* deriva de caçar ou lutar, o que remete à natureza da predação (i.e. tirar à força a nutrição/comida de outro organismo; GARVEY; WHILLES, 2016). Atualmente, o termo "grupo trófico" é utilizado como forma de agrupar determinados organismos que possuem as mesmas demandas energéticas e nutricionais (GARVEY; WHILLES, 2016).

Historicamente, o termo "ecologia trófica" é mais utilizado por cientistas que estudam a fisiologia de organismos, com particular interesse em incluir o organismo em um contexto ecossistêmico (GARVEY; WHILLES, 2016). Para isso, estuda-se como variáveis bióticas e abióticas influenciam o consumo dos organismos (GARVEY; WHILLES, 2016). Dessa forma, esses estudos desempenham um papel fundamental para entender como a fauna e a flora influenciam no fluxo de energia em comunidades biológicas (GERKING, 1994; GASALLA; SOARES, 2001; GARVEY; WHILLES, 2016). A ecologia trófica está presente em todos os níveis da ecologia, visto que ela pode ser utilizada para testar hipóteses que integram esses diferentes níveis fornecendo uma visão ampla (i.e. reducionista e holística) para a ecologia.

Histórico da ecologia trófica

Não podemos definir ao certo quando foram realizados os primeiros registros das relações tróficas pelos cientistas. Porém, o que sabemos é que estudos das relações alimentares são mais antigos que a própria ecologia. Possivelmente, as pinturas rupestres, feitas há milênios pelo ser humano, foram os primeiros registros dessas relações alimentares entre organismos (**Fig. 1**). Essas pinturas retratam—dentre muitos outros momentos do cotidiano do humano pré-histórico—os comportamentos de caça e alimentação de animais. Certamente, essas observações das relações alimentares no passado, possibilitaram o desenvolvimento da agricultura e domesticação de animais, o que proporcionou o desenvolvimento da sociedade moderna.

Figura 1 – Pinturas rupestres encontrada em A) Tassili n'Ajjer Argélia ilustrando um homem juntamente com cachorros caçando um outro animal; e B) humanos caçando com arco e flecha — Piauí, Brasil (Fonte: desconhecido).

Provavelmente, os primeiros registros da ecologia trófica em notações científicas foram feitos por naturalistas entre os séculos XVII e XVIII—como Carolus Linnaeus—ao descreverem e classificarem as espécies em seus estudos. Esses registros, embora apenas trouxessem uma informação qualitativa, auxiliaram Charles Elton, em 1927, a formalizar o que hoje conhecemos como "ecologia trófica". Através do desenvolvimento dos conceitos de pirâmide e teia trófica, Elton foi o primeiro pesquisador a trabalhar com interações entre organismos, tendo uma visão ecossistêmica (GARVEY; WHILLES, 2016).

Em 1939, Viktor Ivlev conecta a escolha do alimento com o fluxo energético em comunidade de peixes. Seu objetivo foi desenvolver e testar meios de quantificar o fluxo de energia e como essa energia influenciava no crescimento e reprodução da população do predador, ou seja, uma visão reducionista (GARVEY; WHILLES, 2016). Esse estudo influenciou o estudo de Raymond Lindeman (1942) —publicado postumamente— quando elaborou a lei da dinâmica trófica, que diz respeito à uma atenuação progressiva da energia passando dos produtores e consumidores primários até chegar aos predadores de topo (i.e. visão holística, GERKING, 1994). Em contrapartida, Hairston et al., em 1960, elaboraram um mecanismo baseado na hipótese do "mundo verde", que determina que a abundância em cada nível trófico seja controlada, direta ou indiretamente, pelos consumidores no topo das cadeias alimentares (também seguindo uma visão holística). Atualmente, graças aos estudos de Lindeman (1942) e Hairston et al. (1960), temos o entendimento que o fluxo de energia em cadeias alimentares naturais é diretamente influenciado pelos dois mecanismos tróficos, chamados "*Bottom-up*" e "*Top-down*" (POLIS; STRONG, 1996).

Certamente, Lindeman e Ivlev foram essenciais para o desenvolvimento dos estudos de ecologia trófica como conhecemos atualmente. Através de suas diferentes visões (i.e. Lindeman defendia uma visão holística enquanto Ivlev uma visão reducionista), esses cientistas influenciaram a forma de se estudar ecologia trófica de pesquisadores subsequentes. Por exemplo, influenciaram George Hutchinson (1957), a propor que o alimento é uma das n-dimensões do nicho ecológico de uma espécie. Também possibilitaram que MacArthur e Pianka (1966), elaborassem a teoria do forrageio ótimo para entender a obtenção de alimento levando em consideração a maximização do ganho de energia (GERKING, 1994). Além disso, influenciaram Eugene Odum (1969), na sua abordagem holística da ecologia trófica e foco na transformação de energia e matéria em um sistema (GASALLA; SOARES, 2001; GARVEY; WHILLES, 2016).

A partir da década de 80, com o surgimento da hipótese do efeito cascata trófica —uma visão holística de pensar na qual uma pequena mudança nos predadores de topo leva à uma reação em cadeia afetando os níveis inferiores de toda a cadeia trófica ocasionando mudanças ecossistêmicas— e consequente tentativa de integrar as visões holística e reducionista, houve uma demanda em direcionar a ecologia trófica para uma abordagem quantitativa, trabalhando a relação entre matéria e energia. Nesse contexto, a teoria metabólica surge para entendermos a relação entre o consumo e as demandas energéticas dos organismos seguindo as leis da termodinâmica (BROWN et al., 2004; GARVEY; WHILLES, 2016). Essa teoria prevê que a progressão de energia entre os níveis de uma cadeia trófica deve seguir uma função da relação entre tamanho corporal, temperatura e taxa metabólica. Os organismos retiram o alimento do ambiente, convertem e acumulam esse material orgânico para manter seu metabolismo, ou seja, assegurar as funções vitais, crescer e se reproduzir.

A escolha do alimento por parte de um predador envolve diversos filtros ambientais e morfológicos (FERRY-GRAHAM et al., 2002, **Fig. 2**). Inicialmente, o predador deve encontrar, detectar e reconhecer outro organismo como alimento. Para isso, o predador precisa compartilhar a mesma escala temporal e espacial com sua presa. Após isso, o predador precisa ponderar os custos energéticos e tomar a decisão de atacar ou recuar (**Fig. 2**). Caso decida atacar, o predador precisa ter a capacidade morfológica de capturar sua presa (**Fig. 2**). Os modelos de forrageio ótimo são relacionados a esses filtros, uma vez que eles influenciam diretamente na maximização do ganho de energia por parte do predador (GERKING, 1994). Também, determinam a eficiência energética com que o alimento será transferido para os níveis superiores em uma cadeia trófica (GARVEY; WHILLES, 2016).

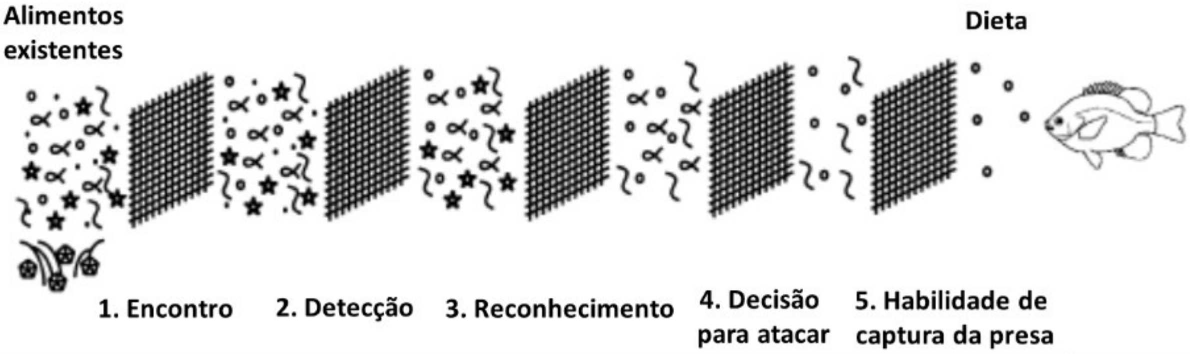


Figura 2 - Filtros ambientais e biológicos que influenciam na dieta de uma espécie (adaptado de FERRY-GRAHAM et al., 2002).

Métodos para estudar ecologia trófica

Diferentes métodos foram, e ainda são utilizados para se estudar a ecologia trófica dos organismos heterotróficos ao longo da história. A escolha do melhor método a ser empregado deve ser ponderada pelas características biológicas dos organismos que se pretende estudar, assim como características ambientais que podem influenciar nas amostragens. Por exemplo, amostragens em ambientes recifais devem considerar, além da biologia do organismo a ser estudado, o tempo limitado de amostragem inerente a mergulhos com cilindro de ar; em uma floresta tropical a acessibilidade e visibilidade também podem ser fatores impeditivos para amostragens de certos organismos.

Para qualificar e quantificar "onde" o organismo heterotrófico forrageia, são utilizados métodos como análise da atividade alimentar e substrato preferencial de forrageio. Esses métodos são amplamente empregados para analisar a ecologia trófica das espécies devido a facilidade em se obter dados, uma vez que não envolve uma triagem de material em laboratório. Permitem, por exemplo, fazer uma relação direta entre disponibilidade do recurso no ambiente e a pressão de predação; também permitem medir a taxa de consumo de um organismo. Porém, vale ressaltar que essas análises inferem apenas o substrato no qual as espécies forrageiam, não podendo ser determinado o que é ingerido (KENT; SHERRY, 2020). Para qualificar e quantificar "como" um organismo heterotrófico obtém seu alimento, é analisado seu comportamento alimentar. São avaliados os aspectos morfológicos e fisiológicos que determinam e possibilitam a escolha de um alimento (LEHNER, 1996). Esse comportamento é altamente influenciado pelos filtros ecológicos descritos acima.

Para qualificar e quantificar "o que" é ingerido por um organismo heterotrófico, são utilizados métodos como: análise de conteúdo gástrico (estômago e/ou intestino), sequenciamento genético através de Metabarcoding e exame de fezes. A análise de conteúdo gástrico, apesar de laboriosa, é amplamente utilizada devido ao baixo custo monetário e analítico. Essa análise gera bons resultados sobre os recursos alimentares utilizados por uma determinada espécie em um momento prévio a sua captura. Apesar do baixo custo dessa análise, o pesquisador deve levar em consideração o tempo necessário para triar os itens alimentares e identificá-los. Além disso, o processo digestivo do predador poderá dificultar a identificação taxonômica dos itens alimentares. A análise de Metabarcoding é uma ferramenta utilizada atualmente, que apresenta facilidade analítica, em comparação à análise de conteúdo gástrico, porém com um custo material e monetário elevado. Através dessa análise, é possível uma melhor identificação dos itens alimentares presentes na dieta da espécie, já que é utilizado sequenciamento genético (LERAY et al., 2015). O exame de fezes também é comumente utilizado por pesquisadores que estudam organismos que possuem uma vida longa, ou são pouco abundantes e bem dispersos em uma área (MAEHR et al., 1990).

No entanto, estes três métodos revelam apenas os recursos consumidos pela espécie no momento anterior ao da amostragem. Pouca informação pode ser resgatada dessas análises para responder o quanto desse alimento ingerido está, de fato, sendo assimilado pelo animal em uma escala temporal. Nesse contexto, as análises de isótopos estáveis (principalmente Carbono e Nitrogênio), aminoácidos essenciais e ácidos graxos surgem como ferramentas para determinar a assimilação do item alimentar por parte dos predadores (DALSGAARD et al., 2003; LAYMAN et al., 2012). Diferenças nas razões isotópicas de carbono e nitrogênio, por exemplo, entre consumidores e níveis tróficos inferiores proveem informação sobre o fluxo de energia, fonte de nutrientes e relações tróficas (LAYMAN et al., 2012). A variação de Carbono estável ($d^{13}C$) no predador revela quais são os itens alimentares consumidos, enquanto a variação de nitrogênio ($d^{15}N$) revela a posição trófica de um organismo na cadeia alimentar (LAYMAN et al., 2012). Dessa forma, essa ferramenta é útil, e vem sendo cada vez mais utilizada para responder perguntas relacionadas ao fluxo de energia em ecossistemas, à absorção de nutrientes de fontes de alimento diversos e à conectividade populacional, indicando diferentes habitats onde os organismos podem se alimentar (POST, 2002; PEREIRA; BENEDITO, 2007; LAYMAN et al., 2012). Contudo, análises de isótopos, além de apresentarem custos monetários e analíticos elevados, também falham em determinar precisamente e quantitativamente o item alimentar consumido.

Taxas de consumo em um mundo em mudança

Como descrito anteriormente, estudar o consumo de animais no ambiente natural pode ser desafiador. Para muitas espécies, os indivíduos precisam ser seguidos exaustivamente pelo pesquisador, até ter um número amostral representativo, e posteriormente sacrificados para determinar seu conteúdo estomacal (FERREIRA et al., 1998; GARVEY; WHILES, 2016). A contagem de mordidas desempenhadas no substrato é notoriamente um dos métodos mais utilizados para se medir indiretamente a taxa de consumo de peixes recifais (BARNECHE et al., 2009). Durante as amostragens, além dos dados de mordidas, o pesquisador pode obter dados abióticos e dados espécie-específicos que podem influenciar a taxa de mordidas. Esses dados são essenciais para estudar o consumo alimentar em um nível ecossistêmico. A temperatura do ambiente, por exemplo, é um fator determinante para animais ectotérmicos (BROWN et al., 2004; GARVEY; WHILLES, 2016). Com base na teoria metabólica, é esperado que animais tenham uma taxa de consumo maior conforme aumenta a temperatura do ambiente em que vivem. Também, desconsiderando variações ontogenéticas, a teoria metabólica prediz que indivíduos que possuem uma massa corporal maior tenham uma taxa de consumo proporcionalmente menor (PAWAR et al., 2012). As relações entre o aumento da temperatura dos oceanos, o metabolismo dos organismos e suas implicações para funções e serviços ecossistêmicos são de fundamental interesse para a ciência (BARNECHE et al., 2018). Dessa forma, as mudanças climáticas do antropoceno poderão alterar a taxa de consume dos peixes recifais, com possíveis consequências diretas para o fluxo de energia nas cadeias tróficas.

Peixes recifais como modelos de estudo

No ambiente marinho, recifes são ecossistemas heterogêneos e complexos que podem ser considerados os mais produtivos e com maior diversidade de organismo do planeta (REAKA-KUDLA, 1997). Há séculos esses ambientes oferecem serviços ecossistêmicos às populações humanas, que exploram suas águas através de atividades como o extrativismo e, mais recentemente, o turismo (REAKA-KUDLA, 1997). Consequentemente, em diferentes locais do globo, os recifes estão sobre constante exploração/pressão predatória de seus recursos (MORBERG; FOLKE, 1999; MARTÍNEZ et al., 2007). Essa exploração causa problemas associados à perda da biodiversidade e ao desequilíbrio nas cadeias tróficas (JACKSON et al., 2001; ESTES et al., 2011). Dentre os milhares de táxons que compõe os recifes, possivelmente um dos mais afetados pela exploração predatória seja o grupo dos peixes.

Esse grupo apresenta elevada riqueza de espécies e está presente em todos os ambientes recifais do mundo. Estão, direta ou indiretamente, envolvidos em interações com todos os níveis da cadeia trófica recifal, atuando como consumidores em todos os níveis (KOTRSCHAL 1988; GERKING 1994). Isso é possível devido a processos evolutivos que conferiram aos peixes uma variedade de características morfológicas e comportamentais que os permitem explorar diversos ambientes e recursos alimentares (**Fig. 3**; KOTRSCHAL 1988; GERKING, 1994; WAINWRIGHT; BELLWOOD, 2002). Dessa forma, os peixes influenciam diretamente na estruturação das comunidades biológicas visto que podem controlar a abundância de suas presas através de uma pressão predatória (BELLWOOD; CHOAT, 1990; STENECK et al., 1991; BURKEPILE; HAY, 2006). Devido ao fato de os peixes serem essenciais em cadeias tróficas recifais, é essencial estudar sua ecologia trófica para entender a importância dessas relações para o funcionamento desse ambiente.

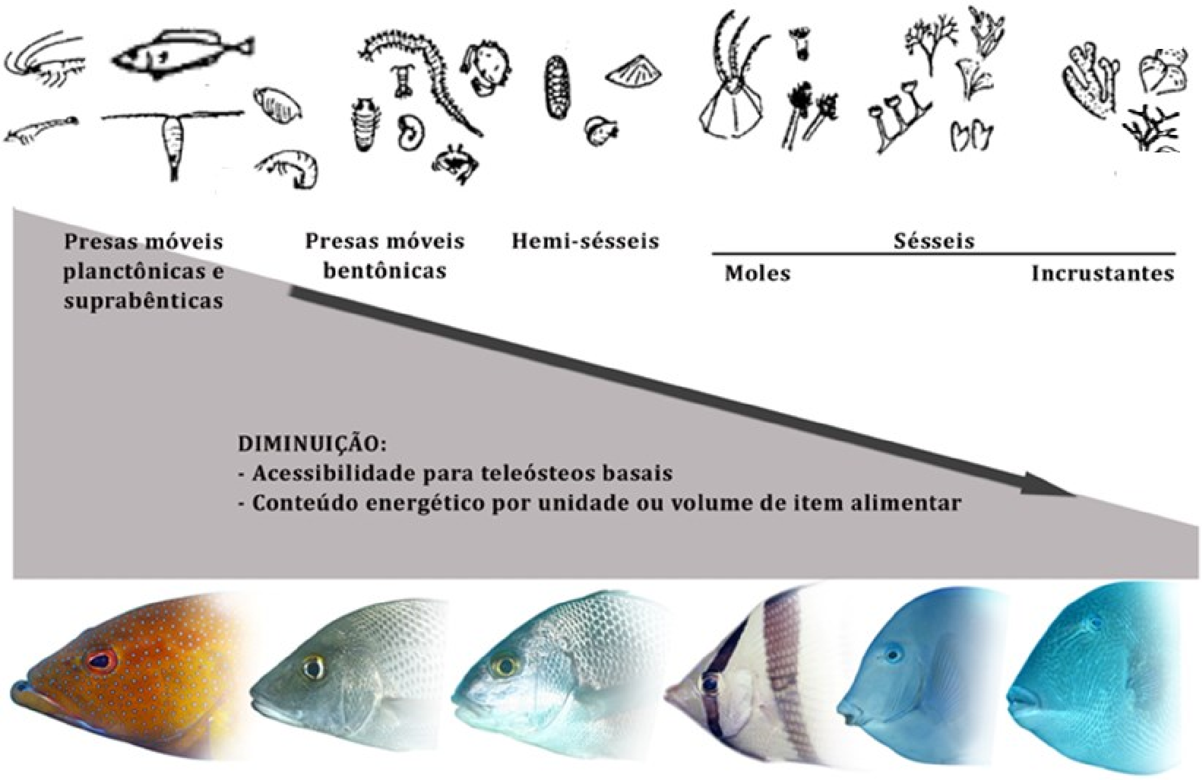


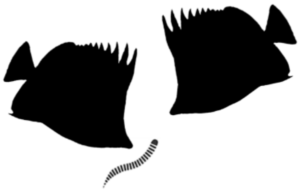
Figura 3 – Adaptações morfológicas da boca e corpo dos peixes recifais, em uma escala evolutiva, que possibilitam explorar diferentes recursos alimentares. O conteúdo energético por volume do item alimentar, diminui conforme aumenta a quantidade de matéria de difícil digestão, como conchas e paredes celulares (adaptado de KOTRSCHAL, 1988).

Duas famílias de peixes recifais se destacam devido a intrínseca relação das espécies que as compõe com o ambiente recifal. A família Chaetodontidae é composta por aproximadamente 134 espécies de peixes recifais, popularmente conhecidos como Peixes-borboleta (FROESE; PAULY, 2020) e ocorre em ambientes recifais tropicais e subtropicais tendo sua evolução estritamente relacionado com esses ambientes (BELLWOOD et al., 2010). Também é uma das famílias de peixes recifais mais estudadas em termos evolutivos e ecológicos (PRATCHETT et al., 2013). Nesses estudos ecológicos, as espécies são usualmente divididas em quatro níveis tróficos: comedores de coral da ordem Scleractinia, comedores de cnidários diversos, comedores de outros invertebrados e generalistas (PRATCHETT, 2005).

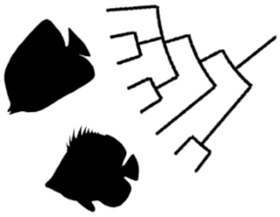
A família Blenniidae está presente em todos os ambientes recifais do mundo, sendo composta majoritariamente por peixes com tamanho corporal pequeno que vivem associados ao substrato recifal (peixes criptobênticos; BRANDL et al., 2018). É uma das famílias mais diversas de peixes recifais contando com aproximadamente 402 espécies (FROESE; PAULY, 2020). Ocupam diversos níveis tróficos de consumidores (i.e. herbívoros, detritívoros e invertívoros), sendo importantes na transferência de energia de níveis basais para os predadores superiores em ambientes recifais (BRANDL et al., 2018). Nessa família, o gênero *Ophioblennius* contém seis espécies das quais cinco ocorrem no oceano Atlântico, sendo cada espécie endêmica a uma província biogeográfica marinha (MUSS, et al. 2001; LASTRUCCI, et al. 2018).

Estrutura da tese

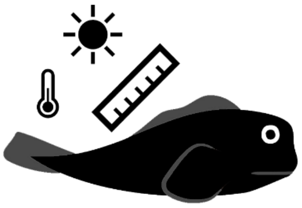
Nesta tese, eu tenho como objetivos gerais: utilizar a ecologia trófica para integrar os diferentes níveis de organização da ecologia (**Fig. 4**); e demonstrar que uma visão ambígua (reducionista e holística) é importante para entender o consumo alimentar das espécies. Para isso, em três capítulos, meus coautores e eu abordamos diferentes hipóteses e objetivos utilizando o consumo alimentar das duas famílias de peixes recifais, descritas acima, como tema central (**Fig. 4**).



O primeiro capítulo é intitulado "***Ecology of Prognathodes obliquus, a butterflyfish endemic to mesophotic ecosystems of St. Peter and St. Paul's Archipelago***". Este peixe-recifal é endêmico do Arquipélago de São Pedro e São Paulo - Brasil sendo uma das espécies mais abundantes na zona mesofótica desse local. A espécie pertence a um dos gêneros menos estudados entre os peixes recifais, possivelmente devido às dificuldades metodológicas advindas do estudo de recifes na zona mesofótica do oceano. Por explorar o consumo e comportamento dos indivíduos, juntamente com parâmetros populacionais como abundância e distribuição vertical, este capítulo é uma interface, conectando a ecologia de indivíduos a populações (**Fig. 4**).



O segundo capítulo é intitulado "***The influence of species abundance, diet and phylogenetic affinity on the co-occurrence of butterflyfishes***". Nesse capítulo utilizamos a história evolutiva e característica tróficas das espécies para entender os padrões globais de co-ocorrência de peixes-borboleta. Para entender esses padrões, propomos duas perguntas: 1) a proximidade filogenética juntamente com a dieta das espécies explica a co-ocorrência de peixes-borboleta numa escala de habitat? Como hipótese, acreditamos que a co-ocorrência e a distância filogenética são positivamente relacionadas. Além disso, espécies com dieta generalistas co-ocorrem mais frequentemente do que espécies especialistas; 2) a dieta das espécies-irmãs de peixes-borboleta do Atlântico e Leste do Pacífico são filogeneticamente conservadas? Como hipótese, acreditamos que espécies distantes filogeneticamente possuirão dietas diferentes devido à conservação de nicho filogenético. Estas hipóteses permeiam entre a ecologia de populações e comunidades, visto que buscam entender a influência de características tróficas e populacionais das espécies na co-ocorrência de espécies em diferentes localidades (**Fig. 4**).



O terceiro capítulo é intitulado "***Size scalling, temperature dependence, and diet correlates of consumption rates***". Nesse capítulo investigamos como o tamanho corporal, temperatura e ecologia trófica influenciam na taxa de consumo alimentar de peixes recifais criptobentônicos. Como hipótese propomos que a taxa alimentar: 1) será maior conforme o aumento da temperatura da água; 2) diminuirá com o aumento do tamanho corporal individual; e 3) será menor em populações cuja dieta é composta por material animal (i.e. presas com valor proteico comparativamente maior). Este terceiro capítulo conecta os níveis de população e indivíduo com o ecossistema, visto que testa como a taxa alimentar de indivíduos e populações responde a variações abióticas e bióticas (**Fig. 4**).

Figura 4 – Desenho esquemático dos diferentes níveis da Ecologia (retângulos coloridos) e a forma como o consumo (setas pretas) dentro desses níveis pode influenciar o seguinte nível. A ecologia trófica atua conectando os diferentes níveis da ecologia através de testes de hipóteses ecológicas.

CAPÍTULO I

Coral Reefs (2019) 38:955–960

Ecology of *Prognathodes obliquus*, a butterflyfish endemic to mesophotic ecosystems of St. Peter and St. Paul's Archipelago

Lucas T. Nunes, Isadora Cord, Ronaldo B. Francini-Filho, Sérgio N. Stampar, Hudson T. Pinheiro, Luiz A. Rocha, Sergio R. Floeter, Carlos E.L. Ferreira

Endemic to the smallest and most isolated archipelago in the Atlantic Ocean, the butterflyfish *Prognathodes obliquus* inhabits waters bellow 40 meters of depth. Until now little was known about this species' ecology. To investigate that, we used submarines, remote-operated vehicles and rebreather diving to better understand the vertical distribution, foraging habits and diet of this Brazilian species. By analyzing the stomach content we found that this species is a generalist invertivore. We also found the first record of a tube-dwelling anemone for the Saint Paul's Rocks. Although this is a relatively deep-water species in a remote location, we found microplastics in its diet, showing that anthropogenic pressures reach fishes even here.

Photos by: Ronaldo Francini-Filho and Luiz Rocha

DOI: 10.1007/s00338-019-01822-8

Abstract

Chaetodontidae is among the most conspicuous families of fishes in tropical and subtropical coral and rocky reefs. Most ecological studies focus in the genus *Chaetodon*, while *Prognathodes* remains poorly understood. Here we provide the first account on the ecology of *Prognathodes obliquus*, a butterflyfish endemic to St. Peter and St. Paul's Archipelago (SPSPA), Mid-Atlantic Ridge. We studied the depth distribution and foraging behaviour of *P. obliquus* through technical diving, remote-operated vehicles and submarines. Also, we characterized its diet by analysing stomach contents. *Prognathodes obliquus* is mostly found below 40 m, with abundance peaking between 90–120 m and deepest record to date at 155 m. It forages mostly over sediment, epilithic algal matrix and complex bottoms formed by fused polychaete tubes, preying mostly upon polychaetes, crustaceans, hydroids and bryozoans. Branching black corals were rarely consumed and used mostly as refuge. In conclusion, *P. obliquus* is a generalist invertebrate feeder typical of mesophotic ecosystems of SPSPA.

Keywords: Chaetodontidae, Diet, Deep reefs, Microplastics, Mid-Atlantic Ridge, St. Paul's Rocks

Video abstract: www.youtube.com/watch?v=y-bDlM6ogyM

Introduction

Chaetodontidae (butterflyfishes) is an iconic and diverse fish family inhabiting tropical and subtropical reefs. It contains approximately 130 species (Froese and Pauly 2018), most of them living in shallow coral ecosystems (SCEs; 0–30 m depth) and about 10% in the mesophotic coral ecosystems (MCEs; 30–150 m; Pratchett et al. 2014). Because they are easily identifiable to species and are closely associated with reefs (Reese 1975), Chaetodontidae is among the most studied families of reef fishes (Pratchett et al. 2014). However, most knowledge on their ecology is based on the genus *Chaetodon* from shallow tropical reefs of the Indo-Pacific and Caribbean (Pratchett et al. 2014).

Butterflyfishes are usually classified into four major trophic categories: hard-coral feeders, soft-coral feeders, non-coral feeders or generalists (Pratchett 2005). Here we consider "generalist" as those feeding on a variety of sessile and mobile invertebrates, without preference for specific taxonomic preys. In the Atlantic Ocean, ecological investigations were performed for only three species of *Chaetodon* and *Prognathodes aculeatus*, all generalist feeders (e.g. Randall 1967; Birkeland and Neudecker 1981; Liedke et al. 2016; 2018).

The genus *Prognathodes* includes 13 species, seven from the Atlantic Ocean (Copus et al. 2019), including three (*P. brasiliensis*, *P. guyanensis* and *P. obliquus*) present in Brazil. All these latter species preferentially inhabit deep waters, with a few individuals recorded shallower than 15 m, mostly in oceanic islands (Pinheiro et al. 2015) or in subtropical areas affected by upwelling (authors pers. obs.). In Brazil, *P. guyanensis* and *P. obliquus* are associated with lower MCEs (80–150 m) and upper MCEs (150–180 m; Rosa et al. 2016; Francini-Filho et al. 2018), while *P. brasiliensis* is found both on shallow and MCEs (Pinheiro et al. 2015). The trophic ecology of this genus is still poorly studied, with the exception of P. aculeatus in the Caribbean (Randall 1967; Birkeland and Neudecker 1981) and *P. carlhubbsi* in Ecuador (Nalbant 1995). The lack of basic ecological information for most *Prognathodes* species is explained by the inherent logistical challenges of sampling depths >30 m.

Prognathodes obliquus (Lubbock and Edwards 1980) is endemic to the St. Peter and St. Paul's Archipelago (SPSPA), Mid-Atlantic Ridge, Brazil. It is among the most common species in the MCEs (50–90 m) of the SPSPA, being particularly abundant in areas dominated by branching black corals (*Tanacetipathes* spp.) and encrusting sponges (Rosa et al. 2016), with rare sightings in waters <30 m (Luiz et al. 2015). In this study, we characterized for the first time the vertical distribution, foraging behaviour and diet of *P. obliquus*.

Materials and methods

The SPSPA is located in the Mid-Atlantic Ridge, about 1000 km from the NE Brazilian coast (0°55.01'N; 29°20.76'W). Benthic assemblages over rocky reefs of the SPSPA are divided in three depth strata (Magalhães et al. 2015): 1) SCEs (<30 m) dominated by *Palythoa caribaeorum*, *Caulerpa racemosa*, crustose coralline algae and *Bryopsis* spp., 2) upper MCEs (30–50 m) dominated by *Caulerpa* spp., two Scleractinia and algal turfs and 3) lower MCEs (50–90 m) dominated by sponges, black corals, bryozoans and intricate bottoms formed by fused polychaete tubes. Sampling occurred in eight expeditions between 2010 and 2018, using remote-operated vehicles (ROV), closed-circuit rebreathers and submarines (Triton and Deep Rover). All dives occurred during daytime (0900 to 1500 hrs) in depths between 0–600 m and sea temperatures were obtained by diving computers.

The behaviour of 37 haphazardly chosen individuals of *P. obliquus* (Fig. 1A) was video-recorded (footages obtained by divers = 35, footages obtained by ROV = 2). For each individual we recorded a 30s to 1min video, totalling 30 minutes of footage. In each video, the individual recorded was engaging in foraging, but generally alternating with other behaviours, such as sheltering within black-corals and engaging in agonistic interactions. All foraging records were obtained in the upper mesophotic zone (30-60 m). Data from ROV and submarine operations were used for understanding bathymetric distribution of *P. obliquus*. For diet analysis, 19 individuals were collected with hand spear and frozen at the end of the dive to avoid enzymatic digestion of food items. Only adults were collected, as juveniles were never sighted. In the lab, total length was measured and individuals were dissected for obtaining stomach and intestine contents. The intestine total length was measured from the pyloric cecum to the anus. The relative intestine length was obtained as a ratio between intestine and body length (Berumen et al. 2011).

The fullness of each stomach was visually estimated and assigned to one of the following four categories: 0-25%, 25.1–50%, 50.1–75% and 75.1%–100% (Liedke et al. 2018). Stomachs were then dissected in Petri dish under stereomicroscope and all food items were identified to lowest taxonomic level possible. Amorphous organic matter was analysed with an optical microscope to identify diagnostic structures, such as nematocysts and spicules (Liedke et al. 2016). The Digested Organic Matter (DOM) category was assigned when taxonomic identification was not possible. The Mixed Cnidaria category included DOM with cnidocytes from different groups (different forms of holotrichs and microbasic b-mastigophores).

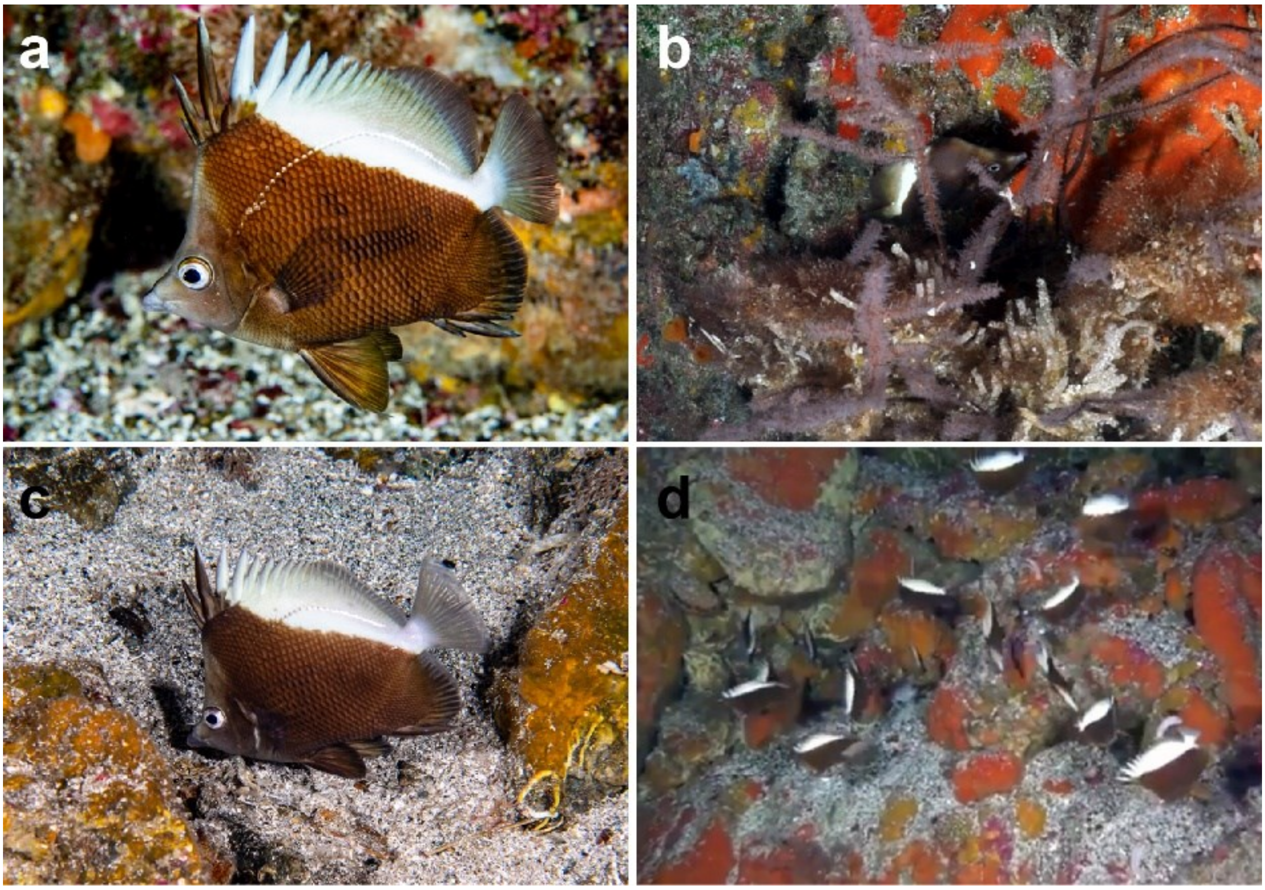


Figure 1 – a) Individual of *Prognathodes obliquus*; b) One individual hidden in the branches of Antipatharia black coral; c) Feeding over sediment in 50 m; d) Aggregation of 15 individuals (photos b by R. Francini-Filho and a, c, d by L.A. Rocha).

Diet was quantified using the frequency of occurrence (%FO; i.e. how often a food item is present in the sampled stomachs) and volumetric index (%V; i.e. summed volume of each item pooled across individuals divided by the total volume of the sampled stomachs; Hynes 1950; Hyslop 1980). The volume of each food item, in each stomach, was measured through a millimetre petri dish where each item was placed between two 1mm thick coverslips and kneaded with a microscope slide, then the number of 1mm^3 grids were counted (Liedke et al. 2016). To determine the importance of each food category we used the Feeding Index equation: $\%IAi = ((\%FOi \cdot \%Vi) / \sum(\%FO \cdot \%V)) \cdot 100$, whereas %FOi and %Vi are the frequency of occurrence and volume of the food category i, respectively (Kawakami and Vazzoler 1980; Liedke et al. 2016).

To evaluate the abundance of *P. obliquus* across depth strata, we performed 31 underwater visual censuses (20 x 2 m transects), 13 transects < 30m depth; six between 30-59m; eight between 60-89; four between 90-120 using rebreathers (dives performed by LAR and HTP). Kruskal-Wallis and post hoc Dunn test were used to test for differences among depth strata. All analyses were performed in R software (R Core Team 2019).

Results and Discussion

Of the 37 individuals recorded in the videos, 13 were sheltering among branches of black coral colonies (Fig. 1B); seven isolated individuals or in pairs were feeding on sediment and epilithic algal matrix (EAM) interspersed with polychaete tubes (Fig. 1C) and 17 were swimming close to the rocks, generally in pairs or in groups up to 15 individuals (Fig. 1D; https://www.youtube.com/watch?v=y-bDlM6ogyM). Despite black corals being abundant in the MCEs, no bites were recorded on them, suggesting that they are used as refuge instead of preferential prey.

The vertical distribution of *P. obliquus* starts with rare occurrences at 30m, but more regular sightings at 40m, with abundance peaking in the lower MCEs (60–120 m; Fig. 2) and maximum depth recorded with submarines at 155 m. This species is thus restricted to mesophotic depths around the SPSPA. A similar distribution pattern was found for the endemic *Prognathodes basabei* from the Hawaiian archipelago, which reaches 200 m of depth and presents a high abundance between 120 and 140 m (Pyle and Chave 1994; Pyle and Kosaki 2016). The vertical distribution of *P. obliquus* coincides with stratification in water temperature, with warmer waters between 0–30 m (26–30 °C), intermediate conditions between 30–60 m (18–26 °C), cold waters between 60–120 m (14–18 °C) and relatively colder waters below 150 m (< 14 °C).

In fact, water temperature is an important determinant of species composition in mesophotic reefs (Simon et al. 2016). Anecdotally, we explored several habitats around ASPSP (i.e. exposed and sheltered, tidal pools, deep reefs) in different seasons, but never observed any juveniles, thus information about recruitment habitat and early life history remains unknown.

The 19 individuals collected for diet analyses had an average total length of 12.92 cm ± 1.87 (mean ± SE). The average relative intestine length was 2.32 ± 0.49, which is characteristic of fishes that eat both animal and plant material. Most of the stomachs were not completely full, but none were empty, which indicates that *P. obliquus* forages during the day, such as other Chaetodontidae species (Reese 1975). We identified 15 feeding items, 14 of which were animals (five of them: Polychaeta, Crustacea, Eggs, Hydrozoa and Bryozoa with summed importance > 95%), whereas algae were unimportant, occurring in only three individuals (IAi <1%; Table 1; Fig. 3) and possibly ingested incidentally.

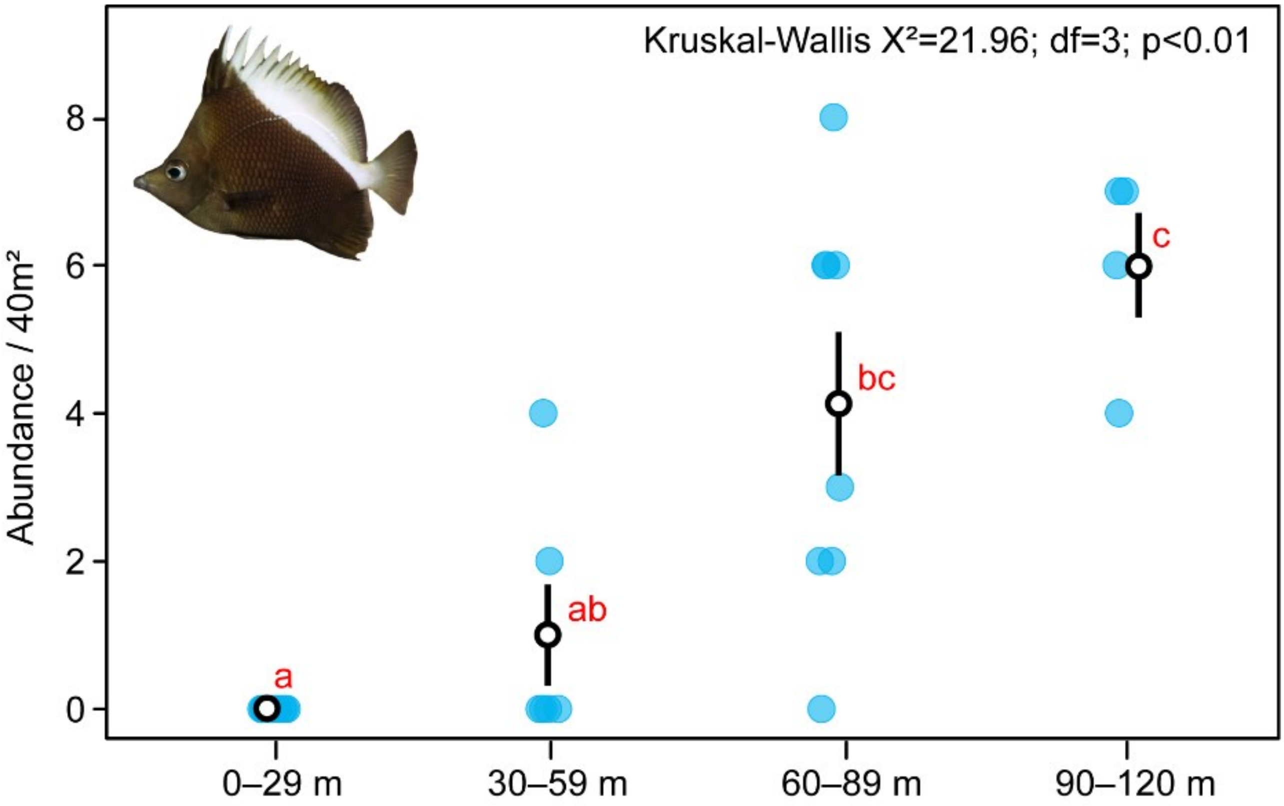
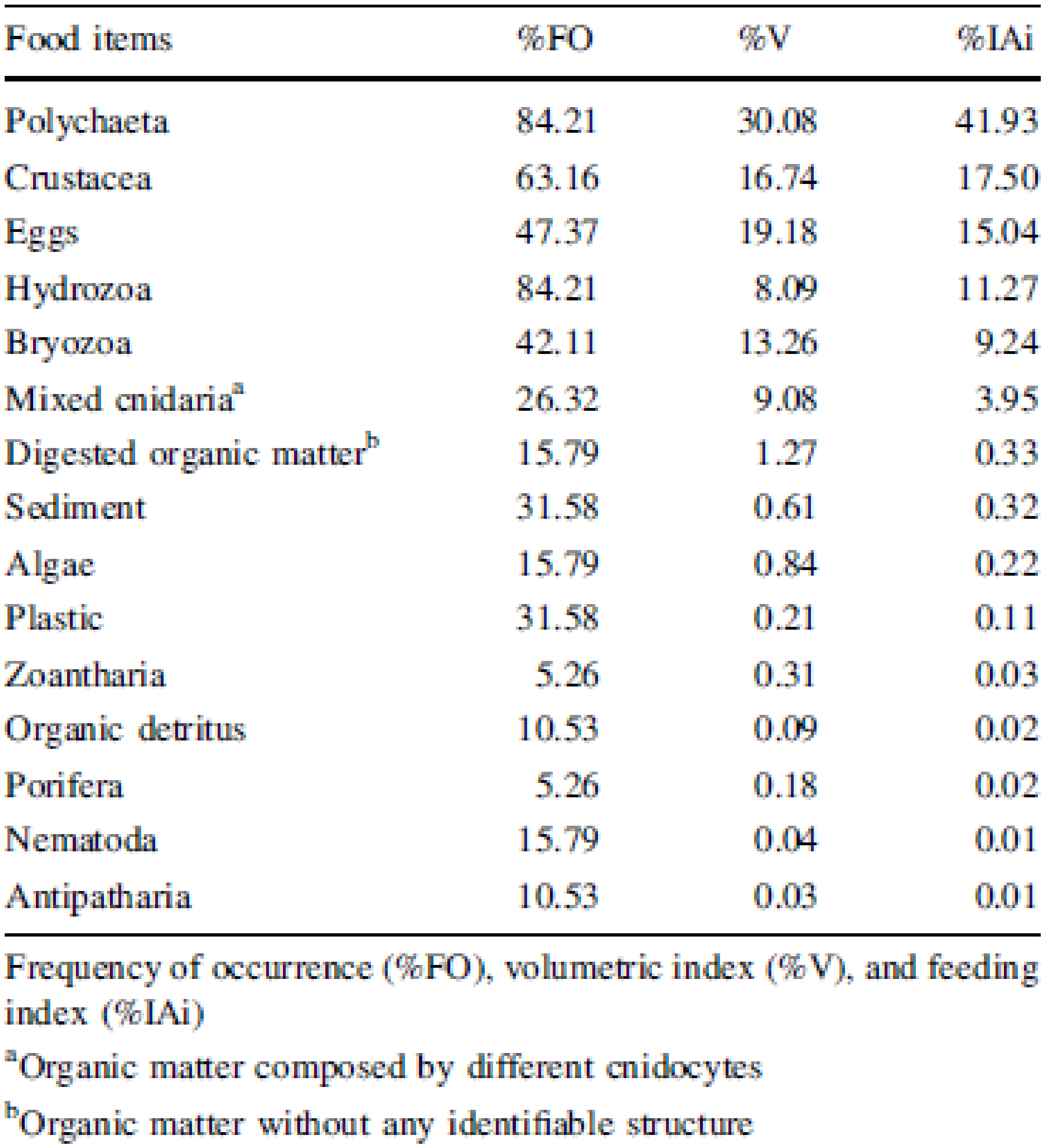


Figure 2 – Vertical distribution of *P. obliquus*. Blue dots are values for each transect. White circles and black bars represent the mean abundance (number of individuals per 40m²) and the standard error, respectively.

The incongruence between the omnivore intestine length and a carnivore diet could be explained by the relatively large amount of Cnidaria material ingested by *P. obliquus* (IAi = 14.47%). Cnidaria is a poor caloric resource (19.6 J mg-1) compared to other invertebrates such as polychaetes (22.3 J mg-1) and crustaceans (22.4 J mg-1; reference values in Beukema

1997). The large intestine length found in hard and soft-coral feeders could help them to deal with chemical defences (i.e. cnidocytes) and to improve the digestion/absorption of nutrients from cnidarians (Berumen et al. 2011).

Table 1 - Diet of 19 individuals of *Prognathodes obliquus* in St. Peter and St. Paul's Archipelago.



Food items	%FO	%V	%IAi
Polychaeta	84.21	30.08	41.93
Crustacea	63.16	16.74	17.50
Eggs	47.37	19.18	15.04
Hydrozoa	84.21	8.09	11.27
Bryozoa	42.11	13.26	9.24
Mixed cnidaria[a]	26.32	9.08	3.95
Digested organic matter[b]	15.79	1.27	0.33
Sediment	31.58	0.61	0.32
Algae	15.79	0.84	0.22
Plastic	31.58	0.21	0.11
Zoantharia	5.26	0.31	0.03
Organic detritus	10.53	0.09	0.02
Porifera	5.26	0.18	0.02
Nematoda	15.79	0.04	0.01
Antipatharia	10.53	0.03	0.01

Frequency of occurrence (%FO), volumetric index (%V), and feeding index (%IAi)

[a] Organic matter composed by different cnidocytes

[b] Organic matter without any identifiable structure

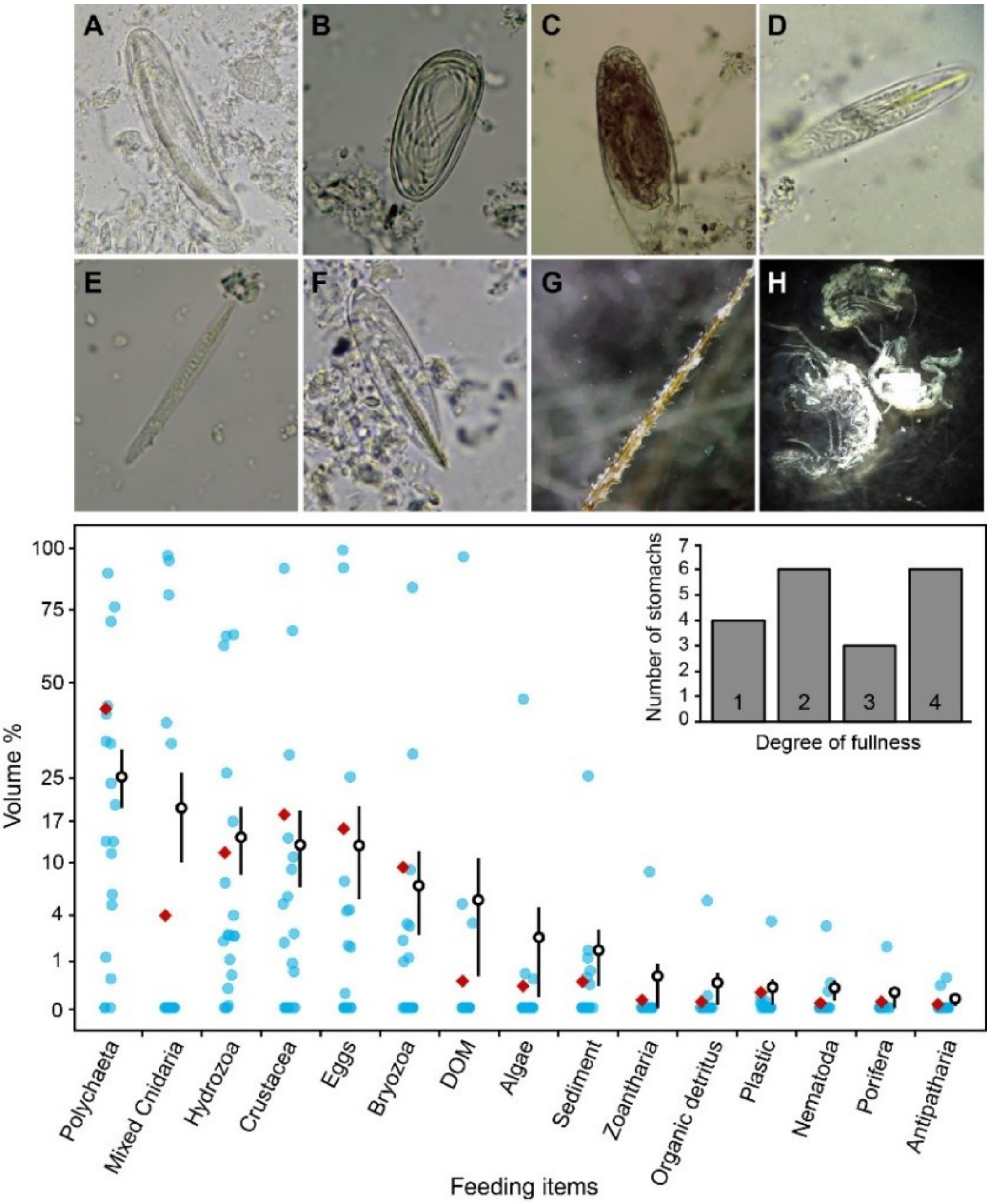


Figure 3 – The importance of feeding items in the diet of *P. obliquus*. Blue dots are the volume of each item for each stomach. Red diamonds represent the Feeding Index (%IAi). White circles and black bars represent the mean volume percentage of each item and the standard error, respectively. DOM = Digested organic matter. Grey bars represent the stomachs' degree of fullness, in four categories: (1) 0–25%, (2) 25.1%–50%, (3) 50.1–75%, (4) 75.1–100%. Photos of cnidocytes found in the mixed cnidaria: A) p-mastigophore, B) Holotrichous, C) Ptychocyst, D) p-mastigophore, E) b-mastigophore, F) b-mastigophore; and G) *Tanacetipathes* spp., H) Crustacea Amphipoda.

DOI: 10.1007/s00338-019-01822-8

Polychaeta was the most important item in the diet of *P. obliquus*, followed by Crustacea. A similar result was found for the diet of *P. aculeatus* in the Caribbean, which is composed mainly by Serpulidae Polychaeta (volume = 38.5%) and Crustacea (23.5%; Randall 1967). Due to decomposition, it was not possible to identify polychaetes to more precise taxonomic categories. Since we did not find tubes or radioles in the stomach content, which are characteristic of sessile polychaetes (Webb 1969), we believe material in *P. obliquus* stomachs were mobile polychaetes. These decomposed items could be better identified by using barcoding analyses in future studies (Leray et al. 2015). In contrast, Atlantic *Chaetodon* inhabiting shallow reefs eat more sessile polychaetes (e.g. Serpulidae and Sabellidae) and cnidarians (mostly Hexacorallia; Randall 1967; Liedke et al. 2018). Despite these differences, members of both genera in the Atlantic could be considered generalist feeders when compared to highly specialized hard-coral feeders of the Indo-Pacific, such as *C. baronessa* and *C. trifascialis* (Pratchett 2005).

Other animal items, such as sponges and black corals were probably accidentally ingested by *P. obliquus* given their low IAi values. This is a plausible explanation considering the high abundance of epibionts over sponges and black corals (M.R. Rosa et al., in preparation). Although there is no information about fishes eating ceriantharians in the Atlantic Ocean, we found cnidocytes of Isarachnanthus (Arachnactidae) in the diet of *P. obliquus*. This is the first record of a ceriantharian for the SPSPA, with the nearest record for this group in Rocas Atoll (Stampar et al. 2012). Surprisingly, even though this is a relatively deep-water species in a remote location, we found microplastics in six stomachs. Despite its geographical isolation, anthropogenic plastic pollution is prevalent in the SPSPA due to permanent human occupation and fishing activities. Great amounts of microplastic occur around the archipelago (Ivar do Sul et al. 2013) and fishing lines entangled in branching black corals are common (Francini-Filho et al. 2019), corroborating that pollution is an important threat to mesophotic reefs (Rocha et al. 2018).

In conclusion, we found that *P. obliquus* is a generalist carnivore, with diet composed mainly of sessile and mobile invertebrates, particularly Polychaeta and Crustacea. The first record of a ceriantharian in the SPSPA highlights the fact that trophic studies bring not only information about the studied species, but also about the environment where they live.

Acknowledgements

We thank Caio Ribeiro, Gilberto Amado-Filho (In memoriam), Mauritius Bell, Moyses Barbosa and Renato Morais for assisting in field work. We thank Bárbara Segal and Alberto Lindner for assistance on food items identification. We thank ICMBio for permission to sampling individuals of P. obliquus (SISBIO nº 41327-12). We thank the Brazilian Navy, SECIRM and the crew of the MV Alucia for logistical support. The Alucia expedition (2017) was funded by the generous support of donors to the California Academy of Sciences' Hope for Reefs Initiative. Other expeditions were funded by the projects: Fontes Hipertérmicas do Arquipélago de São Pedro e São Paulo (SISBIO nº 58069-1), Programa de Monitoramento de Longa Duração das Comunidades Recifais de Ilhas Oceânicas – PELD/ILOC (CNPq 403740/2012-6; CELF-PI) and Programa Arquipélago (CNPq 557185/2009-2 and 405386/2012-5; RBFF-PI). SNS is supported by a grant from FAPESP 2015/24408-4. LTN received a scholarship from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brazil (CAPES).

Conflict of interest

We declare that there is no conflict of interest.

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CAPÍTULO II

Marine Biology (2020) 167:107

The influence of species abundance, diet and phylogenetic affinity on the co-occurrence of butterflyfishes

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We studied global co-occurrence patterns of butterflyfishes in relation to species abundance, trophic characteristics and evolutionary histories, specifically examining two questions 1) Does phylogenetic affinity and/or abundance explain co-occurrence at the habitat scale?; and 2) Diets of sister species from Atlantic Ocean and Eastern Pacific are phylogenetically conserved?
We found that phylogenetic distance per se fails to explain the co-occurrence of butterflyfish species pairs. Instead, species abundance exerted a major influence in species network centrality. We also found no correlation between phylogenetic distance and diet similarities for Atlantic and East Pacific butterflyfishes, thus, in these regions, species' diets do not seem to be phylogenetically conserved. This suggests that evolutionary processes are not the main drivers of butterflyfishes co-occurrence highlighting species' abundance and niche-related processes as the most important factors in determining whether species co-occur at the habitat scale.

Photos: SR Floeter, LT Nunes

DOI: 10.1007/s00227-020-03725-7

Abstract

Understanding "why species are where they are" at different scales is one of the main focuses of ecological and biogeographical studies. Although ecological features, such as trophic group and species abundance, are thought to be more important for driving co-occurrence patterns at the habitat scale, it is not yet known if phylogenetic constraints can also exert some influence. Here, we studied global co-occurrence patterns of butterflyfishes in relation to species abundance, trophic characteristics, and evolutionary histories, specifically examining two questions: Question 1) Does phylogenetic affinity and/or abundance explain co-occurrence at the habitat scale? To answer this, we used abundance data from 23 global localities to evaluate whether phylogenetic affinity alone as well as after accounting for differences in diet among sympatric species explains co-occurrences at the habitat scale. Question 2) Are the diets of sister species from the Atlantic Ocean and the Eastern Pacific phylogenetically conserved? To examine this, we used a more detailed diet classification of species present within these realms. We found that phylogenetic distance per se fails to explain the co-occurrence of butterflyfish species pairs. Instead, species abundance exerted a major influence in interspecific co-occurrences. We also found no correlation between phylogenetic distance and diet similarities for Atlantic and East Pacific butterflyfishes, thus, in these regions, species' diets do not seem to be phylogenetically conserved. This suggests that evolutionary processes are not the main drivers of butterflyfish co-occurrence highlighting species' abundance and niche-related processes as the most important factors in determining whether species co-occur at the habitat scale.

Keywords: Chaetodontidae, escala do habitat, espécies-irmãs, nicho trófico, peixes recifais, *Prognathodes*

Introduction

Understanding species' distributions across scales has always been one of the main focuses of ecological and biogeographical studies. The presence or absence of a species in a community can be influenced by several macroecological (McGill and Collins 2003), biogeographical (Ekman 1953), evolutionary (Whittaker 1972) and species-related processes (Whittaker 1972; Brown 1984; Burns and Strauss 2011). In most studies, however, these processes have been examined to disentangle species co-occurrences in a regional/geographical scale (e.g. Hodge et al. 2014; Hodge and Bellwood 2016; Gaboriau et al. 2018). So far, few studies have examined species co-occurrences at the smaller habitat scale (e.g. Early and Keith 2019; Eurich et al. 2019), particularly considering evolutionary and ecological processes simultaneously. According to Darwin's naturalization conundrum, species have higher chances to occur in habitats where close relatives are present, due to facilitation by favourable niche conditions. However, this occurrence could be impaired by competition with closely related species due to similarities in resource requirements (Diez et al. 2008; Thuiller et al. 2010).

Two species that share a direct common ancestor tend to have similar traits that could intensify competition for resources when in sympatry, leading to competitive exclusion (Harper et al. 1961; Abrams 1983; Germain et al. 2016). Based on this assumption, the "Limiting similarity" theory posits that there is a maximum level of similarity between species that would allow coexistence by minimizing competition (Abrams 1983). Relatedly, the "Character displacement" theory suggests that sympatric sister species will differ ecologically or morphologically to co-exist to minimise/avoid competitive pressures (Brown and Wilson 1956; Slatkin 1980; Abrams 1983). Besides these evolutionary theories, abundance is known to influence species co-occurrence by affecting the strength of interactions (Vazquez et al. 2009). Assuming interaction neutrality, resulting from the random encounter of individuals, abundant species will tend to co-occur more frequently than the rare ones, thus being central to co-occurrence networks (Vazquez et al. 2007; 2009). Thus, both ecological and evolutionary processes should contribute to co-occurrence patterns in high-diversity biological systems.

Among high-diversity systems, coral and rocky reefs stand out as the most productive ecosystems in marine shallow waters, supporting hundreds of thousands of species (Reaka-Kudla 1997; Roberts et al. 2002). Such biologically complex systems provide ideal models to

DOI: 10.1007/s00227-020-03725-7

test co-occurrence theories, being important for studies of pairwise species patterns (e.g. Auster et al. 2005) as well as species-habitat relationships (e.g. Reese 1981) at different temporal and spatial scales (e.g. Nickell and Sayer 1998; Mariani et al. 2001). Among the most conspicuous fishes on reefs, the Chaetodontidae (butterflyfishes) comprises around 134 species. It is one of the most studied reef fish families, known as a good model for ecological studies due to their close association with the benthic substrate, prevalence of diurnal foraging behaviour and the ability to explore different habitats (Blowes et al. 2013; Konow and Ferry 2013). In addition, the Chaetodontidae family has been relatively well studied in terms of phylogenetic relationships (Fessler and Westneat 2007; Bellwood et al. 2010; Floeter et al. 2018). Most of these studies, however, focused on butterflyfishes from the Indo-Pacific Ocean (e.g. Pratchett et al. 2014), where species diversity is higher (Findley and Findley 1989; Kulbicki et al. 2013), while species from the Atlantic Ocean and Eastern Pacific have received relatively less attention.

Butterflyfishes are usually divided into four major feeding guilds: hard-coral feeders, soft-coral feeders, non-coral feeders and generalists (Pratchett 2005). Species that feed almost exclusively on hard corals, such as *Chaetodon trifascialis* (Berumen and Pratchett 2008), tend to feed on a single taxonomic group or species (Schoener 1971; Nagelkerken et al. 2009). Although specialists may assimilate energy from their prey more efficiently compared to generalists (Berumen and Pratchett 2008) this feeding strategy could make them vulnerable to stochastic fluctuations in food resources (Schoener 1971; Munday 2004; Berumen and Pratchett 2008). Contrastingly, generalist species consume a variety of prey and are distributed in a way that is not strictly related to a specific food resource (Schoener 1971). Thus, the generalist strategy may ensure population persistence, especially in unstable or hostile environments. Moreover, a generalist habit can allow the co-occurrence of sister species by minimizing competition pressure for feeding resources (Pratchett et al. 2004; Berumen and Pratchett 2008). For instance, the generalist invertivore *Chaetodon striatus* is widely distributed in the western Atlantic Ocean, from southern Brazil to Florida-USA, including oceanic islands. Throughout its distribution, *C. striatus* co-occurs with six other butterflyfishes, including its sister species *C. capistratus* in the Caribbean (Bellwood et al. 2010), which does not seem to affect population abundances (Liedke et al. 2016; 2018).

In this study, we aimed to understand the relationship between co-occurrence and evolutionary history of butterflyfishes, accounting for their abundance and trophic characteristics. We explored the global co-occurrence patterns of Chaetodontidae by asking:

Question 1) Does phylogenetic affinity and/or species abundance explain co-occurrence at the habitat scale? We hypothesize that co-occurrence will be positively related to both phylogenetic distance and abundance (Fig. 1a and 1b). Also, we expect that generalist species will co-occur more frequently than specialist ones (Fig. 1c). Question 2) Are the diets of sister species from the Atlantic Ocean and the Eastern Pacific phylogenetically conserved? To answer that, we used a more detailed diet classification of species present within these less studied realms. We hypothesize that distantly related species will have different diets due to phylogenetic niche conservatism (Fig. 1d).

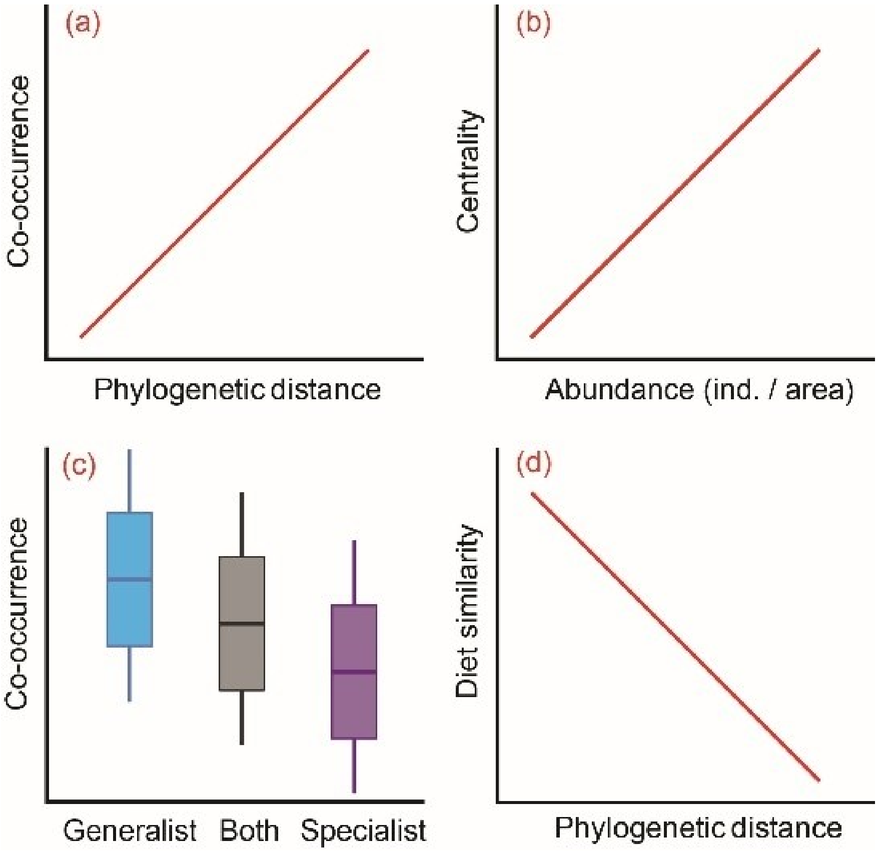

Fig. 1 Hypothetical relationships between: (a) co-occurrence and phylogenetic distance; (b) species centrality and abundance; (c) co-occurrence and diet of the *Chaetodon* species-pair; (d) phylogenetic distance and diet similarity for Chaetodontidae species from the Atlantic and Eastern Pacific Oceans.

Material and Methods

Does phylogenetic affinity and/or species abundance explain co-occurrence at the habitat scale?

We used global visual censuses from 23 localities to obtain habitat scale abundance data of *Chaetodon* species (Fig. 2a; Table 1; derived from Morais et al. 2017; Barneche et al. 2019). The visual census method consists of belt transects in which a diver records and counts all the species inside an area on the reef. The transect area (m^2) differed among the localities but not within a locality (please refer to Table 1 for more information). We defined the "habitat scale" as the area of the transect, which ranged from 40 to 500 m^2 within a certain depth and reef type.

We used solely localities with two or more *Chaetodon* species inhabiting the same reef and only censuses in which at least one *Chaetodon* species was present. The *Prognathodes* genus was not included in this analysis since most species inhabit mesophotic reefs (Copus et al. 2019; Nunes et al. 2019). In total, 60 *Chaetodon* species were present in the censuses, which represent approximately 70% of the genus' diversity. The possible combinations of co-occurring species (i.e. species-pairs) at localities ranged from 3 (Ceará - Brazil) to 300 (central great barrier reef - Australia). To infer the proportion of censuses with species-pairs, we used the Bray-Curtis index through the equation: $BCij = 1 - (1 - (2Cij / (Si + Sj)))$ where i and j are two *Chaetodon* species potentially co-occurring in a given habitat; C is the sum of only the lower abundance for each census found for both species; Si is the sum of the abundance of species i; and Sj is the sum of the abundance of species j. Abundance data was used in the model for co-occurrences due to its importance for species centrality in co-occurrence networks (see the statistical analysis below for details).

The phylogenetic distances between each species-pair was extracted from the phylogeny of Cowman and Bellwood (2011), using the 'ape' R package (Paradis 2004). Distances represent the sum of branch lengths separating two species in the phylogeny. We imputed five species that were not present in the phylogeny by utilizing morphologically similar and phylogenetically closely related species. These species were all considered part of the same clade (Kuiter 2002) and subgenus (Bellwood and Pratchett 2013) as the ones not included in the phylogeny.

Since diet can vary according to food item availability in each locality (Anderson et al. 1981) and is dependent on taxonomic resolution, we adopted a broader categorization for comparisons among localities. Species were classified as specialists or generalists according to their diet, which was obtained from literature (see Online Resource 1). Here we define as “specialists” those species that feed preferentially (more than 75% of their diet) on a single taxon (e.g. Scleractinia). We considered a species as “generalist” when its diet was composed of a variety of sessile and mobile invertebrates, without clear preference for specific taxonomic groups (Schoener 1971; Nunes et al. 2019).

Are the diets of sister species from the Atlantic Ocean and the Eastern Pacific phylogenetically conserved?

We sampled eight species of *Chaetodon* and four species of *Prognathodes* that occur in the Atlantic and Eastern Pacific Oceans. Among the *Chaetodon* species, *C. capistratus* and *C. striatus* occur in the Western Atlantic but are found in sympatry only in the Caribbean (**Online Resource 2**). *Chaetodon ocellatus* and *C. humeralis* occur in the Western Atlantic and Eastern Pacific, respectively (**Online Resource 2**). *Chaetodon robustus, C. hoefleri* and *C. marleyi* occur in West Africa, but only *C. robustus* and *C. hoefleri* overlap their ranges (**Online Resource 2**). Finally, the closely related species *Chaetodon sanctaehelenae* and *C. sedentarius* occur separately in the Mid-Atlantic Ridge and Western Atlantic, respectively. In *Prognathodes*, *P. brasiliensis* and *P. aculeatus* are sister species that occur at the Brazilian and Caribbean provinces, respectively (**Online Resource 3**). *Prognathodes obliquus* is endemic to the St. Peter and St. Paul’s Archipelago, while its sister species, *P. dichrous,* occurs in the Mid-Atlantic Ridge (**Online Resource 3**).

To quantify the diet of each species, we combined literature and stomach content analyses. Literature data was obtained for *C. striatus, C. capistratus* and *P. aculeatus* in the Caribbean (Birkeland & Neudecker 1981 ; Liedke et al. 2018); *P. obliquus* in St. Peter and St. Paul’s Archipelago (Nunes et al. 2019) and *C. marleyi* in South Africa (Vine 1998). Additionally, we sampled stomach contents of four *Chaetodon* and two *Prognathodes* species in six localities of the Atlantic as well as *Chaetodon humeralis* in the Eastern Pacific. The individuals were collected using hand spear and frozen to cease enzymatic action. Only adult individuals were sampled to avoid the effect of ontogenetic diet differences. All individuals were dissected in the laboratory where their stomachs were removed and fixed in 10% formaldehyde. The stomachs were subsequently sectioned in a petri dish under a stereomicroscope, where its content was separated and identified to the lowest taxonomic category possible. Amorphous or partially digested food items were investigated under an optic microscope, in search of any cellular structures that could be used to better define a taxonomic group, such as spicules and nematocysts (Liedke et al. 2016; Nunes et al. 2019).

We quantified the diets according to the frequency of occurrence (%FO), that indicates how often a food item is present in the sampled stomachs; and the volumetric index (%V), which relates the volume of each item to the total volume of the sampled stomach (Hynes 1950; Hyslop 1980). The volume of food items was measured through a millimetre Petri dish, where each item was placed between two 1 mm thick coverslips and kneaded with a microscope slide, then the number of 1 mm^3 grids were counted (Nunes et al. 2019). We assessed the importance of each food item through the Feeding Index equation: $\%IAi = ((\%FOi \cdot \%Vi) / \sum(\%FO \cdot \%V)) \cdot 100$, where %FOi and %Vi represent the frequency of occurrence and volume of the food category *I*, respectively (Kawakami and Vazzoler 1980; Liedke et al. 2016; Nunes et al. 2019).

Table 1 Localities in which we obtained *Chaetodon* co-occurrence data. Census: total number of censuses in which at least one *Chaetodon* species occur. Area: census area in squared meters. Total area: Number of censuses multiplied by the area, which indicates the total reef area sampled in each locality. Species: richness of *Chaetodon* species. **R** and **p**: the correlation and significance, respectively. 1) Co-occurrence matrix; 2) Phylogenetic matrix; 3) Diet matrix. Values in red indicate significative results ($p<0.05$).

Province	Locality	Census	Area	Total area	Species	R_{12}	p_{12}	R_{13}	p_{13}	R_{32}	p_{32}	$R_{12\|3}$	$p_{12\|3}$
Brazil	Ceara	15	40	600	3	-0.846	0.340	*na*	*na*	*na*	*na*	*na*	*na*
	Manuel Luis	15	40	600	3	0.500	0.002	*na*	*na*	*na*	*na*	*na*	*na*
Caribbean	Curaçao	53	40	2120	3	-0.932	0.313	*na*	*na*	*na*	*na*	*na*	*na*
	Mexico	150	100	15000	4	-0.938	0.044	*na*	*na*	*na*	*na*	*na*	*na*
	Virgin Islands	199	100	19900	4	0.211	0.439	*na*	*na*	*na*	*na*	*na*	*na*
Central Pacific	Fiji island	257	40	10280	22	-0.108	0.058	-0.050	0.221	-0.505	0.001	-0.155	0.009
	Rose Atoll	16	500	8000	9	-0.289	0.077	0.667	0.002	-0.431	0.007	-0.003	0.500
	Samoa	307	150	46050	20	0.049	0.253	-0.099	0.080	-0.380	0.001	0.013	0.434
Hawaiian	Hawaii	359	150	53850	13	-0.033	0.396	-0.075	0.255	-0.279	0.008	-0.057	0.311
Indo-Pacific	Aceh	50	500	25000	24	0.109	0.018	-0.112	0.061	-0.332	0.001	0.078	0.118
	Bali	18	500	9000	19	-0.088	0.113	0.073	0.176	-0.467	0.001	-0.062	0.185
	Raja Ampat	82	500	41000	24	-0.021	0.364	0.007	0.422	-0.398	0.001	-0.019	0.375
North-western Indian	Eilat	5	500	2500	4	-0.713	0.099	0.283	0.261	-0.488	0.337	-0.687	0.132
	Red Sea	5	500	2500	8	0.126	0.263	0.050	0.389	-0.102	0.306	0.132	0.275
Polynesian	French Polynesia	135	40	5400	14	-0.190	0.050	0.014	0.399	-0.472	0.001	-0.208	0.031
	Pitcairn	185	100	18500	11	-0.261	0.041	-0.015	0.444	-0.403	0.001	-0.292	0.017
	Society Islands	20	500	10000	15	0.039	0.355	-0.107	0.131	-0.449	0.001	-0.010	0.471
South-western Pacific	Central GBR	140	500	70000	25	-0.063	0.135	-0.019	0.364	-0.322	0.001	-0.073	0.100
	New Caledonia	840	42	35280	22	-0.198	0.008	0.049	0.232	-0.404	0.001	-0.195	0.003
	Queensland	66	500	33000	23	0.040	0.264	0.036	0.284	-0.442	0.001	0.062	0.165
Western Indian	Mozambique	29	100	2900	16	-0.034	0.365	0.054	0.304	-0.384	0.001	-0.014	0.447
	Seychelles	76	100	7600	15	0.008	0.499	-0.147	0.059	-0.430	0.001	-0.062	0.269
	Tanzania	7	500	3500	10	0.149	0.187	-0.007	0.477	-0.434	0.001	0.162	0.137

DOI: 10.1007/s00227-020-03725-7

Statistical analyses

To test for an effect of abundances on co-occurrence strengths, we used network analyses and calculated the centrality of species in each locality. High centrality scores indicate species that are strongly connected to other species in the network, with these connected species also being strongly connected to other species (Delmas et al. 2019). Undirected, unipartite co-occurrence networks with weighted edges were created based on the Bray Curtis co-occurrence matrices described above, with weights being the Bray Curtis co-occurrence strength. Species' centrality was calculated through eigenvector centrality within each locality network. The centrality measure (dependent variable) was then regressed against species abundance (independent variable) to assess whether abundant species would co-occur more frequently when compared to the less abundant ones. In this study, connection strengths within networks are based on co-occurrences, therefore a relationship between centrality and abundance will suggest an influence of abundances on estimated co-occurrence strengths (i.e. more abundant species co-occur more often than less abundant species).

To correlate co-occurrence (dependent variable) with phylogenetic relationships (independent variables) after accounting for diet types at each locality, we performed a partial mantel test with 999 permutations and the Pearson correlation method, using the 'ncf' R package (Bjornstad 2018). Additionally, we investigated possible differences among the proportion of species pairs (samples) in each diet type by performing Chi-Squared with Goodness-of-Fit test. Due to discrepancies in the total number of samples among the graphical quadrants (see results) we performed a bootstrap analysis with 1000 resamples (**Online Resource 4**). Finally, we verified differences between co-occurring diet types using Kruskal-Wallis and post hoc Dunn tests.

To verify similarities in species diets, we performed a cluster analysis with the IAi value grouped in nine major categories: Algae, Ectoprota, Hydrozoa, Octocorallia, Hexacorallia, Polychaeta, Crustacea, Eggs; and "Others" (i.e. items with low importance for the diet). We used a simprof (Similarity Profile Analysis) test with Euclidian distance to unravel significant groups. To correlate the diet matrix (i.e. Euclidian distances among species) with the phylogenetic distance matrix, we performed a mantel test. All analyses were performed using R software version 3.4.3, through the packages "ade4", "boot", "clustsig", "dunn.test", "ggdendro", "ggplot2", "gridExtra", "igraph", "map", "maptools", "plotrix", "plyr", "reshape" and "vegan" (R core team 2019).

Results

Among the 2618 species-pairs analysed, we only found a correlation between co-occurrence and phylogenetic distance in a few localities (**Table 1**). Despite this, some patterns emerged when we analysed each quadrant of Fig. 2b separately. The top left quadrant represents closely related species (phy dist < 15) that co-occur in more than 50% of the census. In this quadrant, only five species-pairs were found, which represent less than 1% of the total species-pairs analysed, showing that closely related species never co-occur in high frequency. The top right quadrant represents distantly related species (phy dist > 15) that co-occur in more than 50% of the census. In this quadrant, only 33 species-pairs were found which represents 1.26% of the total analysed (**Fig. 2b**). The bottom left quadrant represents closely related species (phy dist < 15) that co-occur in less than 50% of the census. In this quadrant, 363 species-pairs were found, representing about 14% of the total (**Fig. 2b**). The bottom right quadrant represents phylogenetically distant species (phy dist > 15) that co-occur in less than 50% of the census. In this quadrant, 2217 species-pairs were found which represents the majority of co-occurring species analysed (**Fig. 2b**).

When we looked at the proportion of species according to diet types, we found significant differences between quadrants (Quad. 2 $X^2 = 7.09$, $p = 0.03$; Quad. 3 $X^2 = 491.85$, $p < 0.01$; Quad. 4 $X^2 = 623.75$, $p < 0.01$), with predominance of generalist pairs in closely related co-occurring species (Quadrants 1 and 3; **Fig. 2c**). Specialist species-pairs, on the other hand, were mainly found in the distantly related quadrants (**Fig. 2c**) and tended to co-occur more frequently than pairs involving generalist species (**Fig. 2d**). Finally, in most localities, we found that species abundance exerted a major influence in the co-occurrence patterns (**Fig. 3**).

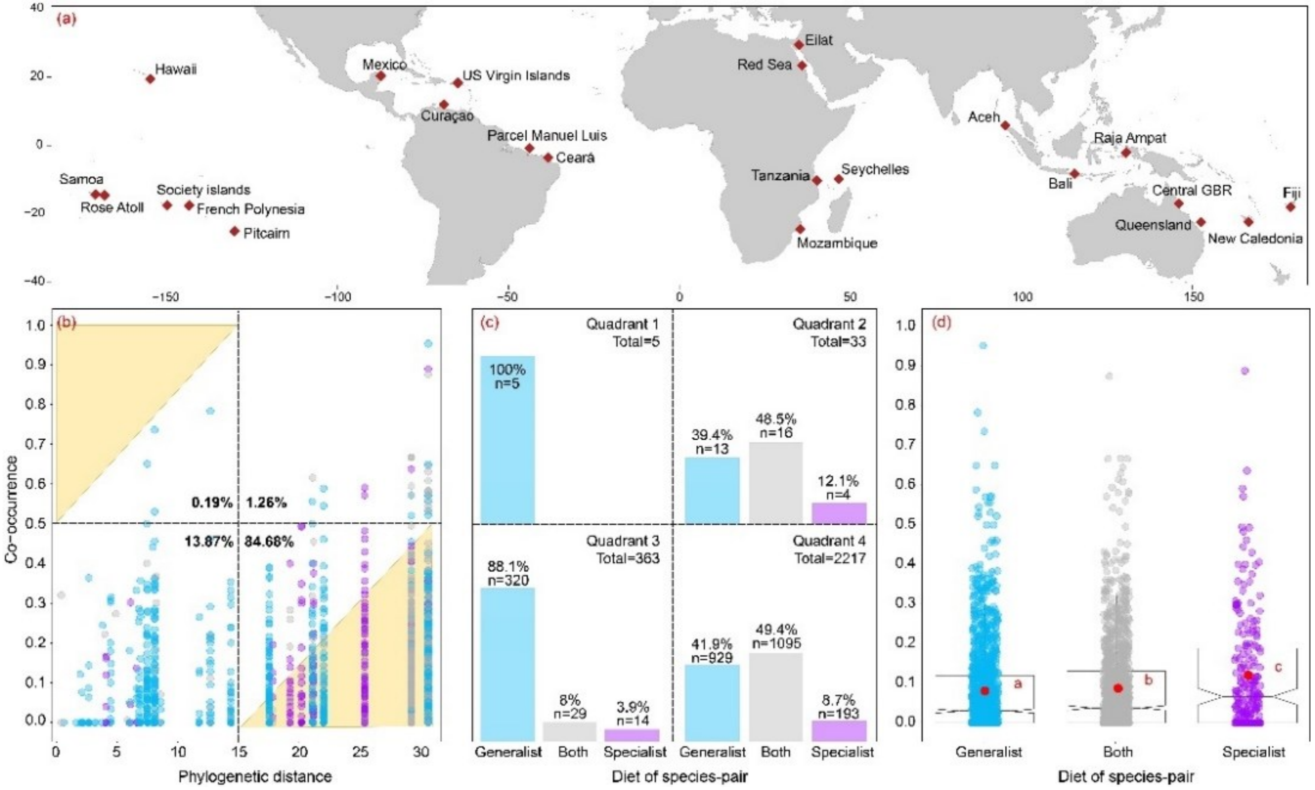

Fig. 2 (a) Global map showing the 23 sampled localities; (b) The correlation between co-occurrence and phylogenetic distance between species pairs (points) obtained through the Bray-Curtis index. Blue and purple points represent generalist and specialist species-pairs, respectively. Grey points represent species-pairs in which one is a generalist and the other is a specialist. The yellow triangle in the first quadrant represents a hypothetical area in which species-pairs do not occur, while there is no impediment for a given species-pair to occur in the lower triangle; (c) Proportion of diet types for each quadrant. n indicates the total number of pairs in the diet type. Percentages represent the proportional number of species-pairs in each quadrant; (d) Correlation between diet types and co-occurrences. Notched boxplot represents median and confidence intervals. Red circles represent the mean co-occurrence of each diet type, Dunn test results represented by letters in red.

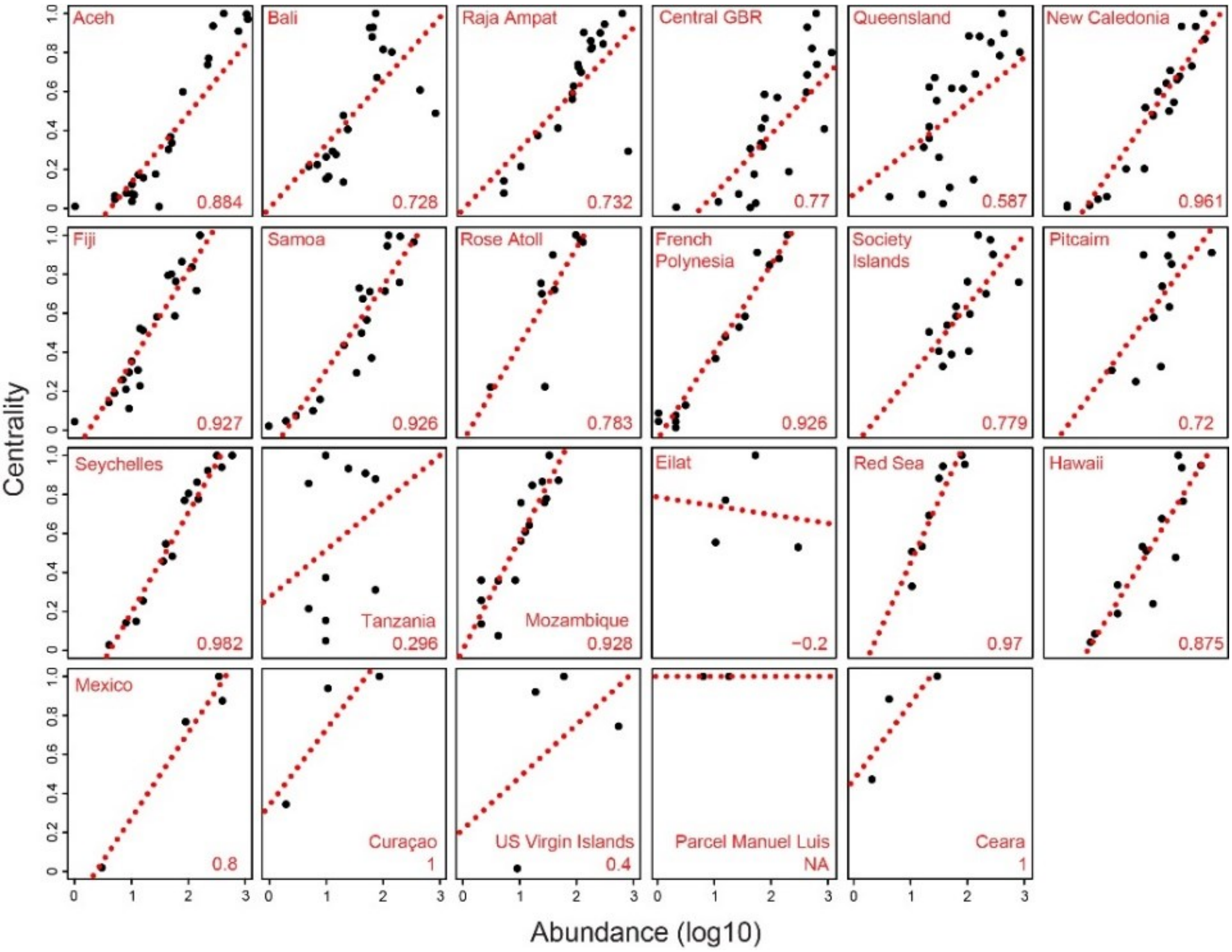

Fig. 3 Relationship between *Chaetodon* abundance and centrality, demonstrating that abundant species typically co-occur more frequently with other *Chaetodon* species. Black dots represent *Chaetodon* species in each locality. Values in red indicate the Pearson correlation.

We also found no correlation between phylogenetic distance and diet similarity among butterflyfishes from the Atlantic and the Eastern Pacific (r = 0.04, p = 0.29). Even though the diets of the 12 Chaetodontidae species consisted of several mobile and sessile invertebrates (from 4 to 30 feeding items depending on the species), Hexacorallia and Polychaeta were the preferred food resource for most species. Among Atlantic species, we found three *Chaetodon* and two *Prognathodes* that can be considered as specialists. The diet of *C. ocellatus* is the most specialized within the *Chaetodon* clade, being mainly composed of Zoanthids (IAi ~ 84%; **Fig. 4**). Its Eastern Pacific sister species, *C. humeralis*, is a generalist feeding predominantly on Hexacorallia, Polychaeta and Algae. Despite having different preferred items, the species *Chaetodon striatus* and *C. capistratus* also display a somewhat generalist diet, with no item showing an importance higher than 75%. *Chaetodon marleyi* is a specialist consuming Polychaeta (~73%), while its closely related *C. robustus* consumed mostly Hexacorallia (~90%; **Fig. 4**). The only individual of *Prognathodes dichrous* analysed in this study consumed mostly Hexacorallia (91%) while its sister species *P. obliquus* have a generalist diet composed of Polychaeta, Crustacea, Ectoprocta and Cnidaria. Algae was present in almost all species analysed, however, always with a low importance, which suggests accidental ingestion.

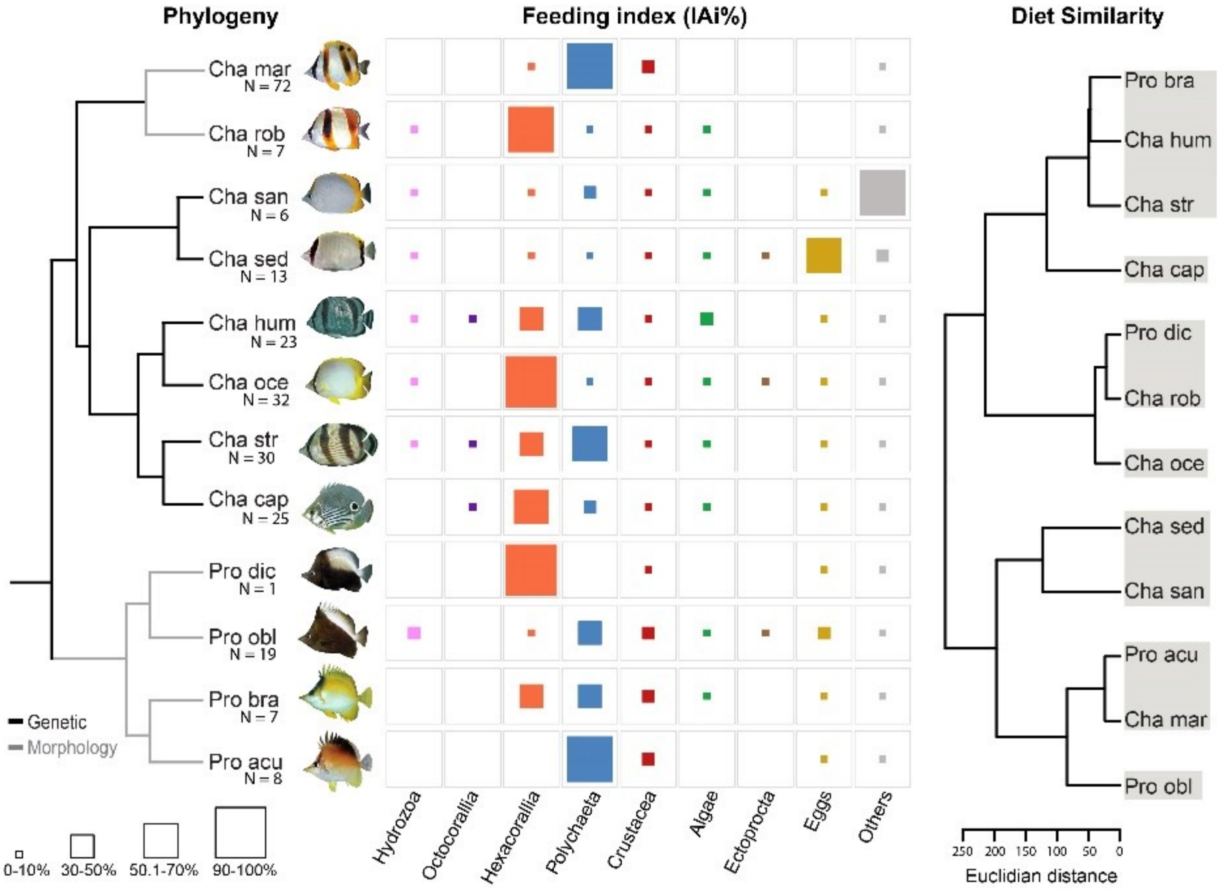

Fig. 4 Molecular phylogeny of *Chaetodon* species from the Atlantic and Eastern Pacific (pruned from Cowman & Bellwood 2011) with respective number of individuals used for diet analyses (N). Coloured squares represent the feeding index (%IAi) of the eight most important diet items, plus "Others" (i.e. all other items found for species' diet). Squares are proportional to the feeding index of each item. Empty squares represent absence of item in the diet. Cluster according to diet similarities, grey boxes represent simprof significant groups. Cha mar: *Chaetodon marleyi* (data from Vine 1998), Cha rob: *Chaetodon robustus*, Cha san: *Chaetodon sanctaehelenae*, Cha sed: *Chaetodon sedentarius*, Cha hum: *Chaetodon humeralis*, Cha oce: *Chaetodon ocellatus*, Cha str: *Chaetodon striatus* and Cha cap: *Chaetodon capistratus* (Liedke et al. 2018), Pro dic: *Prognathodes dichrous*, Pro obl: *Prognathodes obliquus* (Nunes et al. 2019), Pro bra: *Prognathodes brasiliensis*, Pro acu: *Prognathodes aculeatus* (Randall 1967).

Discussion

Does phylogenetic affinity and/or species abundance explain co-occurrence at the habitat scale?

Phylogenetic distance between butterflyfishes fails to explain their co-occurrence at the habitat scale, although closely related species never co-occur at high frequency (i.e. Quadrants 1; Fig. 2b). The same lack of correlation was found in other studies for freshwater green algae (Narwani et al. 2013) and plant species (Germain et al. 2016), suggesting that evolutionary processes do not influence species co-occurrence at the habitat scale. Thus, we suggest that co-occurrences at this small scale might be modulated by: (1) “trait-matching” (Vazquez et al. 2009), where species co-occurrence will be linked to biological traits such as diet type or territorial behaviour (e.g. Keith et al. 2018); or (2) neutral processes resulting from the random encounters among individuals, where locally abundant species co-occur more frequently just by chance (Vazquez et al. 2009). Based on our results (Fig. 3), the abundance of species is highly correlated with its centrality in the co-occurrence network, which provides support for the neutral hypothesis. This is supported by studies that demonstrated the central role of abundance in structuring biological interactions in several animal and plant groups (Vazquez et al. 2007; Floeter et al. 2007).

Although we did not find a correlation between co-occurrence and phylogenetic distance, we found that specialist pairs tend to co-occur more frequently than generalists or between generalist and specialist pairs. It is likely that the overlap in resource use may explain why generalist pairs co-occur less than specialist pairs, considering that specialists might show less overlap in food items consumed (Pratchett 2005). In that case, specialist species-pairs would diverge in their preferred food items to avoid competition (Blowes et al. 2013), while generalists would only be able to co-occur with some degree of resource partitioning (Anderson et al. 1981; Bouchon-Navaro 1986). Thus, we suggest that species abundance and resource partitioning are more important in determining whether species can co-occur at the habitat scale (Anderson et al. 1981; Bouchon-Navaro 1986; Pratchett 2005; Early and Keith 2019) than phylogenetic relationships (Germain et al. 2016).

Are the diets of sister species from the Atlantic Ocean and the Eastern Pacific phylogenetically conserved?

For Atlantic and East Pacific butterflyfishes, species' diet does not seem to be phylogenetically conserved (Fig. 4). Our results diverge from a previous study where the authors found a significant correlation between phylogenetic distance and diet among *Chaetodon* species (Blowes et al. 2013). This difference, however, was likely related to the fact that Blowes et al. (2013) used the preferential substrate for foraging as a proxy for species diet, instead of stomach content analyses. Although quantifying diet through stomach content analysis might also have associated issues (e.g. difficulty to identify digested items; Liedke et al. 2018), it is still a very important approach for identifying the actual food intake when used in combination with substrate selection, even for specialist species. In addition to stomach content analysis, we suggest that future studies should also use other methods, such as isotopic analyses and metabarcoding, to access species trophic ecology. For instance, the generalist *C. striatus* in South Brazil prefers to feed over Porifera and Calcareous articulated algae substrates but its diet is composed mainly of Cnidaria (Liedke et al. 2016). Through a broader feeding categorization (i.e. specialist and generalist) we were able to find an inverse correlation between phylogenetic distance and diet for *Chaetodon* species in most studied localities. This result corroborates our hypothesis that closely related species evolved to exploit similar substrates for foraging, such as scleractinian corals (Floeter et al. 2018), but not necessarily the same food resource within this substrate (Nagelkerken et al. 2009).

Chaetodon sedentarius and *C. sanctaehelenae* were the only closely related species grouped based on diet. However, this clustering was not based on similarities between their diets, but rather based on differences between their contents and the other butterflyfishes. These two species are thought to have separated from their shared ancestral lineage from the Indo-Pacific as a result from a recent invasion of the Atlantic (Floeter et al. 2008; Bellwood and Pratchett 2013). Despite not co-occurring throughout their distributions, both species share a more pelagic habit and are commonly found in schools in the water column (authors' personal observation). This differs from other analysed *Chaetodon* species that are benthic feeders and always forage solitarily or in pairs. The sister species *C. ocellatus* and *C. humeralis* are thought to have been separated by the rise of the Isthmus of Panama and, therefore, do not co-occur anywhere along their distributions (Bellwood et al. 2010). *Chaetodon ocellatus* is a specialist feeding on Zoanthids while *C. humeralis* is a generalist. In the Caribbean, the sister species *Chaetodon striatus* and *C. capistratus* both possess a generalist diet. Both are syntopic species feeding over a variety of invertebrates (Liedke et al. 2018). *Chaetodon capistratus* is commonly recorded on the reef flat eating preferentially Hexacorallia while *C. striatus* is mostly found on the reef interface eating mostly Polychaeta (Findley and Findley 1989; Liedke et al. 2018). The African clade of *Chaetodon* species is represented in this study by two species with a relatively more specialized diet: *Chaetodon marleyi*, which feeds mostly on Polychaeta, and its close relative *C. robustus*, a specialist in Hexacorallia. Both species occur along the African coast, but there is no overlap in their distribution (Online Resource 2). Species within the *Prognathodes* genus are distributed in different biogeographical provinces in the Atlantic Ocean (Online Resource 3). They also inhabit reefs with very distinct characteristics, which may have influenced the divergent diets found between sister species. Although we provide a better resolution about the diet of these poorly known species, we emphasize the need for a better phylogenetic resolution within the genus *Prognathodes* for better investigation of evolutionary patterns related to the ecology of this genus.

Both ecological and evolutionary processes could promote divergence in the diet of Atlantic and East Pacific butterflyfish sister species. This differentiation could be mediated by the opportunity to fill available niches following speciation and the emergence of coral reefs, with species being able to explore other food items in addition to scleractinian corals (Lobato et al. 2014; Floeter et al. 2018). But also, the availability and fluctuations in the abundance of food resources, which can alter predator's food plasticity (Pfennig et al. 2006).

Conclusions

Our study provides insights about the ecology and evolution of butterflyfishes, one of the most widely distributed and iconic reef fish families. Particularly, we bring new information about the less studied Atlantic and Eastern Pacific species. Co-occurrence patterns of butterflyfishes cannot be explained by the phylogenetic affinity, suggesting that resource partitioning and species abundance provide a better explanation for *Chaetodon* species-pairs. Additionally, we found that diets of Atlantic and Eastern Pacific butterflyfishes are not phylogenetically conserved. These species are mostly generalists feeding on invertebrates, except for a few specialized species that consume different species of Hexacorallia.

Compliance with Ethical Standards

We declare that there is no conflict of interest. The sampling was supported by Chaetodon project [CNPq #483682/2010-1 to SRF], SISBIOTA-Mar [CNPq #563276/2010-0 and FAPESC #6308/2011-8; to SRF], Long Term Ecological Research of Brazilians Oceanic Islands – PELD/ILOC [CNPq #403740/2012-6 to CELF], PROSPEC-Mar [CNPq #458548/2013-8 to Dr. Leticia Veras Costa Lotufo]. LTN and IC received a scholarship from the Brazilian Ministry Educational Council – [CAPES Finance Code 001]. We also declare that all individuals were sampled according to the international and national guidelines for sampling. Permission for sampling in Brazil was given by the ICMBio Institute (SISBio #55911-3 and #29953-10 to CEFL; and SISBio #41327-9 to SRF); In Ascension island permission was given by the Conservation Centre of the Ascension Government (ERP-2015-09 to Dr. Renato Morais).

Acknowledgments

We thank Mauricio Cantor and Luiz Gustavo Rodrigues Oliveira Santos for statistical help and insights. We thank Alana Fraga for assistance with the stomach content analyses. We thank A Bernardi, G Bernardi, E Faria, R Freitas, A Jackson, AM Millán, R Morais, L Rocha and P Vasconcelos for sampling and field support. We thank A Lindner, B Segal, S Stampar and T Silveira for helping with the identification of food items, insights and lab equipment. We thank the three anonymous reviewers who helped to improve the manuscript.

Authors contributions

LTN and SRF conceived the ideas and designed the study; LTN, ACS and BMF collected the data and/or performed statistical analyses; LTN and IC performed the stomach content analyses. LTN, IC, AMRL and CELF contributed to sampling effort; LTN led the writing; All the authors contributed to the writing and discussions. All authors gave final approval for publication.

Data accessibility

All the data and scripts will be available at the Zenodo platform (https://zenodo.org).

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Online resource material

The influence of species abundance, diet and phylogenetic affinity on the co-occurrence of butterflyfishes

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ESM1 - Diet of *Chaetodon* species obtained from the literature.

Species	Diet type	Reference
Chaetodon adiergastos	Generalist	Bellwood and Pratchett (2013)
Chaetodon andamanensis	Specialist	Bellwood and Pratchett (2013)
Chaetodon aureofasciatus	Specialist	Bellwood and Pratchett (2013)
Chaetodon auriga	Generalist	Bellwood and Pratchett (2013); Berumen et al. (2011); Bouchon-Navaro (1986)
Chaetodon austriacus	Specialist	Bellwood and Pratchett (2013)
Chaetodon baronessa	Specialist	Bellwood and Pratchett (2013); Berumen et al. (2011); Nagelkerken et al. (2009)
Chaetodon bennetti	Specialist	Bellwood and Pratchett (2013); Berumen et al. (2011); Bouchon-Navaro (1986)
Chaetodon blackburnii	Generalist	Bellwood and Pratchett (2013)
Chaetodon capistratus	Generalist	Bellwood and Pratchett (2013); Liedke et al. (2018)
Chaetodon citrinellus	Generalist	Bellwood and Pratchett (2013); Berumen et al. (2011); Harmelin-Vivien and Bouchon-Navaro (1983)
Chaetodon collare	Specialist	Bellwood and Pratchett (2013)
Chaetodon decussatus	Generalist	Bellwood and Pratchett (2013)
Chaetodon dolosus	Generalist	Bellwood and Pratchett (2013)
Chaetodon ephippium	Generalist	Bellwood and Pratchett (2013); Berumen et al. (2011); Nagelkerken I et al. (2009); Bouchon-Navaro (1986)
Chaetodon falcula	Generalist	Bellwood and Pratchett (2013)
Chaetodon fasciatus	Generalist	Bellwood and Pratchett (2013)
Chaetodon flavirostris	Generalist	Bellwood and Pratchett (2013)
Chaetodon fremblii	Generalist	Bellwood and Pratchett (2013)
Chaetodon guentheri	Generalist	Bellwood and Pratchett (2013)

Chaetodon guttatissimus	Generalist	Bellwood and Pratchett (2013)
Chaetodon interruptus	Generalist	Bellwood and Pratchett (2013)
Chaetodon kleinii	Generalist	Bellwood and Pratchett (2013); Berumen et al. (2011); Harmelin-Vivien ML (1989)
Chaetodon lineolatus	Generalist	Bellwood and Pratchett (2013)
Chaetodon lunula	Generalist	Bellwood and Pratchett (2013); Bouchon-Navaro (1986)
Chaetodon lunulatus	Specialist	Berumen et al. (2011); Nagelkerken et al. (2009)
Chaetodon madagaskariensis	Generalist	Bellwood and Pratchett (2013)
Chaetodon melannotus	Generalist	Bellwood and Pratchett (2013); Berumen et al. (2011)
Chaetodon mertensii	Generalist	Bellwood and Pratchett (2013)
Chaetodon meyeri	Specialist	Bellwood and Pratchett (2013); Berumen et al. (2011)
Chaetodon miliaris	Generalist	Bellwood and Pratchett (2013)
Chaetodon mitratus	Generalist	Bellwood and Pratchett (2013)
Chaetodon multicinctus	Specialist	Bellwood and Pratchett (2013)
Chaetodon ocellatus	Generalist	Bellwood and Pratchett (2013); Pratchett (2013)
Chaetodon ocellicaudus	Specialist	Berumen et al. (2011); Pratchett (2013)
Chaetodon octofasciatus	Specialist	Bellwood and Pratchett (2013); Berumen et al. (2011)
Chaetodon ornatissimus	Specialist	Bellwood and Pratchett (2013); Berumen et al. (2011); Bouchon-Navaro (1986)
Chaetodon oxycephalus	Generalist	Bellwood and Pratchett (2013); Berumen et al. (2011)
Chaetodon paucifasciatus	Generalist	Bellwood and Pratchett (2013)
Chaetodon pelewensis	Generalist	Bellwood and Pratchett (2013); Berumen et al. (2011); Bouchon-Navaro (1986)
Chaetodon plebius	Specialist	Bellwood and Pratchett (2013)
Chaetodon punctatofasciatus	Specialist	Bellwood and Pratchett (2013); Berumen et al. (2011)
Chaetodon quadrimaculatus	Generalist	Bellwood and Pratchett (2013); Bouchon-Navaro (1986)
Chaetodon rafflesii	Generalist	Bellwood and Pratchett (2013); Berumen et al. (2011)
Chaetodon rainfordi	Specialist	Bellwood and Pratchett (2013)
Chaetodon reticulatus	Specialist	Bellwood and Pratchett (2013); Bouchon-Navaro (1986)
Chaetodon sedentarius	Generalist	Bellwood and Pratchett (2013)
Chaetodon semeion	Generalist	Bellwood and Pratchett (2013)
Chaetodon semilarvatus	Specialist	Bellwood and Pratchett (2013)

Chaetodon smithi	Generalist	Bellwood and Pratchett (2013)
Chaetodon speculum	Generalist	Pratchett (2013)
Chaetodon striatus	Generalist	Liedke et al. (2018)
Chaetodon triangulum	Specialist	Pratchett (2013)
Chaetodon trichrous	Generalist	Bellwood and Pratchett (2013)
Chaetodon trifascialis	Specialist	Bellwood and Pratchett (2013); Berumen et al. (2011); Harmelin-Vivien and Bouchon-Navaro (1983); Harmelin-Vivien (1989); Bouchon-Navaro (1986)
Chaetodon trifasciatus	Specialist	Bellwood and Pratchett (2013); Bouchon-Navaro (1986)
Chaetodon ulietensis	Generalist	Bellwood and Pratchett (2013); Berumen et al. (2011); Bouchon-Navaro (1986)
Chaetodon unimaculatus	Generalist	Bellwood and Pratchett (2013); Berumen et al. (2011); Bouchon-Navaro (1986)
Chaetodon vagabundus	Generalist	Bellwood and Pratchett (2013); Berumen et al. (2011); Harmelin-Vivien and Bouchon-Navaro (1983); Harmelin-Vivien (1989); Nagelkerken et al. (2009); Bouchon-Navaro (1986)
Chaetodon xanthocephalus	Generalist	Bellwood and Pratchett (2013)
Chaetodon xanthurus	Generalist	Bellwood and Pratchett (2013)

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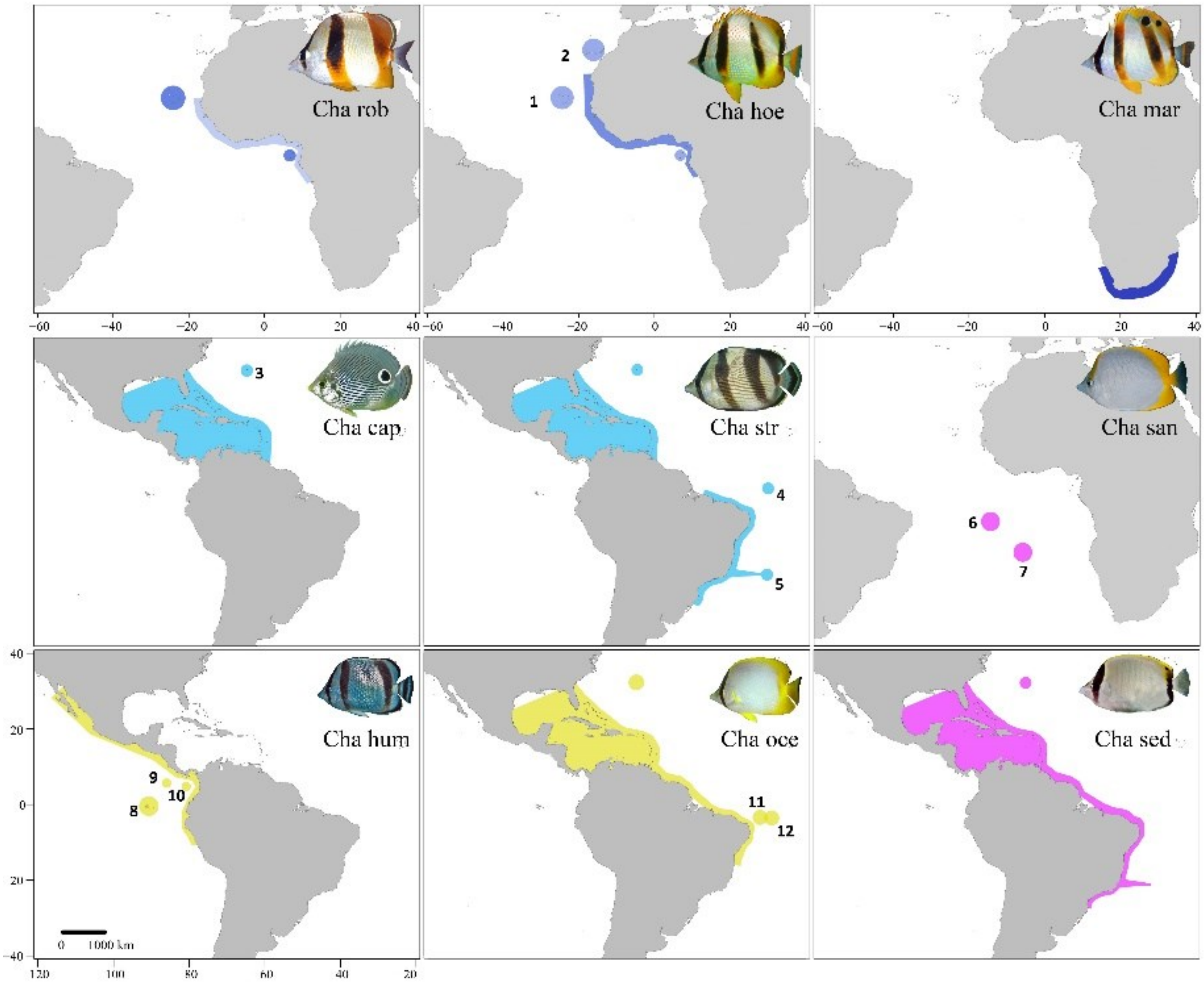
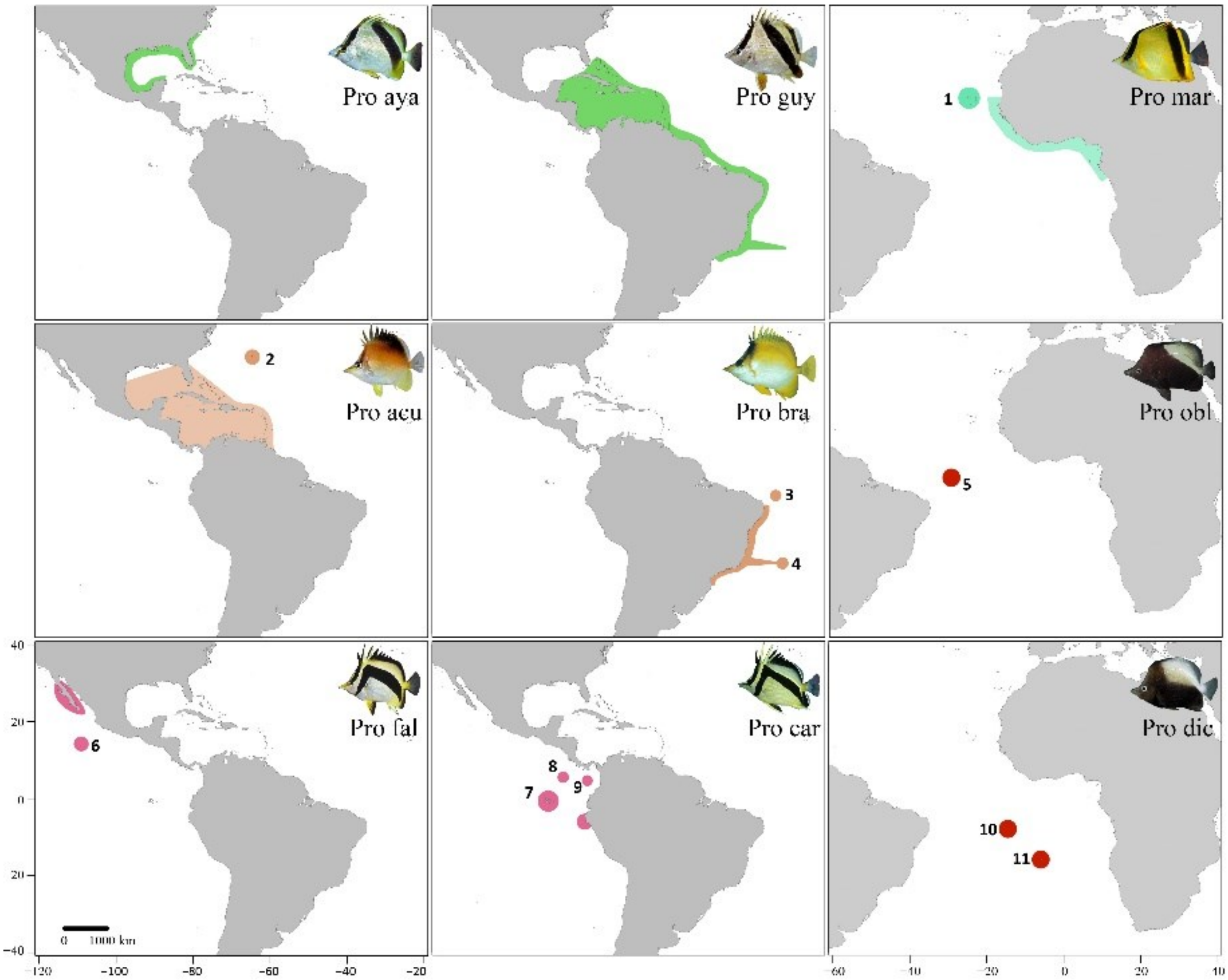
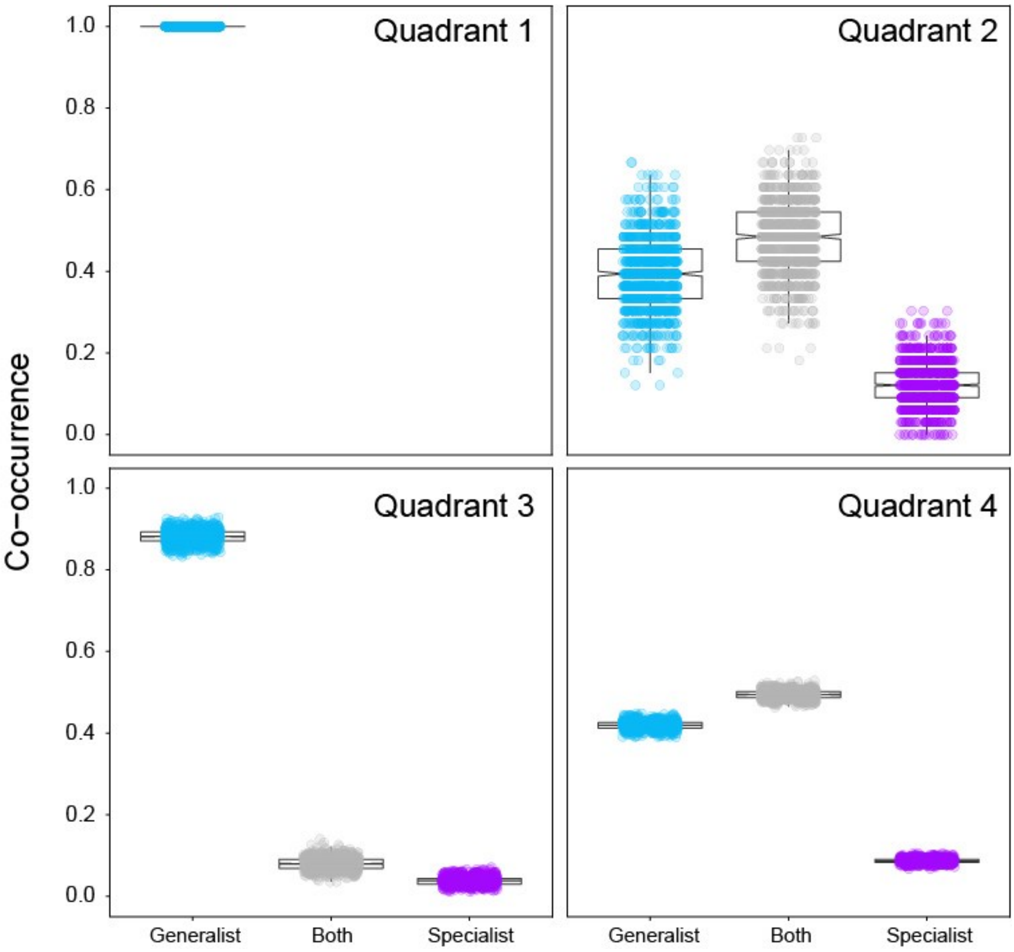


ESM 2 - Distribution of *Chaetodon* species in the Atlantic and the Eastern Pacific. Cha rob: *Chaetodon robustus*, Cha hoe: *Chaetodon hoefleri*, Cha mar: *Chaetodon marleyi*, Cha cap: *Chaetodon capistratus*, Cha str: *Chaetodon striatus*, Cha san: *Chaetodon sanctaehelenae*, Cha hum: *Chaetodon humeralis*, Cha oce: *Chaetodon ocellatus*, Cha sed: *Chaetodon sedentarius*. Numbers represent the islands: Cabo Verde (1), Canarias (2), Bermuda (3), Saint Peter and Saint Paul's archipelago (4), Trindade and Martin Vaz archipelago (5), Ascension (6), Saint Helena (7), Galapagos archipelago (8), Cocos (9), Malpelo (10), Rocas atoll (11) and Fernando de Noronha archipelago (12). Similar colours indicate sister species based on phylogeny (Bellwood et al. 2010, Fessler & Westneat 2007) or morphology and colour patterns.



ESM 3 - Distribution of *Prognathodes* species in the Atlantic and the Eastern Pacific. Pro aya: *Prognathodes aya*, Pro guy: *Prognathodes guyanensis*, Pro mar: *Prognathodes marcellae*, Pro acu: *Prognathodes aculeatus*, Pro bra: *Prognathodes brasiliensis*, Pro obl: *Prognathodes obliquus*, Pro fal: *Prognathodes falcifer*, Pro car: *Prognathodes carlhubbsi* and Pro dic: *Prognathodes dichrous*. Numbers represent islands: Cabo Verde (1), Bermuda (2), Fernando de Noronha archipelago (3), Trindade and Martin Vaz archipelago (4), Saint Peter and Saint Paul's archipelago (5), Revillagigedo (6), Galapagos archipelago (7), Cocos (8), Malpelo (9), Ascension (10) and Saint Helena (11). Similar colours indicate sister species according to morphology and colour patterns.



ESM 4 - Bootstrap analyses (1000 resamples) among diet types for each quadrant of Figure 1c. Blue and purple points represent generalist and specialist species pairs, respectively. Grey points represent species pairs in which one is generalist and the other is specialist

CAPÍTULO III

Para ser submetido ao periódico Ecology Letters

Size scalling, temperature dependence, and diet correlates of consumption rates

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Size scaling, temperature dependence, and diet correlates of consumption rates

The consumption rates of reef fishes can be guided by different factors affecting their metabolism. Here we analysed how water temperature, body mass and diet can influence the bite rates of cryptobenthic fishes from the genus *Ophioblennius*. For this we counted the bites in the substratum of four *Ophioblennius* species in eight localities of the Atlantic Ocean. We also sampled individuals from two species to quantify their diets. Bite rates were not correlated to species diet, but it were positively related to temperature and inversely related to body size, indicating the influence of these factores in species consumption rate. We found a specialist detritivore diet for all *Ophioblennius* populations. Algae and animals were also found but with little importance for the diet featuring an accidental ingestion probably when feeding on the algal matrix.

Photos: SR Floeter, JP Krajewski, J Greenfield, RA Morais

Abstract

Consumption rates constitute a fundamental, yet elusive quantity in ecophysiology and ecosystem ecology. We often rely on consumption-rate proxies such as bite rates; however we lack a theoretical framework that formally bridges these quantities. Here, we expanded a model based on the Metabolic Theory of Ecology to quantitatively assess how feeding rates are related to consumption rates, and predict how they should change with body size, temperature, and diet. We test our predictions using data from eight populations of redlip blennies across the Atlantic Ocean. Our results confirm that bite rates vary predictably with body size but increase at a faster rate with rising temperatures than predicted from theory. We found no evidence of a diet effect in feeding rates of this clade. Our results suggest that climate change will predictably alter consumption rates of animals, with direct consequences for how energy moves through food webs.

Keywords: Bite rates, body size, diet, feeding rates, *Ophioblennius*, reef fish, temperature

Introduction

The ecological function of individuals in an ecosystem is largely determined by how much energy and nutrients they consume in order to grow, maintain bodily functions, and reproduce. Consumption rates thus constitute a centrepiece in the pursuit to link individual function to ecological processes at higher levels of organisation. In food webs, the consumption rates of heterotrophic organisms can control myriads of ecological processes, from net primary production to the recycling of energy and nutrients (Vanni 2002; Taylor et al. 2006; Roman & McCarthy 2010; Estes et al. 2011). However, measuring consumption rates is often challenging—particularly in the wild (Garvey & Whiles 2016)—because, for most organisms, individuals need to be observed exhaustively to determine their feeding period, and later sacrificed to analyse their gut content (e.g. Ferreira et al. 1998a; Wootton 1997; Garvey & Whiles 2016). Therefore, consumption rates need to be quantified indirectly, for instance, via functional response curves (Pawar et al. 2012), or by counting bite rates (i.e. number of bites on the substratum per fixed unit time; Ferreira et al. 1998a, b). This latter quantity has been notoriously used as an empirical proxy for consumption rates because it is much simpler to be tallied (e.g. Barneche et al. 2009; Longo et al. 2019). However, we still lack a theoretical framework that bridges bite rates with consumption rates formally and, in doing so, sets quantitative predictions about how bite rates vary with biotic and abiotic variables. Such framework would constitute a fundamental step towards predicting the role of individuals in food webs by better linking a widely-tallied feeding metric (bite rates) with consumption rates, which is a centrepiece in individual physiology as well as population, community, and ecosystem ecology.

By virtue of being an energy-intake rate, bite rates are expected to scale with individual body mass (Pawar et al. 2012; Medeiros et al. 2014), and to vary with abiotic variables, chief among which is temperature (Mendes et al., 2009; Ferreira et al., 1998b; Brown et al. 2004; Garvey & Whiles 2016). For example, studies focusing on terrestrial mammals (Pelletier & Festa-Bianchet 2004), marine iguanas (Wikelski & Carbone 2004), and reef fishes (Floeter et al. 2005; Barneche et al. 2009; Medeiros et al. 2014) suggested that bite rates scale negatively with increasing body size and/or positively with increasing temperature. Qualitatively, these temperature effects seem to follow the same direction as those of many other rates, such as metabolic and growth rates (Gilooly et al. 2001; Brown et al. 2004; Barneche et al. 2014; Barneche & Allen 2018). On the other hand, the size scaling of bite rates is inversely related to that of consumption rates, which scale positively with body size (Pawar et al. 2012). Hence, this warrants further theoretical investigation.

In addition to body size and temperature, the nutritional quality or energy content of diet is expected to play a role in explaining consumption—and by extension, bite—rates (Otto & Svensson 1981; Wilson et al. 2003; Hood et al. 2005; Sala et al. 2012). The energy content of primary producers and sessile invertebrates are expected to be lower than mobile invertebrates and vertebrate animals (Cumminns & Wuycheck 1971; Harmelin-Vivien 2002). Studies indicate that consumption rates can be lower when the nutritional quality of food is higher because metabolic requirements will be achieved faster. For example, herbivorous/detritivorous insect larvae may eat less often when plants exhibit higher N content (Otto & Svensson 1981). Moreover, populations of Magellanic penguins may invest less time diving and searching for food when the nutritional quality of their prey is higher (Sala et al. 2012).

In coral reef fishes, the often-observed high consumption rates of nominally detritivores has been associated with the low energy content of organic detritus and other primary producers (Wilson 2003). Detritivores are particularly important in the recycling of organic matter in both aquatic (Schaus et al. 1997; Taylor et al. 2006) and terrestrial ecosystems

(Seastedt & Crossley 1984). In reef environments, for instance, abundant crypto-benthic fishes generate a fundamental link to the maintenance of ecosystem-wide biomass by ingesting large quantities of detritus (Wilson 2003, Depczinsky et al. 2007). This group is generally characterised by species of small body sizes and is particularly abundant in tropical reefs (Brandl et al., 2018). In theory, those characteristics alone are expected to determine high biomass consumption, production, and turnover (Brown et al. 2004; Allen et al. 2005). However, we are yet to determine the relative roles of individual body size, environmental temperature, and prey type on consumption rates of detritivorous fishes. Doing so will constitute a fundamental step in formally predicting their ecosystem function at both micro- and macro-ecological scales.

In this study, we first develop a theoretical framework to derive quantitative hypotheses and predictions regarding the size scaling and temperature dependence of bite rates. We then empirically evaluate these effects, as well as those of food prey type, on the bite rates of multiple Atlantic species belonging to the crypto-benthic reef fish genus *Ophioblennius* (Perciformes: Blennidae; Fig. 1). In brief, our mathematical model predicts that bite rates will scale negatively with body size and positively with temperature. We also predict qualitatively that, holding everything else constant, populations who exhibit higher proportions of animal prey in their diet will exhibit lower bite rates. We conclude our study by discussing the potential implications of our findings in light of future ocean warming.

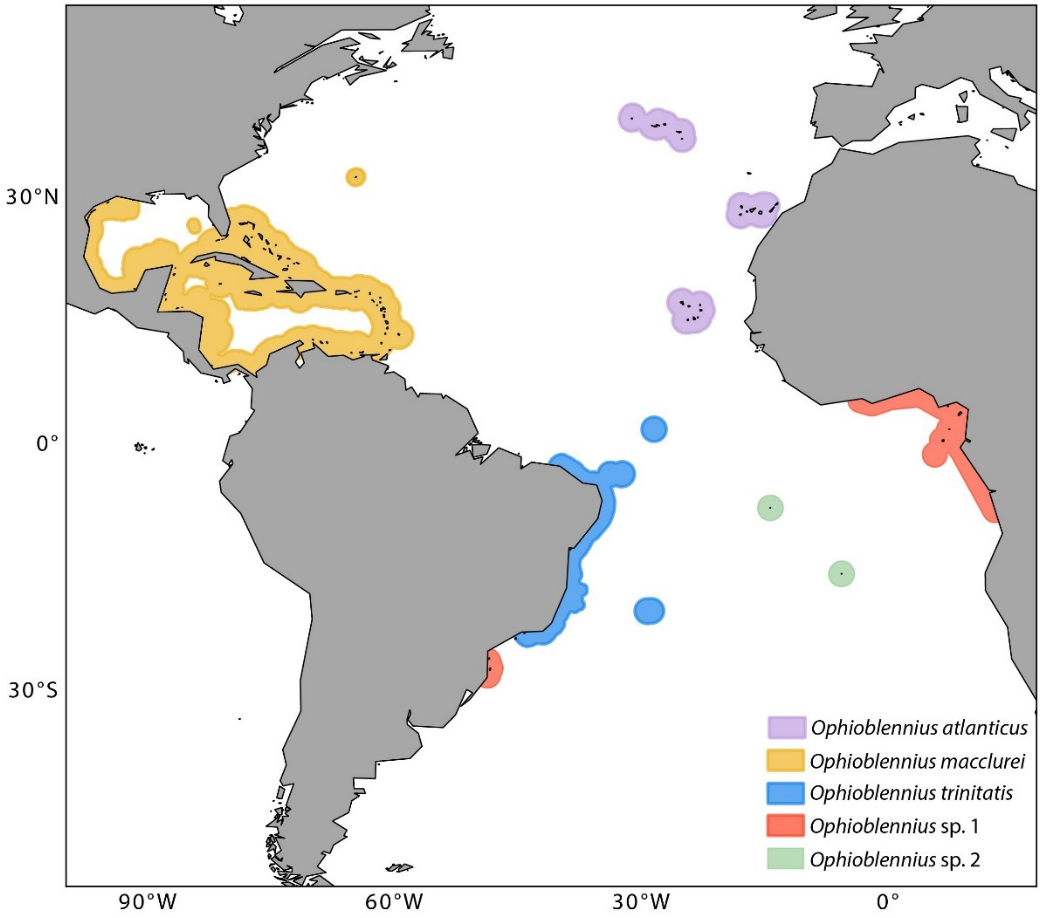

Figure 2. Distribution of five *Ophioblennius* species occurring in the Atlantic Ocean.

Material and Methods

Theory and hypotheses

Hypothesis H1: *Feeding rates are expected to exhibit negative body size scaling with a power-law scaling exponent* $-0.39 \leq \rho \leq -0.18$. Individual-level consumption rates, C_i (mm^3 of food minute^{-1}), like most physiological rates (Brown et al. 2004), are partly determined by the body size, M_i (grams), of the individual following a power function of the form:

$$C_i = c_0 {M_i}^{\alpha}, \quad (1)$$

where c_0 (mm^3 min^{-1} g$^{-\alpha}$) is a normalisation constant that is interpreted as the consumption rate of an individual whose body size is 1 gram, and α is the scaling exponent. Traditionally, bodies of theory such as the Metabolic Theory of Ecology (MTE; Brown et al. 2004) assumed that consumption rates exhibited the same size scaling of whole-organism metabolic rates. In such cases, α would take a value between 0.5 and 1, averaging at approximately 0.75 (Barneche et al. 2014). More recent developments have demonstrated that α can either be < 1 (i.e. sublinear or hypo-allometric averaging at 0.85) or > 1 (i.e. superlinear or hyper-allometric averaging at 1.06) if the individual forages respectively in 2 or 3 dimensions (Pawar et al. 2012).

Consumption rates can be directly determined by bite rates, F_i (bites minute^{-1}), if the average volume of the bite, V_i (mm^3 bite^{-1}), is known:

$$C_i = F_i V_i. \quad (2)$$

Eqn 2 assumes that the intake energy density of the food is constant (please refer to the Discussion for an in-depth consideration about violation of this assumption). The volume of the bite is also expected to exhibit size scaling:

$$V_i = v_0 M_i^{\delta}, \ (3)$$

where v_0 (mm^{-3} bite^{-1} g$^{-\delta}$) is a normalisation constant and δ is the scaling exponent. Combining equations 2 and 3 yields

$$F_i = f_0 M_i^{\rho}, \ (4)$$

where $f_0 = c_0/v_0$ is the bite rate of an individual whose body size is 1 gram, and $\rho = \alpha - \delta$. The scaling exponent of consumption rates of crypto-benthic detritivorous fishes is unknown. Based on Pawar et al. (2012), we could expect $\alpha \approx 0.85$ a priori because crypto-benthic fishes are expected to search for food on 2D surfaces. Although it is also possible that $\alpha \approx 1.06$ (or some other value in between) due to a number of factors not included in our simplified model, it is important to highlight that our theoretical prediction serves as a benchmark against which deviations can be analysed in order to generate future directions and insights. As we demonstrate in the Results section below, based on body size and mouth volume data, mean $\delta = 1.24$, and, if we constrain $0.85 \leq \alpha \leq 1.06$ (Pawar et al. 2012), then our model predicts a mean scaling exponent, ρ, contained within the -0.39 – -0.18 interval.

Hypothesis H2: *Feeding rates are expected to exhibit the same temperature dependence of whole-organism metabolic rates with an activation energy* $E_f \approx 0.6$ *eV.* Temperature is a fundamental driver of many physiological rates which determines myriads of ecological processes at higher levels of organisation, such as population growth, community biomass turnover, and ecosystem carbon residency times (Brown et al. 2004; Savage et al. 2004; Allen et al. 2005; Barneche et al. 2014; Barneche & Allen 2018). In general, physiological rates exhibit a positive exponential-like increase with increasing temperature within most of the natural range of temperatures experienced by an organism in the environment (i.e. below the optimum; Gillooly et al. 2001; 2002; Barneche et al. 2014; Barneche & Allen 2018). Here we borrow MTE's model to *empirically* characterise such effects on bite rates as:

$$f_0 = f_0(T_c)e^{\frac{E_f}{k}\left(\frac{1}{T_c} - \frac{1}{T}\right)}, (5)$$

where $f_0(T_c)$is $f_0$at an arbitrary standardising temperature T_c (Kelvin), E_f(electronvolts) is an "activation energy"-like parameter that defines the rate of exponential increase, k is the Boltzmann constant (8.62×10^{-5} eV K^{-1}), and T is the environmental temperature (K). In fishes, the temperature dependence of metabolic rates is characterised by activation energies between 0.4 – 0.8 eV (Brown et al. 2004; Barneche et al. 2014; Barneche & Allen 2018). We therefore predict that $E_f \approx 0.6$ eV by assuming that feeding rates will exhibit the same temperature dependence of metabolic rates.

Hypothesis H3: *Populations which exhibit higher proportions of animal prey in their diet will exhibit lower bite rates.* The diversity and relative abundance of diet items for most *Ophioblennius* species and populations in the Atlantic Ocean remain unexplored. *Ophioblennius macclurei*, endemic to the Caribbean, constitutes an exception to this because it is known to feed almost exclusively on organic detritus (Randall 1967). Other studies indicate that animal prey may also be ingested incidentally or in small quantities (Mendes 2000); however, there are no quantifications of whether these proportions change among populations. We therefore quantify the proportion of different diet items across populations of the *Ophioblennius* spp. Atlantic cluster, and hypothesise that populations exhibiting higher proportions of animal prey in their diet should exhibit lower bite rates.

Testing hypotheses

***Hypotheses H1* and *H2*.** The *Ophioblennius* genus encompasses 16 crypto-benthic reef fish species, five of which occur in the Atlantic Ocean (Muss et al. 2001; Lastrucci et al. 2018). The genus is distributed across all tropical and subtropical Atlantic marine provinces, and each of the five species is endemic to a single province, with the exception of one species found in both southwestern Atlantic (SWA) and the Gulf of Guinea (Lastrucci et al. 2018). Species in this genus are an ideal model to study feeding activity because they inhabit shallow reefs, are easy to observe and follow continuously, and are distributed along a range of environmental temperatures and reef types (Nursall 1977; Medeiros et al. 2014).

We estimated the bites rates of four *Ophioblennius* species in eight locations of the Atlantic Ocean encompassing both oceanic and coastal reefs. Sampling occurred during daylight by snorkelling in shallow reefs (between 3–6 m, see Table 1 for details) from 10:00 to 15:00. Separate sampling periods for summer and winter were conducted in Santa Catarina (south Brazil) because this was the only location that exhibited seasonality in the sea surface temperature, which ranged from 14 to 29ºC (Faria-Junior & Lindner 2019).

In each location, we employed the "focal-animal" method (adapted from Lehner 1996), which entailed following one *Ophioblennius* individual for three or five minutes (depending on the location) while tallying its total number of bites in the substratum. Multiple individuals were observed across locations (n = 304). To avoid possible interference in the feeding activity, the observer waited one minute before each observation for the fish to become accustomed to their presence, and subsequently followed the individual at a minimum distance of 2 m. Each individual was only sampled once. A bite was tallied when the fish hit the substratum with its jaw open, regardless of further ingestion (Longo et al. 2019). Considering that *Ophioblennius* individuals feed by taking several bites in quick succession between pauses (i.e. the "foray" mode), each bite was counted individually as opposed to considering bursts of quick bites as a single bite each.

Table 1 – Species of *Ophioblennius* and sampled locations. SST: Mean sea surface temperature (˚C) during sampling; Depth: maximum depth (m) sampled; Bite: number of individuals whose bite rates were observed; Diet: number of specimens collected for the diet analysis; Intestine: number of individuals whose intestines were measured.

Species	Location	Latitude	Longitude	SST	Depth	Bite	Diet	Intestine
O. macclurei	Bocas del Toro	9°18'38"N	82°11'41"W	29.0	1.0	15	-	-
Ophioblennius sp1.	Principe Island	1°41'29"N	7°26'29"E	29.0	1.5	50	3	3
O. trinitatis	SPSPA*	0°55'01"N	29°20'44"W	27.7	8.0	36	12	18
O. trinitatis	Rocas Atoll	3°51'37"S	33°49'07"W	29.6	0.5	48	9	30
O. trinitatis	Fernando de Noronha	3°50'20"S	32°25'0.8"W	28.5	1.5	43	-	-
Ophioblennius sp2.	Ascension Island	7°53'33"S	14°22'51"W	24.0	1.0	16	-	-
O. trinitatis	Salvador	13° 0'13"S	38°32'03"W	27.0	2.0	65	17	17
Ophioblennius sp1.	Santa Catarina	27°47'09"S	48°30'28"W	24.5	3.0	31	9	7

* St Peter and St Paul Archipelago

In addition to the number of bites, we recorded the sea surface temperature (ºC) during observations using a dive computer (Mares® Puck Pro model). Also, we visually estimated the total length L_i (cm) of each fish individual to the nearest 1 cm to calculate its body mass (M) through well-established relationships of the form $M_i = aL_i^b$ (Froese & Pauly 2019).

We combined eqns 4 and 5 and transformed it to the natural log scale to test the effects of body size and temperature on bite rates:

$$\ln F_i = \Delta \ln f_0(T_c) + \ln f_0(T_c) + \rho \ln M_i + \frac{E_f}{k}\left(\frac{1}{T_c} - \frac{1}{T}\right) + \beta \ln Y_i. \quad (6)$$

We adopted a hierarchical linear model based on eqn 6, which was implemented in a Bayesian framework using the package *brms* (Bürkner 2018) in R (R Core Team 2019) to determine posterior distributions and associated 95% credible intervals (C.I.s) for the fitted parameters. Parameters $\ln f_0(T_c)$, ρ and E_f were treated as fixed with normal priors that were weakly informative relative to the parameter space (mean = 1, standard deviation = 2). The fixed-effect parameter, β, was added in order to account for the effects of log-transformed observation time (minutes), $\ln Y_i$. Additional uncertainty for the normalised (i.e. size- and temperature-independent) bite rate, $\ln f_0(T_c)$, was estimated at the location level (please see the online supplementary information for a model selection of random effects). This *random* effect ($\Delta \ln f_0(T_c)$) was assumed to be normally distributed, with a mean of 0, hence $\ln f_0(T_c)$ corresponds to a mean among locations. The posterior distributions of model parameters (Table S1) were estimated using Markov chain Monte Carlo (MCMC) methods by constructing four chains of 5,000 draws each, with 2,500 warm-up draws, so a total of 10,000 draws were retained to estimate posterior distributions (i.e. 4 × (5,000 - 2,500) = 10,000). Model convergence was deemed as achieved when the Gelman–Rubin statistic, $\hat{R}$ (Gelman & Rubin 1992), was 1. We used Bayesian R^2 in order to estimate the amount of explained variation of each model (Gelman et al. 2019). Posterior predictive checks are provided in the online supplementary information (Fig. S1).

To estimate the size-scaling exponent of bite volume, δ (eqn 3), we also measured the upper-bound bite size of multiple *Ophioblennius* individuals (n = 23) which were independently collected from the individuals observed to tally bite rates (see collection methods to test *Hypothesis H3* below). We opened the mouth of each collected specimen and carefully filled them with modelling dough until they were completely full, while ensuring that the dough did not invade the oesophagus. Each dough was placed between two thick coverslips and kneaded with a microscope slide to a height of 1 mm, such that the number of 1 mm^2 grids occupied by the dough on the Petri dish represented the mouth volume in mm^3 (Nunes et al. 2019). We measured the total length (cm) of the individuals which were transformed to body mass following the above-mentioned length-weight relationship (Froese

& Pauly 2019). We then transformed eqn 3 to the natural log scale to estimate the effects of size on mouth volume using a linear model:

$$\ln V_i = \ln v_0 + \delta \ln M_i. \quad (7)$$

No random effects were included. Fitting specifications followed the same procedure as described above for eqn 6. See Fig. S2 in the supplementary online information for posterior predictive checks.

***Hypothesis H3*.** We collected adult individuals from two species in five locations to evaluate gut content and mouth volume (n = 50 individuals). Individuals were collected with a hand spear, then immediately frozen—to cease enzymatic action that could degrade the gut content—and transported to the laboratory. We were not able to collect individuals from which we tallied bite rates.

In the laboratory, all individuals were measured and dissected, had their gut removed, and were fixed in 10% formaldehyde. The fullness of each gut was visually estimated and assigned to one of four proportion bins according to the amount of food: 0.25 (almost empty), 0.5 (half full), 0.75 (almost full), 1 (full; Nunes et al. 2019). The guts were sectioned in a petri dish under a stereomicroscope, where their content was separated and identified to the lowest taxonomic category possible (Nunes et al. 2019). The volume of each food item was then measured following the exact same procedure described above for the quantification of mouth volume.

For each collected specimen, we calculated the relative proportion of animal prey volume in the gut relative to all other items (excluding plastic and inorganic sediment). Individuals whose diet did not exhibit any animal content (n = 15 out of 50 individuals) were excluded from the analysis. We then took the natural logarithm of these ratios and used a hierarchical linear model to test whether these log-ratios vary across locations, which were treated as random effects on an average, across-location mean intercept. Fitting specifications followed the same procedure as described above for the bite rate model (see Fig. S3 in the supplementary online information for posterior predictive checks). A model selection procedure indicated that these ratios were not explained by gut fullness, body mass, nor temperature (supplementary online information). We then tested whether the estimated location-level log-ratios were negatively correlated with location-level normalised bite rate using a Pearson's product-moment correlation (*n* = 5 locations), hence directly testing hypothesis *H3*.

In addition to the log-ratio analysis, we also assessed the population-averaged importance of each food item, d, for all studied *Ophioblennius* populations. To do so, we calculated the feeding index, I_d (%) by relating feeding items' frequency of occurrence to the volume (Nunes et al. 2019):

$$I_d = \frac{O_d \, J_d}{\sum_{d=1}^{n} O_d \, J_d} 100, \quad (8)$$

where O_d (%) is the frequency of occurrence of food item d relative to the frequency of all n registered items at a given location, and J_d (%) is the volumetric index, which is defined as the volume (mm^3) of item d summed across individuals relative to the summed volume of all n registered items.

Hypothesis evaluation criteria. We evaluated hypotheses *H1* and *H2* based on the region of practical equivalence (ROPE) around the null value of each parameter of interest (Kruschke 2018). We accepted a hypothesis if a parameter's posterior 95% highest density interval (hereafter 95% HDI) was fully contained within the ROPE. We rejected a hypothesis if a parameter's 95% HDI fell outside the ROPE. We considered having insufficient evidence to either accept or reject a hypothesis as the 95% HDI both overlapping and exceeding the ROPE. Ideally, a ROPE should be guided by both theoretical expectations and empirical knowledge (Kruschke 2018). Thus, for hypothesis *H1*, we adopt a ROPE of $-0.5 \leq \rho \leq -0.01$ because of the inherent uncertainty contained in both δ (see Results below) and α (Pawar et al. 2012). For hypothesis *H2*, we consider a ROPE of $0.4 \leq E_f \leq 0.8$ eV because it contains many of the empirically observed temperature dependence estimates for fish metabolic rates (Brown et al. 2004; Barneche et al. 2014). Finally, we decided to accept hypothesis *H3* if the Pearson's product-moment correlation p-value, P, was < 0.05.

Results

Hypothesis H1

We observed substantial variation in bite rates among locations (Fig. S4). This variation was captured by our hierarchical modelling approach (eqn 6): specifically, our mean estimate of 0.51 for the standard deviation of the location-level deviation in normalised bite rate, $\Delta \ln f_0(T_c)$, implies that bite rate varied by about 2.8-fold ($e^{2}\times^{0.51}$) among locations after accounting for the effects of body size, temperature, and observation time.

The model fit of eqn 6 also revealed that bite rates varied systematically with body size, temperature, and observation time (Bayesian $R^2 = 0.38$; 95% HDI: 0.31 – 0.45; Table S1; Fig. 2a). In agreement with hypothesis *H1*, the mass scaling exponent of bite rates, ρ, was substantially negative and its 95% HDI was contained within the ROPE -0.5 – -0.01 (mean = -0.18; 95% HDI: -0.26 – -0.09). The model fit of eqn 7 revealed that the mass scaling exponent of mouth volume, δ, was substantially higher than 1, characterising a hyper-allometric relationship (mean = 1.24; 95% HDI: 1.16 – 1.33; Bayesian R^2 = 0.98; 95% HDI: 0.97 – 0.98; Fig. 3; Table S2).

Hypothesis H2

The mean temperature dependence of bite rates, which is characterised by the empirical activation energy E_f (eqn 6), was substantially steeper than the expected value of 0.6 eV (mean = 1.15 EV; Fig. 2b). However, we lacked sufficient evidence to either accept or reject hypothesis *H2* because the 95% HDI (0.53 – 1.77 eV) fell both within and outside the ROPE 0.4 – 0.8 eV.

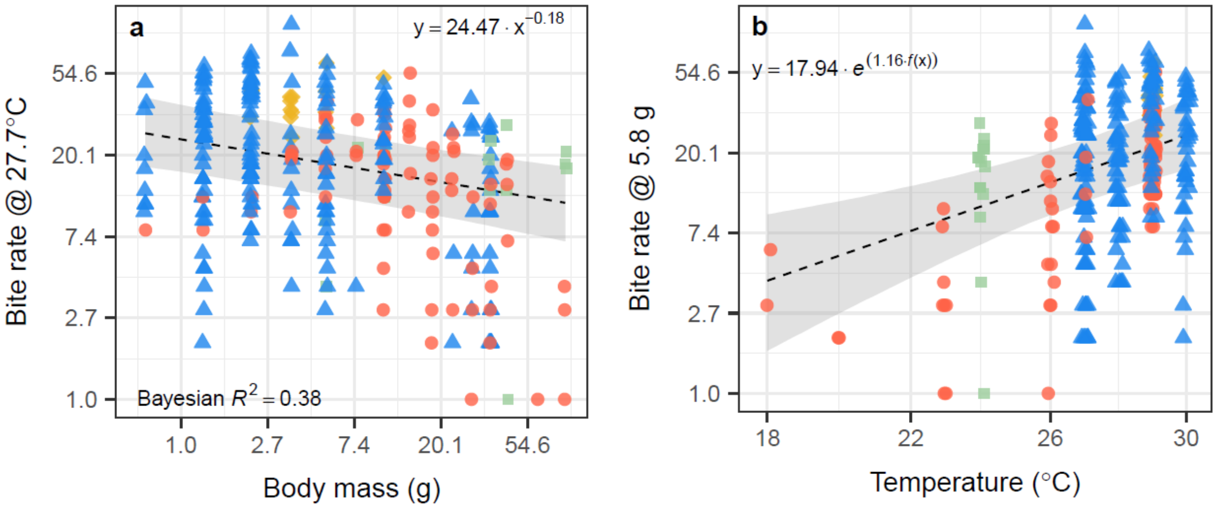

Figure 2. Scaling of bite rates of *Ophioblennius* spp. with respect to (**a**) body mass and (**b**) and temperature. Parameter estimates (listed in Table S1) were obtained using a Bayesian hierarchical linear model (eqn 6). Following eqn 5, the effect of temperature on bite rate in (**a**) was controlled for by standardising the temperature measures, T (in K), to the mean temperature in the dataset, T_c= 300.87 K (= 27.7˚C). In (**b**), the effect of body mass was controlled for by standardising measures to the mean observed body size on natural log scale (5.82 g). $f(x)$ is the Boltzmann relationship in eqn 5 assuming T_c = 300.87 K. Both plots have been corrected for the mean observation time on natural log scale (3.57 min). Colours

and symbols represent different species: *Ophioblennius trinitatis* (blue triangles), *Ophioblennius macclurei* (golden diamonds), *Ophioblennius* sp. 1 (red circles), and *Ophioblennius* sp. 2 (green squares).

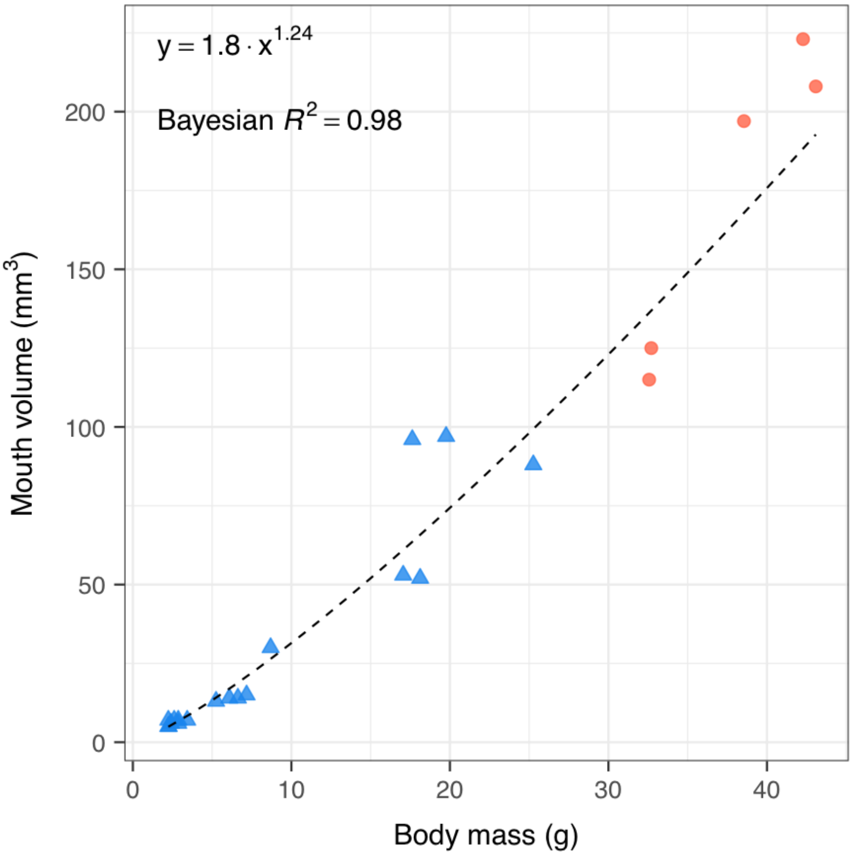

Figure 3. Scaling of mouth volume of *Ophioblennius* spp. with respect to body mass. Parameter estimates (listed in Table S2) were obtained using a Bayesian linear model following eqn 7. Colours and symbols as in Fig. 2.

Hypothesis H3

We identified 11 feeding items in the diet of *Ophioblennius* spp. Organic detritus, which was composed of morphic and amorphic forms, was the most important item across all locations, with a mean feeding index, I_d, of 87.35% (ranging between 62.03 – 98.59%; Fig.

4). Algae and animal material were also found in the diet but in low proportions, indicating either unusual or accidental ingestion. We also found plastic in the stomachs for most of the locations (Fig. 4). A complementary morphometric analysis revealed that *Ophioblennius* spp. exhibit a primarily omnivorous diet with detritivore tendencies (supplementary online information; Fig. S5).

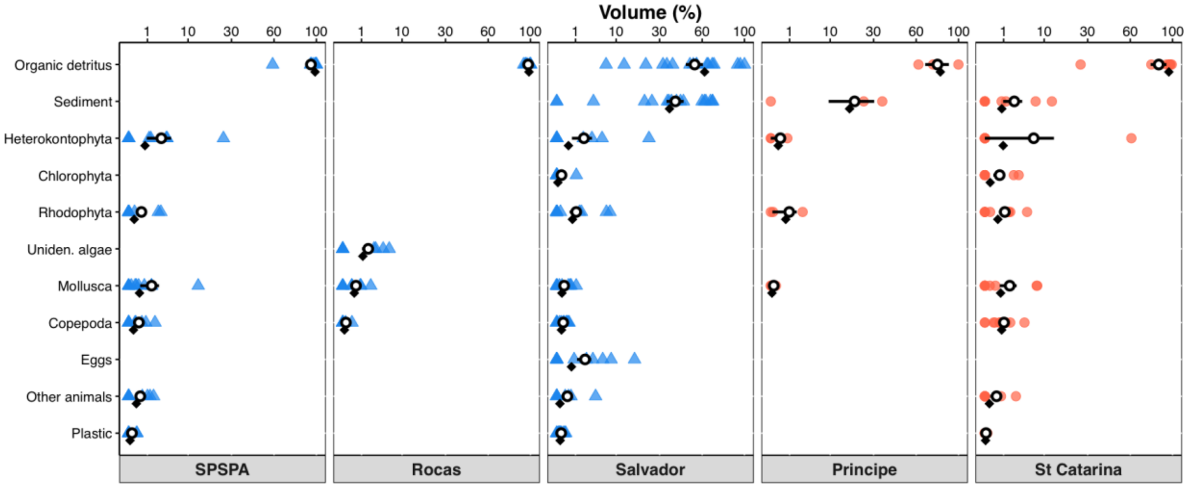

Figure 4. Diet composition of *Ophioblennius* spp. across five locations in the Atlantic Ocean. Points represent individuals and the volume (%) of a diet category in their gut. Black and white circles and black lines represent the mean volume and its standard error, respectively. Black diamonds represent the importance of each diet item at each location, as calculated using the feeding index, I_d (%). Locations: St Peter and St Paul's Archipelago (SPSPA), Rocas Atoll (Rocas), Salvador, Principe Island (Principe), and Santa Catarina (St Catarina). Colours and symbols as in Fig. 2.

The hierarchical modelling approach employed to estimate location-level diet log-ratios revealed that the log-ratios varied by about 7-fold ($e^2 \times^{0.98}$, where 0.98 is the value of the standard deviation of the location-level deviation in log-ratios) among locations (Table S3). We found no evidence of a correlation between the location-level diet log-ratios and normalised bite rates (Pearson's product-moment correlation, r = -0.0699; t = -0.1214; d.f. =

3, $P = 0.9110$; Fig. 5), and therefore we rejected hypothesis *H3*.

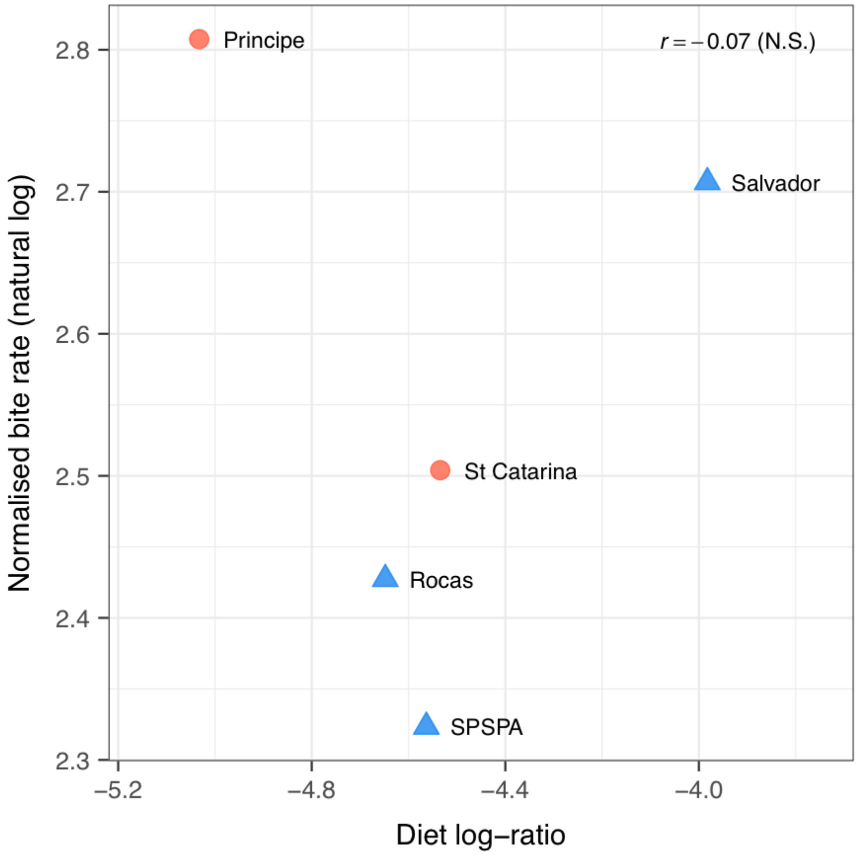

Figure 5. Relationship between location-level diet log-ratio and normalised bite rates (eqn 6). Both diet log-ratios (Table S3) and normalised bite rate (eqn 6; Table S1) estimates were calculated by adding location-level random deviations to an average intercept. Both estimates were each obtained using hierarchical Bayesian linear models with location as a random effect. Locations as in Fig. 4. Colours and symbols as in Fig. 2.

Discussion

We developed a new model inspired by the Metabolic Theory of Ecology to precisely predict how individual bite rates scale with body mass and temperature. After accounting for the effects of size and temperature, we analysed empirically whether population-average bite rates change systematically with the proportion of animal items in the diet. Although our model was put to the test using a specific clade of crypto-benthic reef fish that is widely distributed in the Atlantic Ocean, its simplicity (based on body size and temperature alone) makes it general and should therefore be applicable to most ectothermic animals. In that sense, our findings reported here establish a benchmark against which future studies can test the generality of our theoretical predictions.

In our test study group, the explanatory power of body size and temperature was modest ($R^2 = 0.38$), suggesting that additional sources of variation are influencing bite rates. Yet, the negative size-scaling of bite rates is consistent with previous studies focused on multiple groups of animals (Pelletier & Festa-Bianchet 2004; Wikelski & Carbone 2004; Barneche et al. 2009), and its estimated exponent, ρ = -0.18, matched our theoretical prediction from hypothesis H1. Moreover, based on the equality $\rho = \alpha - \delta$, and our result that δ = 1.24, our results suggest that consumption rates should exhibit a hyper-allometric relationship, with a size-scaling exponent α = 1.06. Such value has been attributed to consumers foraging in 3 dimensions (Pawar et al. 2012). Given that *Ophioblennius* spp. are primarily benthic 2D dwellers, this might suggest that the mouth-filling method used here generates an overestimate of the upper-bound bite volume mass exponent, δ, and in reality $\alpha < 1$. On the other hand, the α = 1.06 corollary could also represent an underappreciated facet of this clade's feeding behaviour. In fact, *Ophioblennius* spp. are often seen feeding on the water column for short periods of time (authors' personal communication). In either case—i.e. 2D or 3D forager—our general model provides future guidance to further investigate the feeding ecology of our test study group.

Environmental temperature is an important driver of metabolic rates in ectothermic animals, thus it should also directly affect consumption rates in predictable ways (Gilooly et al. 2001; Brown et al. 2004; Barneche et al. 2009, 2014; Schaum et al. 2017; Ferreira et al. 2019). The positive relationship between temperature and bite rates observed here is qualitatively consistent with results from other studies focused on nominally herbivorous reef fishes (e.g. Floeter et al. 2005; Mendes et al. 2009; Barneche et al. 2009). However, contrary to our prediction in hypothesis H2, our mean estimate for the temperature dependence of bite rates in *Ophioblennius* spp. (E_f = 1.15 eV) was much steeper than what would be predicted if bite rates were primarily governed by metabolic rates alone. The mechanisms underlying these findings are unclear to us; however, they seem to be consistent with the idea that populations adapted to warmer environments exhibit higher-than-expected grazing pressure on primary producers (Schaum et al. 2017).

Consistent with earlier accounts from other *Ophioblennius macclurei* (Randall 1967), all *Ophioblennius* populations showed a specialist detritivore diet. Algae, plastic, and other materials were less important, and most likely reflected accidental ingestion. Given the specialist detritivore diet of *Ophioblennius* spp., we found no evidence to support the notion that populations eating higher animal content exhibit slower bite rates (hypothesis H3). Detritus is a common component found in the algal matrix, which is the main substratum in most rocky and coral reefs (Wilson et al. 2003; Aued et al. 2018) and is the preferential foraging ground of *Ophioblennius* (Medeiros 2014). Detritus is composed mainly of filamentous algae, but its nutritional value and amino-acid composition can be improved by bacterial activity that degrades the organic matter in the algal matrix (Wilson et al. 2003). The bacteria present in the sediment and organic detritus are important for fish nutrition in coral reefs, accounting for 4 to 10% of the organic matter in blennies' territories (Choat & Clements 1998; Wilson et al. 2003). This suggests that the nutritional value of detritus might change with the environment, and as such should affect the feeding rates of detritivorous animals. We suggest that future studies in this and other groups should assess the nutritional quality of all diet components, and in particular the detritus, by directly measuring their energy density or the relation between carbon and nitrogen (Wilson et al. 2003).

Ocean warming will affect the dynamics of energy transmission in ecosystems in non-trivial ways. For example, higher temperatures will shrink the average size of many fish species (Brown et al. 2004; Allen et al. 2005; Barneche et al. 2014; Audzijonyte et al. 2019). Our results indicate that such shrinkage would drive faster bite rates, which could further compound the impacts of consumers on preys (Schaum et al. 2017; Ferreira et al. 2019), These consequences take particular significance for small cryptobenthic detritivorous such as *Ophioblennius* spp. because these fish comprise one of the most important sources of energy for larger predators in coral reef ecosystems (Brandl et al. 2019).

Conclusions

Here, we built upon and expanded existing ecological theory to predict how the bite rates—a widely employed quantity of feeding behaviour and energetic demand of animal populations—vary with body mass, environmental temperature, and diet. In testing our predictions with laboratory data and field observations from a broad geographical range, we also quantitatively integrated bite rates with the more elusive consumption rates. Therefore, our model serves as a bridge between classic behavioural ecology and ecophysiology, and a means to better predict the effects of environmental change on consumers' feeding pressure. Alterations in energy flows through cryptobenthic fish could cascade through, and help shape the structure, of future reef ecosystems.

Acknowledgements

We thank Cláudio Sampaio, Juan Pablo Quimbayo, Hugulay Maia, Luisa Fontoura, Linda Eggertsen, Moyses Barbosa, Otávio Schlickmann, Renato Morais, and Renan Ozekoski for sampling and field support. We thank Alberto Lindner, Angela Canterle, Bárbara Segal, Giulia Burle, and Paulo Horta for helping with food item identification, insights, and lab equipment. We thank ICMBio for permission to sample *Ophioblennius trinitatis* in Brazil (SISBio #58324-6 and #41327-9; PI: CELF) and Direcção de Pescas of São Tomé & Príncipe for permission to sample in Principe Island.

Funding

The sampling for this work was supported by Conselho Nacional de Desenvolvimento Científico e Tecnológico [563276/2010-0 to SRF; 458548/2013-8 to Leticia Lotufo; 403740/2012-6 to CELF], Smithsonian Tropical Research Institute (STV grant to SRF and CELF), Fundação de Amparo à Pesquisa e Inovação do Estado de Santa Catarina [6308/2011-8 to SRF], California Academy of Sciences [PI: Luiz Rocha], The Rufford Foundation [18424-1 to Renato Morais]. LTN and NSL received a scholarship from the Brazilian Ministry Educational Council – [Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Finance Code 001].

Conflict of interest

The authors declare no conflicts of interest.

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Online Supporting Information

Size scaling, temperature dependence, and diet correlates of consumption rates

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Model selection

Hypothesis H1. The dataset used to test eqn 6 in the main text includes multiple observations within locations, particularly with regards to body size. Thus, it is possible that the average mass-scaling slope, ρ, exhibits substantial within-location variation. We tested whether adding a random effect to ρ (i.e.) would yield a better model than the one presented in the main text, i.e. with only one random effect, $\Delta \ln f_0(T_c)$, on the fixed mass- and temperature-independent bite rate, $\ln f_0(T_c)$. This alternative, more complex model was compared to the simpler model using leave-one-out cross-validation (LOO), which is a fully Bayesian model selection procedure for estimating pointwise out-of-sample prediction accuracy (Hooten & Hobbs 2015; Vehtari et al. 2017). For each model, we calculated the expected log pointwise predictive density ($\widehat{elpd}_{loo}$) using the log-likelihood evaluated at the posterior simulations of the parameter values (Vehtari et al. 2017). We then calculated *p*-values for the pairwise differences in $\widehat{elpd}_{loo}(\Delta\widehat{elpd}_{loo})$ using standard errors (s.e.) and a normal probability density function. This method of calculating s.e. is reliable for data sets with many observations (n =

304 in our analysis) because the distribution of $\Delta\widehat{elpd}_{loo}$ is well approximated by a normal distribution (Vehtari et al. 2017). Although the complex model exhibited higher average predictive accuracy, it was not significantly higher ($\Delta\widehat{elpd}_{loo}$= -5.6; s.e. = 3.8; P = 0.1385), and we therefore retained the simpler model as the most parsimonious model. Model comparison was done using the R package *brms* version 2.12.0 (Bürkner 2018).

Hypothesis H3. We added the environmental temperature, as well as the natural logarithm of individual gut fullness and body mass, as covariates to the log-ratios hierarchical model described in the Materials and Methods section. We then tested whether this more complex model was substantially better than the simpler model (without these same covariates, including only location as a random effect). We employed the leave-one-out cross-validation (LOO) as described above. The simpler model exhibited substantially higher average predictive accuracy ($\Delta\widehat{elpd}_{loo}$= 2.1; s.e. = 0.8; P = 0.0094), and it was therefore retained as the most parsimonious model.

Parameter estimates and posterior predictive checks

Table S1. Point estimates and 95% highest density intervals for the parameters in eqn 6, which were estimated using a Bayesian hierarchical linear model. The model includes fixed-effect parameters: ρ, the mass scaling exponent of bite rate; E_f, the temperature dependence of bite rate; β, the observation time scaling exponent of bite rate; $\ln f_0(T_c)$, the location-level mean for the mass- and temperature-independent bite rate at temperature T_c = 27.7˚C. The random effect corresponds to the standard deviation for location-level variation in mass- and temperature-independent bite rate at T_c ($\Delta \ln f_0(T_c)$).

Parameter	**Mean estimate**	**2.5% HDI**	**97.5% HDI**
Fixed effects			
ρ	-0.18	-0.26	-0.09
E_f (eV)	1.15	0.53	1.77
β	0.31	-0.5	1.06
$\ln f_0(T_c)$ (bites min^{-1} g$^{-\rho}$)	2.81	1.77	3.96
Random effect			
Std. deviation of $\Delta \ln f_0(T_c)$	0.51	0.25	1.02

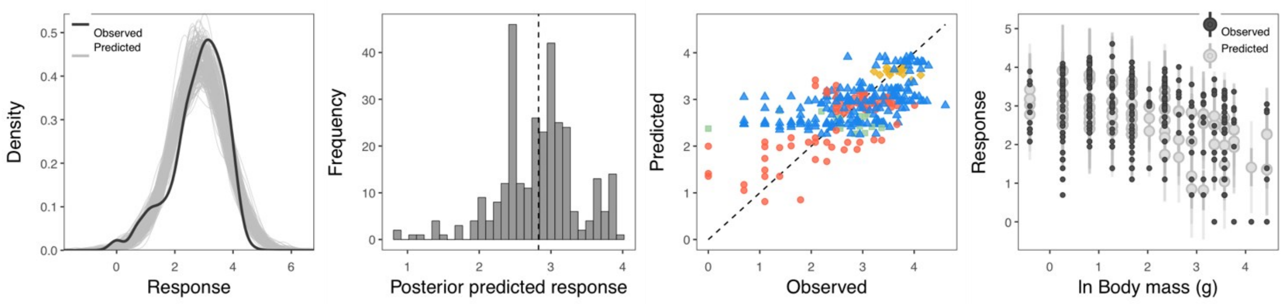

Figure S1. Posterior predictive checks of model fit for the bite-rate model. From left to right: (1) Comparison between density of observed vs. 200 predicted posterior draws of bite rates (response); (2) mean observed value (dashed line) overlaid on posterior distribution of predicted bite rates; (3) Scatter-plot between observed and observation-level mean posterior prediction of bite rates. Dashed line represents a 1-to-1 fit; (4) Posterior predictive 50% intervals (light circles) overlaid on observed (dark circles) bite rates as a function of body mass. Colours and symbols as in Fig. 2.

Table S2. Point estimates and 95% highest density intervals for the parameters in eqn 7 which were estimated using a Bayesian linear model. The model includes fixed-effect parameters: δ, the mass scaling exponent of mouth volume; $\ln v_0$, the mean for the mass-independent mouth volume.

Parameter	**Mean estimate**	**2.5% HDI**	**97.5% HDI**
δ	1.24	1.16	1.33
$\ln v_0$ (mm^3 g$^{-\delta}$)	0.59	0.38	0.80

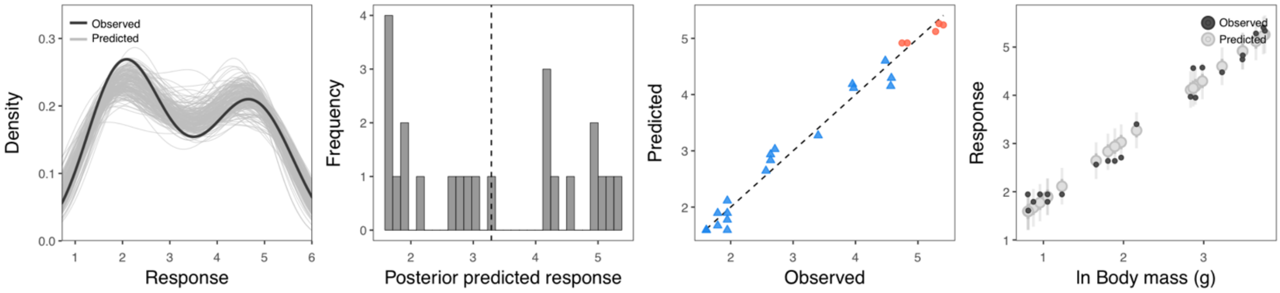

Figure S2. Posterior predictive checks of model fit for the mouth-volume model. From left to right: (1) Comparison between density of observed vs. 200 predicted posterior draws of mouth volume (response); (2) mean observed value (dashed line) overlaid on posterior distribution of predicted mouth volume; (3) Scatter-plot between observed and observation-level mean posterior prediction of mouth volume. Dashed line represents a 1-to-1 fit; (4) Posterior predictive 50% intervals (light circles) overlaid on observed (dark circles) mouth volume as a function of body mass. Colours and symbols as in Fig. 2.

Table S3. Point estimates and 95% highest density intervals for the parameters in the diet log-ratios model which were estimated using a Bayesian hierarchical linear model. The model includes a fixed-effect intercept which corresponds to an among-location mean log-ratio, and the random effect corresponds to the standard deviation for location-level variation on the intercept (*Δ*Intercept).

Parameter	**Mean estimate**	**2.5% HDI**	**97.5% HDI**
Fixed effects			
Intercept	-4.55	-6.13	-3.36
Random effect			
Std. deviation of *Δ*Intercept	0.95	0.04	3.48

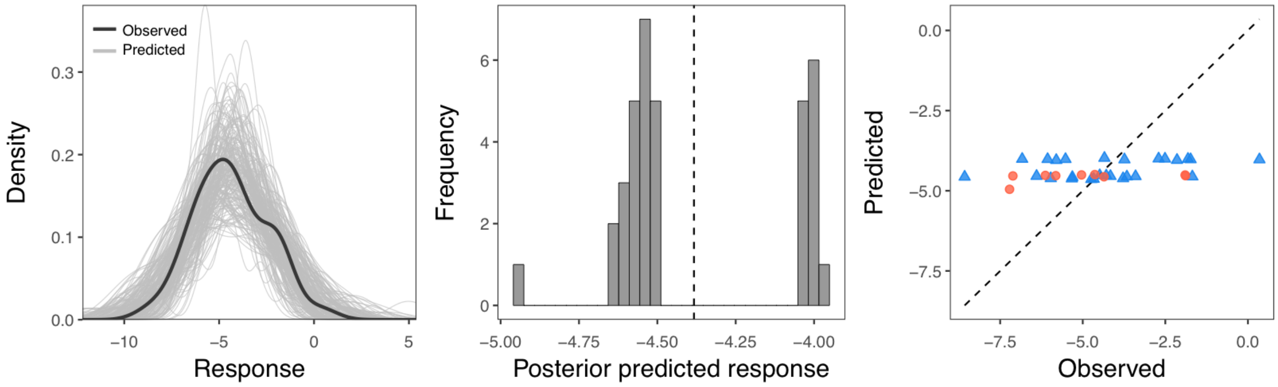

Figure S3. Posterior predictive checks of model fit for the log-ratios model. From left to right: (1) Comparison between density of observed vs. 200 predicted posterior draws of log-ratios (response); (2) mean observed value (dashed line) overlaid on posterior distribution of predicted log-ratios; (3) Scatter-plot between observed and observation-level mean posterior prediction of log-ratios. Dashed line represents a 1-to-1 fit. Colours and symbols as in Fig. 2.

Variation in bite rates among locations

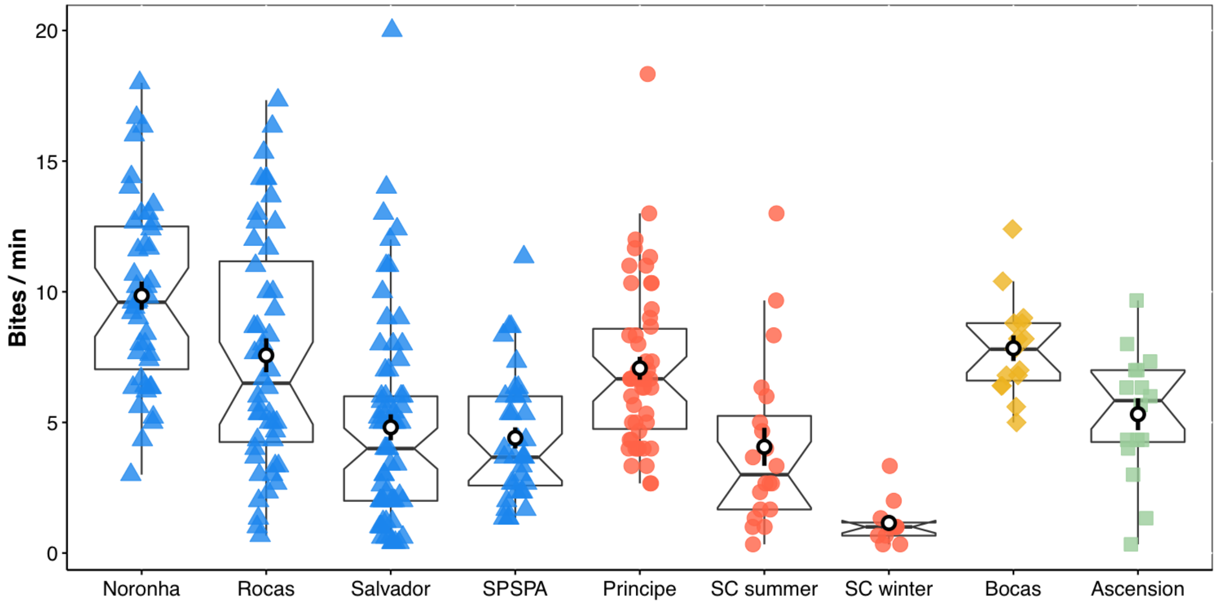

Figure S4. Notched boxplot for *Ophioblennius* spp. bite rates (bites on the substratum / minute) in the Atlantic Ocean. Each point corresponds to an individual bite rate observation. Black and white circles and black lines represent the mean number of bites and their standard error, respectively. Locations: Fernando de Noronha (Noronha), Rocas Atoll (Rocas), Salvador, St Peter and St Paul's Archipelago (SPSPA), Principe Island (Principe), Santa Catarina sampled during the summer and winter (SC summer and SC winter), Bocas del Toro (Bocas), and Ascension Island (Ascension). Colours and symbols as in Fig. 2.

Intestine morphology

The intestine total length of multiple individuals (*n* = 75) was measured and related to the fish total length to obtain the relative intestine length (Intestinal Coefficient; Berumen et al. 2011). Intestinal Coefficient below 1 indicates a carnivore diet, between 1 and 3 indicates an omnivore diet and above 3 an herbivore or detritivore diet (Ward-Campbell et al. 2005). Differences in IC among trophic groups can be explained by food nutritional quality. A longer gut in herbivores and detritivores allows food items for a longer passage, increasing digestion time and absorption of low nutritional quality and hard to digest food items, in comparison to carnivores (Kotrschal & Thomson 1968; Ward-Campbell et al. 2005). Similarly, to other studies of herbivorous and detritivorous reef fish diets (e.g. Crossman et al. 2005), we used the first third of the intestine to obtain the food material when we could not visually differentiate the stomach from the intestine. For all *Ophioblennius* populations the IC values ranged from 1 to 3 indicating an omnivore diet with detritivore tendencies (Fig. S5). Kruskal–Wallis was used to test for differences in the Intestinal Coefficient among localities. We found no evidence supporting differences in IC among locations (χ^2= 74; d.f. = 73; P = 0.45), thus suggesting that the different *Ophioblennius* populations and species feed on similar resources. Moreover, these findings indicate that this cluster of species is characterised by a specialist diet, which corroborates previous evidence obtained for *Ophioblennius macclurei* in the Caribbean (Randall 1967).

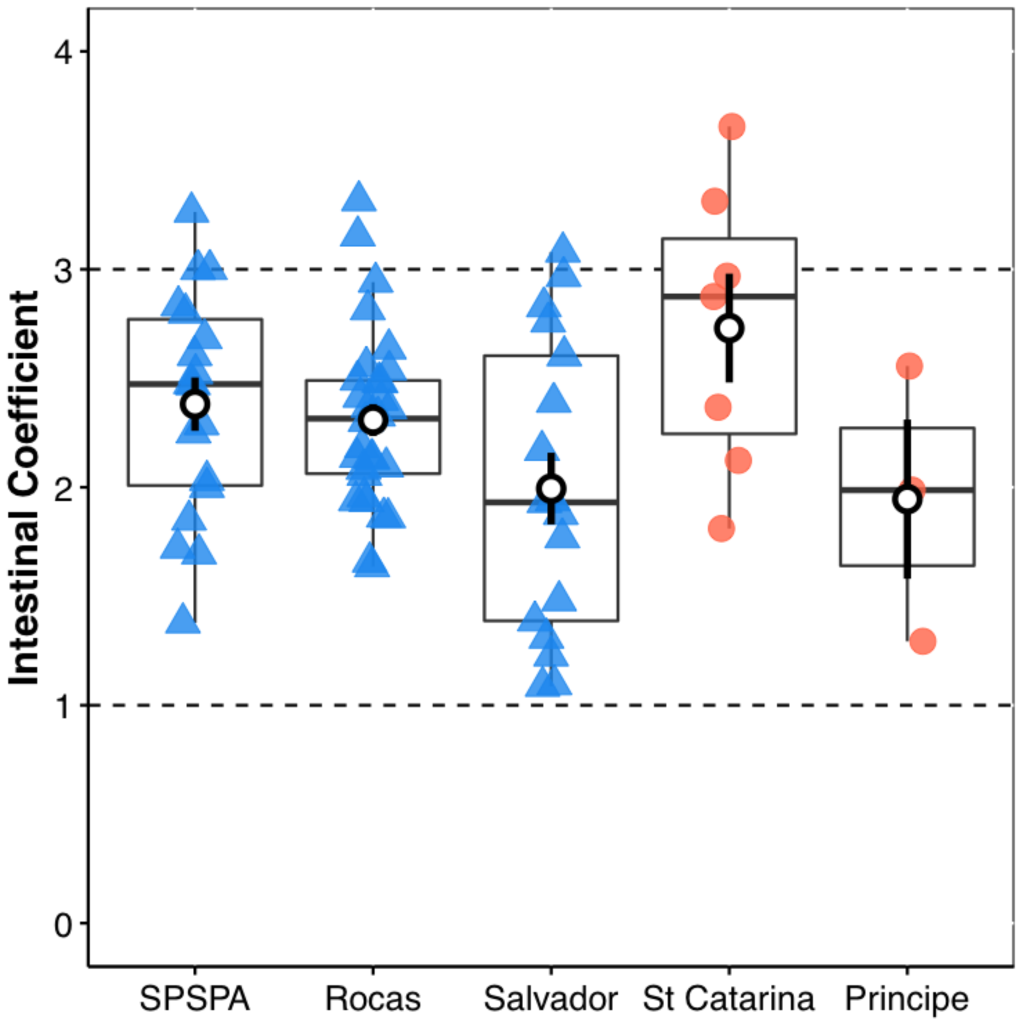

Figure S5. Boxplot for the intestinal coefficient (IC) of *Ophioblennius* spp. Locations: St Peter and St Paul's Archipelago (SPSPA), Rocas Atoll (Rocas), Salvador, Santa Catarina (SC), and Principe Island (Principe). Points represent individuals. Black and white circles and black lines represent the mean IC and their standard error, respectively. Colours and symbols as in Fig. 2.

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CONCLUSÃO GERAL

Em um mundo de mudanças ambientais e biológicas ocasionadas e/ou realçadas por impactos antrópicos, entender a ecologia trófica das espécies em diferentes escalas espaciais é essencial para prever como essas mudanças influenciam no funcionamento do ecossistema. Quantificando e qualificando o consumo de uma espécie podemos determinar, por exemplo, seu papel funcional dentro de um ecossistema e seu papel trófico dentro de uma cadeia trófica. Consequentemente, podemos prever como as relações alimentares, dentro de uma cadeia trófica, podem ser afetadas, por exemplo, por um aumento exponencial na temperatura superficial dos oceanos (SSTºC) em diferentes cenários futuros.

Embora muitas vezes não creditada e reconhecida, a ecologia trófica tem aplicabilidade em todos os níveis de organização (de indivíduos a ecossistemas) e pode ser utilizada para estudar diferentes escalas ecológicas e espaciais em um mesmo trabalho. No primeiro capítulo (NUNES et al., 2019), eu e meus coautores demonstramos que um estudo reducionista, focado em uma única espécie, é importante para entender o ambiente em que essa espécie vive (e.g. presença e importância de organismos sésseis ou crípticos que compõe a dieta da espécie) e seus aspectos populacionais (e.g. distribuição vertical e abundância da população). Nesse capítulo, vimos que a distribuição vertical da população de *Prognathodes obliquus* não é restrita ao alimento, já que essa espécie de peixe-borboleta apresenta uma dieta generalista composta por diversos táxons. Assim, a presença da população, em um determinado local, não é dependente da disponibilidade de um alimento específico, como seria o caso de espécies especialistas.

Entender os padrões de distribuição das espécies tem sido tema central na ecologia, e é importante especialmente para espécies endêmicas, cuja distribuição é dependente de processos evolutivos e ecológicos que levam à especiação em um determinado local. Além de *P. obliquus*, apenas outra espécie de Chaetodontidae ocorre no Arquipélago de São Pedro e São Paulo (ASPSP). A espécie *Chaetodon striatus* habita a zona recifal eufótica (<40m) deste arquipélago, enquanto *P. obliquus* habita a zona mesofótica. Ambas as espécies co-ocorrem apenas entre os 30 e 40 metros de profundidade, ambas com baixa abundância, o que torna difícil inferir padrões de co-ocorrência, na escala do habitat. Também, devido ao fato de ser a única espécie de *Prognathodes* habitando o ASPSP é impossível comparar localmente a ecologia trófica com outras espécies do mesmo gênero.

Embora não seja uma tarefa fácil, avaliar a co-ocorrência e comparar a ecologia das duas espécies que habitam o ASPSP, os dados gerados a partir desse primeiro capítulo, possibilitaram realizar essa comparação em uma escala global no segundo capítulo (NUNES et al., 2020). Para isso, utilizamos uma abordagem mais holística e verificamos que não existe uma relação clara entre a proximidade filogenética e a co-ocorrência das espécies de *Chaetodon*, na escala do habitat, para peixes-borboleta, em diversos recifes do mundo. Possivelmente, o efeito evolutivo atua em outras variáveis que podem afetar mais diretamente essa co-ocorrência. Também vimos que espécies especialistas tendem a co-ocorrer mais que generalistas, possivelmente devido a uma menor sobreposição nos recursos alimentares utilizados. Através da compilação de dados de diversos estudos que utilizam uma abordagem reducionista, comparamos a macroecologia trófica das espécies irmãs de Chaetodontidae que ocorrem no oceano Atlântico, que são menos estudadas comparativamente às espécies que ocorrem no oceano Pacífico. Esse capítulo inovou trazendo informações da ecologia trófica e demonstrando que algumas espécies do Atlântico têm uma dieta especialista em determinados invertebrados, enquanto a maioria das espécies possuem dieta generalista. Embora esse capítulo forneça informações tróficas essenciais, ele não trata de conectar a ecologia trófica das espécies com o ecossistema, sendo focado em avaliar o consumo alimentar, através de conteúdo estomacal, em uma escala de comunidade.

No terceiro capítulo, nós desenvolvemos um modelo para avançar na conexão da ecologia trófica com suas implicações ecossistêmicas, conectando taxa de consumo com a temperatura do ambiente (nível ecossistêmico) e massa corporal do animal (nível individual). Para esse capítulo, utilizamos como modelo espécies do gênero *Ophioblennius* (Família Blenniidae) uma das famílias de peixes mais importantes para a transferência energética em ambientes recifais. Devido à dificuldade de coletar dados de taxa de consumo para diferentes espécies em uma escala macroecológica, não pudemos utilizar a família Chaetodontidae como modelo nesse capítulo. Porém, o modelo desenvolvido e os resultados desse capítulo podem ser aplicados a qualquer animal, incluindo Chaetodontidae e qualquer outra família de peixes recifais que forrageie no substrato bentônico. Os resultados demonstram que o consumo é negativamente relacionado à massa corporal dos indivíduos, com indivíduos maiores tendo uma menor taxa de consumo, o que segue o esperado pela teoria metabólica. Já a temperatura do ambiente está positivamente relacionada ao consumo, com indivíduas mordendo o substrato mais do que o esperado. Para a dieta, não encontramos uma relação clara entre o consumo de itens animais com a taxa de consumo já que todas as espécies se mostraram especialistas em detritos. Devido a essa correlação do consumo com a temperatura e a falta de relação com a dieta, sugerimos que para determinar a taxa de consumo de uma espécie, é imprescindível analisar a qualidade nutricional do alimento. Possivelmente, variáveis abióticas influenciam a qualidade nutricional do alimento, que por sua vez influenciará no consumo das espécies e, consequentemente, influenciará em toda a cadeia trófica recifal. Em resumo, nosso modelo, apresentado no capítulo 3, conecta a ecologia comportamental clássica com a Ecofisiologia. Com a união dessas duas áreas de estudo, fornecemos uma forma de prever os efeitos das mudanças ambientais na pressão alimentar dos consumidores. Consequentemente, podemos prever alterações no fluxo de energia em cadeias tróficas que podem afetar a estrutura da comunidade e alterar os ecossistemas.

Como ressaltado nos capítulos dessa tese, estudar o consumo das espécies utilizando vários métodos é importante para não limitar as perguntas que podem ser feitas. Por isso, utilizei diferentes métodos em conjunto para obter uma melhor resolução da ecologia trófica das espécies. Por exemplo: a análise do comportamento alimentar irá inferir hábitos de forrageio e taxa de consumo; já análise de conteúdo estomacal irá qualificar e quantificar o que foi ingerido; e análise de isótopos estáveis irá inferir o que está sendo assimilado daquilo que foi ingerido. Certamente, o uso de diferentes métodos em um mesmo projeto pode trazer custos amostrais, analíticos e monetários consideráveis, além de consumir um tempo analítico maior para seu desenvolvimento. Porém, esses custos não devem impossibilitar entender holisticamente o ecossistema. Dessa forma, estudos de caso, em escala local, se mostram essenciais, já que a união de diferentes trabalhos pode gerar um maior entendimento dos padrões relacionados à ecologia trófica e expandir o conhecimento do papel trófico e funcional das espécies no ambiente.

Por fim, a importância da ecologia trófica é ímpar para a ciência. Através de estudos de conteúdo estomacal podemos sugerir a importância de uma espécie para o ambiente em que vive, assim como propor sua conservação e/ou seu uso como recurso pela sociedade humana. Compilando diversos estudos ou métodos sobre uma mesma espécie é possível aferirmos com mais precisão a importância dela para dinâmica de nutrientes e fluxo de energia no ecossistema. Historicamente, o ser humano reconhece mais facilmente a importância de estudos holísticos que tragam benefícios diretos, a curto prazo e visíveis para a sociedade. Porém, vale ressaltar que estudos reducionistas são partes fundamentais para montarmos a visão holística, mostrando que todos os trabalhos científicos são importantes independente se enxergamos sua função imediata ou não para a humanidade.

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Produções audiovisuais

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The influence of trophic and phylogenetic affinity on the co-occurrence of butterflyfishes
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2019
Prognathodes obliquus
https://www.youtube.com/watch?v=y-bDlM6ogyM

2017
Cleaning interactions at Rocas Atoll
https://www.youtube.com/watch?v=eXcCHXVWdUw

2017
Marine life of Trindade island
https://www.youtube.com/watch?v=FYNFSGRc6LA&t=96s