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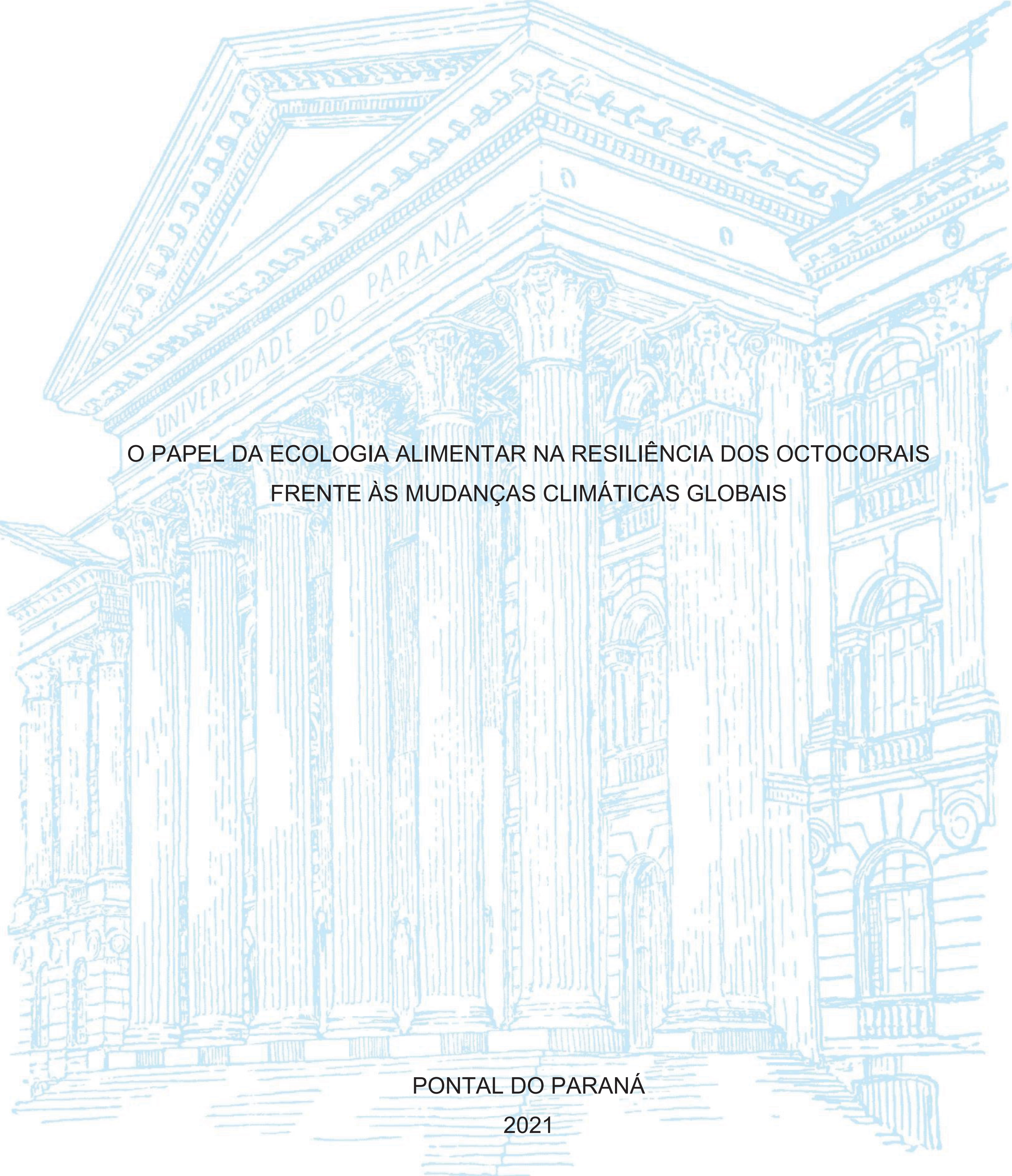
PATRICK DERVICHE



O PAPEL DA ECOLOGIA ALIMENTAR NA RESILIÊNCIA DOS OCTOCORAIS FRENTE ÀS MUDANÇAS CLIMÁTICAS GLOBAIS

PONTAL DO PARANÁ
2021

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O PAPEL DA ECOLOGIA ALIMENTAR NA RESILIÊNCIA DOS OCTOCORAIS FRENTE ÀS MUDANÇAS CLIMÁTICAS GLOBAIS

Dissertação apresentada ao curso de Pós-Graduação em Sistemas Costeiros e Oceânicos, Campus Pontal do Paraná – Centro de Estudos do Mar, Universidade Federal do Paraná, como requisito parcial à obtenção do título de Mestre em Sistemas Costeiros e Oceânicos.

Orientador: Prof. Dr. Paulo da Cunha Lana

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Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação em SISTEMAS COSTEIROS E OCEÂNICOS da Universidade Federal do Paraná foram convocados para realizar a arguição da Dissertação de Mestrado de **PATRICK DERVICHE** intitulada: **O papel da ecologia alimentar na resiliencia dos octocorais frente às mudanças climáticas globais**, sob orientação do Prof. Dr. PAULO DA CUNHA LANA, que após terem inquirido o aluno e realizada a avaliação do trabalho, são de parecer pela sua APROVAÇÃO no rito de defesa.

A outorga do título de mestre está sujeita à homologação pelo colegiado, ao atendimento de todas as indicações e correções solicitadas pela banca e ao pleno atendimento das demandas regimentais do Programa de Pós-Graduação.

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“I was playing when I invented the aqualung. I think play is the most serious thing in the world”

“The reason I love the sea I cannot explain – it's physical. When you dive you begin to feel like an angel. It's a liberation of your weight”

“*What is a scientist after all? It is a curious man looking through a keyhole, the keyhole of nature, trying to know what's going on*”

J Cousteau

RESUMO

Embora os octocorais estejam entre os organismos bênticos suspensívoros mais abundantes em costões rochosos e recifes de coral, além de desempenhar um relevante papel no acoplamento bento-pelágico, seu desempenho alimentar ainda é pouco compreendido. Os octocorais também atuam como engenheiros ecológicos, transformando a estrutura de duas dimensões dos substratos duros em sistemas tridimensionais biologicamente complexos, que fornecem refúgio, alimento e proteção para vários organismos. Neste sentido, entender a sua ecologia alimentar e a interação com seus simbiontes é essencial para modelar o acoplamento bento-pelágico, para estimar o balanço de carbono e para prever potenciais respostas às mudanças ambientais globais. A relação simbiótica entre octocorais e ofiuroides, por exemplo, é amplamente reportada na literatura, sendo comumente considerada mutualística ou comensalística. No entanto, as altas densidades de colonização do ofiuroide não-nativo *Ophiothela mirabilis* Verrill, 1987 reportadas em octocorais nos costões rochosos do Atlântico ocidental levantaram preocupações sobre seus efeitos potencialmente negativos no desempenho alimentar dos hospedeiros e, consequentemente, para todo o ecossistema. Diferentemente dos seus parentes próximos, os corais escleractíneos, recentemente têm se reportado o aumento da distribuição e abundância de octocorais em vários sistemas marinhos, processo chamado de mudança de fase, o que talvez possa ser parcialmente explicado por diferenças na ecologia alimentar. Esta dissertação teve os objetivos de (I) avaliar experimentalmente os efeitos do ofiuroide não-nativo *O. mirabilis* sobre a performance alimentar do abundante octocoral (e possivelmente seu hospedeiro favorito) *Leptogorgia punicea* (Milne Edwards & Haime, 1857) em um sistema de costão rochoso do Atlântico sul-ocidental e (II) realizar uma revisão sistemática e reavaliação de dados da ecologia alimentar dos octocorais, buscando relacioná-la com as tendências de aumento de sua distribuição ao redor do mundo. A dissertação está estruturada em dois capítulos, correspondentes a cada um desses objetivos. No primeiro capítulo, as taxas de alimentação e entradas de carbono heterotrófico em octocorais densamente colonizados por *O. mirabilis* (5,4 ± 0,6 indivíduos cm^{-2} de área de hospedeiro) foram comparados com controles sem ofiuroides, usando um sistema de câmaras de incubação *in situ*. Ao contrário de nossa expectativa, não foram observadas diferenças significativas no desempenho alimentar do octocoral entre o controle e o tratamento. Portanto, embora os octocorais hospedando *O. mirabilis* possam ter a abertura e a extensão dos pólipos prejudicados, seu desempenho alimentar permanece similar. Nesse sentido, o impacto de *O. mirabilis* no fluxo de carbono em sistemas de costão rochoso, se avaliado pela alimentação do principal hospedeiro, é mínimo. No segundo capítulo, fizemos uma reavaliação geral dos balanços de carbono e uma revisão da ecologia alimentar dos octocorais por meio de uma pesquisa sistemática e abrangente da literatura indexada, publicada entre 1960 e 2020. A heterotrofia em octocorais azooxantelados (301 µg C g AFDW^{-1} hora^{-1}) é comparativamente maior do que em octocorais zooxantelados (19 µg C g AFDW^{-1} hora^{-1}). A alimentação em suspensão é responsável por 186% das necessidades metabólicas em octocorais azooxantelados e apenas 29% em octocorais zooxantelados. Em compensação, a autotrofia é responsável por 149% da contribuição do carbono adquirido autotroficamente para os octocorais zooxantelados. Em conclusão, as taxas de ingestão e entradas de carbono heterotrófico identificadas tanto nos experimentos *in situ* quanto na revisão da literatura destacam o papel significativo de octocorais em tais processos de acoplamento bento-pelágico em sistemas rasos de substrato duro. Embora as invasões biológicas possam afetar negativamente espécies-chave ou engenheiros ecológicos, desencadeando efeitos na estrutura e funcionamento de ecossistemas, a ausência de efeitos negativos na performance alimentar de *L. punicea* indica que os sistemas de costão rochoso do Atlântico sul-ocidental também não são significativamente impactados por *O. mirabilis.* Além disso, as mudanças de fase observadas ao redor do mundo podem estar relacionadas com as vantagens dos octocorais em sua ecologia alimentar em comparação com os escleractíneos. Duas hipóteses principais foram identificadas, incluindo a capacidade de diminuir os gastos de energia para superar eventos de estresse e a menor dependência de autotrofia. Assim, os experimentos *in situ* e a revisão da literatura permitiram identificar o relevante papel da ecologia alimentar na resiliência dos octocorais.

Palavras-chave: Octocorallia; Ecologia bêntica; Invasões biológicas; Ecologia alimentar; Alimentação suspensívora; Heterotrofia; Autotrofia; Acoplamento bento-pelágico; Balanço de carbono.

ABSTRACT

Although octocorals are among the most abundant benthic suspension feeders in several rocky shore and coral reef systems and play a relevant role in benthic-pelagic coupling, their feeding performance remains poorly understood. Octocorals also act as ecological engineers, transforming the two-dimensional structure of substrates into biologically complex three-dimensional fouling systems that provide refuge, food, and protection for many organisms. In this sense, understanding their feeding ecology and interaction with their symbionts is essential to model benthic-pelagic coupling, to estimate the carbon balance and to predict their potential responses to environmental changes. The symbiotic relationship between octocorals and brittle stars, for instance, is widely reported in the literature and is commonly considered mutualistic or commensalistic. However, the high colonization densities of the nonnative brittle star *Ophiothela mirabilis* Verrill, 1987 reported in octocorals on the rocky shores of the western Atlantic have raised concerns about potential negative effects on host feeding performance. Unlike their close relatives, the scleractinian corals, octocorals are maintaining and even increasing their abundance and distribution range in many marine systems, which may be partially explained by differences in their feeding ecology. This dissertation aimed to (I) assess the effects of the nonnative brittle star *O. mirabilis* on the feeding performance of the abundant octocoral (and possibly its favorite host) *Leptogorgia punicea* (Milne Edwards & Haime, 1857) in a rocky shore system of the southwestern Atlantic and (II) perform a systematic review and data reassessment on octocoral feeding ecology, seeking to relate it to trends in their range expansion worldwide. The dissertation is structured in two chapters, corresponding to each of these aims. In the first chapter, the feeding rates and heterotrophic carbon inputs from octocorals densely colonized by *O. mirabilis* (5.4 ± 0.6 individuals cm^{-2} of host area) were compared to host controls without brittle stars using an *in situ* incubation chamber system. Contrary to our expectation, no significant differences were observed in octocoral feeding performance between the control and treatment groups. Therefore, although octocorals hosting *O. mirabilis* may potentially impair polyp opening and extension, their feeding performance remains similar. In this sense, the impact of *O. mirabilis* on the carbon budget of the rocky shore system driven by octocoral ingestion is minimal. In the second chapter, we performed a general reassessment of carbon balances and a review of the feeding ecology of octocorals through a systematic and comprehensive search of peer-reviewed literature published between 1960 and 2020. Heterotrophy in azooxanthellate octocorals (301 µg C g AFDW^{-1} hour^{-1}) is comparatively higher than that in zooxanthellate octocorals (19 µg C g AFDW^{-1} hour^{-1}). Suspension feeding is responsible for 186% of the metabolic demand in azooxanthellate octocorals and only 29% in zooxanthellate octocorals. In compensation, autotrophy is responsible for 149% of the contribution of autotrophically acquired carbon to zooxanthellate octocorals. In conclusion, the feeding rates and heterotrophic carbon input assessed both in the *in situ* experiments and in the literature review highlight the significant role of octocorals in such benthic-pelagic coupling processes in shallow hard-bottom systems. Although biological invasions can negatively affect key species or ecological engineers, triggering effects on the structure and functioning of ecosystems, the absence of negative effects on the feeding performance of *L. punicea* indicates that the rocky shore systems of the southwestern Atlantic are not impacted by *O. mirabilis*. Furthermore, the phase shifts reported worldwide may be related to the advantages of octocorals in their feeding ecology compared to scleractinians. Two main hypotheses were identified, including the ability to decrease energy demand to overcome stressful events and less dependence on autotrophy. Thus, the *in situ* experiments and the literature review allowed us to identify the relevant role of feeding ecology in the resilience of octocorals.

Keywords: Octocorallia; Benthic ecology; Biological invasions; Feeding ecology; Suspension feeding; Heterotrophy; Autotrophy; Benthic-pelagic coupling; Carbon budget.

SUMÁRIO

Highlights

Capítulo I. The effects of the nonnative brittle star *Ophiothela mirabilis* Verrill, 1867 on the feeding performance of an octocoral host in a southwestern Atlantic rocky shore

Os efeitos do ofiuroide não-nativo *Ophiothela mirabilis* Verrill, 1867 no desempenho alimentar de um hospedeiro octocoral em um costão rochoso do Atlântico sul-ocidental

- Não houve diferença no desempenho alimentar dos octocorais colonizados ou não por *O. mirabilis*;
- Os efeitos de *O. mirabilis* nos balanços de carbono do costão rochoso são mínimos ou pouco significativos;
- Nossos resultados sugerem que a relação simbiótica entre *O. mirabilis* e *L. punicea* é de comensalismo;
- *L. punicea* desempenha um papel significativo no acoplamento bento-pelágico do costão rochoso;
- Hospedeiros com características morfológicas e funcionais distintas podem reagir de forma distinta à colonização por *O. mirabilis*.

Capítulo II. Current worldwide trends in the expansion of octocorals may be related to their feeding ecology: a literature review and data reassessment

As tendências mundiais atuais na expansão dos octocorais podem estar relacionadas à sua ecologia alimentar: uma revisão da literatura e reavaliação dos dados

- Diferenças nas demandas metabólicas não dependem da simbiose com zooxantelas;
- Octocorais azooxantelados possuem taxas de alimentação suspensívora maiores do que os zooxantelados;
- As características heterotróficas e autotróficas dos octocorais está relacionada com sua morfologia;

- Mudanças de fase entre octocorais e corais escleractíneos podem ser parcialmente explicadas por diferenças na ecologia alimentar;
- Octocorais possuem menor dependência de autotrofia e são capazes de diminuir gastos metabólicos para superar eventos de estresse.

Resumo em linguagem acessível

Embora os corais moles estejam entre os animais mais abundantes em vários costões rochosos e recifes de coral, e desempenhem um importante papel na interação entre o fundo marinho e a coluna d’água, ainda pouco se sabe sobre sua alimentação. Os corais moles se alimentam do plâncton, que são pequenas algas, animais e detritos que flutuam na coluna d’água. Além do plâncton, alguns corais moles ainda adquirem energia através das zooxantelas, microalgas presentes em seus tecidos, que realizam fotossíntese e incorporam carboidratos diretamente utilizados pelos animais hospedeiros. Os corais moles também atuam como engenheiros ecológicos, transformando a estrutura de duas dimensões dos fundos marinhos em estruturas tridimensionais cheias de vida, que fornecem refúgio, alimento, e proteção para vários outros animais. Neste sentido, entender o modo como os corais moles se alimentam e a sua interação com os animais que se hospedam em seu corpo é essencial para entender os fluxos de matéria e energia entre o fundo marinho e a coluna d’água, e para prever possíveis respostas às mudanças ambientais que estão acontecendo globalmente. A relação entre corais moles e ofiuroides (ou serpentes do mar) já foi muito estudada na literatura científica, sendo comumente considerada uma relação que beneficia ambos os animais (mutualismo) ou apenas as serpentes do mar sem oferecer prejuízos ao coral mole (comensalismo). No entanto, as altas densidades de colonização de uma espécie de serpente do mar não-nativa (*Ophiothela mirabilis,* Verrill, 1987) vistas em corais moles nos costões rochosos do oeste do oceano Atlântico têm preocupado os pesquisadores, pela possibilidade dos efeitos negativos no desempenho alimentar dos corais moles. Diferente dos seus parentes próximos, os corais verdadeiros, os corais moles estão mantendo e até aumentando sua distribuição e abundância em vários locais ao redor do mundo, o que talvez possa ser parcialmente explicado por diferenças na maneira como se alimentam. Para abordar estas questões, esta dissertação teve os objetivos de (I) avaliar os efeitos de uma espécie de serpente do mar não-nativa (*O. mirabilis*) sobre a capacidade de obter alimento de um abundante coral mole em um costão rochoso do sudoeste do oceano Atlântico e (II) realizar uma revisão e reavaliação de dados dos modos de alimentação dos corais moles, buscando relacioná-las com as tendências de aumento de sua distribuição ao redor do mundo. Para tal, a dissertação está estruturada em dois capítulos, correspondentes a cada um desses objetivos. No primeiro capítulo, um experimento de campo comparou a quantidade de alimento capturado pelo coral mole *Leptogorgia punicea* (Milne Edwards & Haime, 1857) sem serpentes do mar ou densamente colonizado por elas. Ao contrário do esperado, não foram observadas grandes diferenças no desempenho alimentar do coral mole densamente colonizado por serpentes do mar ou sem as serpentes do mar. Portanto, embora os corais moles hospedando serpentes do mar possam afetar a capacidade de se esticarem para poderem se alimentar, prejudicadas pelas serpentes do mar, seu desempenho alimentar permanece similar. Nesse sentido, o impacto das serpentes do mar no coral mole e no costão rochoso é praticamente nulo ou mal pode ser medido. No segundo capítulo, realizamos uma revisão do modo de alimentação de corais moles por meio de uma pesquisa detalhada da literatura científica, publicada entre 1960 e 2020. Corais moles que não hospedam zooxantelas se alimentam mais do plâncton do que os corais que hospedam zooxantelas. Em compensação, a energia fornecida pelas zooxantelas é capaz de suprir a demanda energética dos corais moles. Em conclusão, a quantidade de alimento que capturam na coluna d’água destaca o seu papel significativo nos processos dos costões rochosos e recifes de coral. Embora as invasões biológicas possam afetar negativamente espécies-chave ou engenheiros ecológicos, desencadeando efeitos na estrutura e funcionamento dos ecossistemas, a ausência de efeitos negativos no desempenho alimentar dos corais-moles indica que os sistemas de costões rochosos do sudoeste do Atlântico não são afetados pelas serpentes do mar não-nativas. Sugerimos que o aumento da abundância e das áreas de distribuiçao de corais moles e a diminuição de corais verdadeiros reportadas ao redor do mundo podem estar relacionados com diferenças no modo como se alimentam. Duas hipóteses principais são oferecidas, incluindo a capacidade de diminuir os gastos de energia para superar eventos de estresse e a menor dependência de autotrofia. Assim, os experimentos de campo e a revisão da literatura permitiram identificar o relevante papel da ecologia alimentar na resiliência dos octocorais.

Introdução geral

Ecologia alimentar dos octocorais e seu papel no acoplamento bento-pelágico

O séston, expressão da atividade biológica dos produtores primários e secundários e da alça microbiana na coluna d’água, é um recurso alimentar muito bem aproveitado pelos animais supensívoros, incluindo os octocorais. Os octocorais são suspensívoros passivos e sua dieta abrange fontes alimentares heterogêneas, desde a fração fina de séston, como matéria orgânica dissolvida (Schlichter et al., 1983) e pico-, nano- e microplâncton (Coppari et al., 2019), até material particulado detrítico (Tsounis et al., 2006) e presas do mesoplâncton (Coma et al., 2001). Alternativamente, vários octocorais também exibem interações simbióticas com as zooxantelas, que são dinoflagelados fotossintéticos principalmente da família Symbiodiniaceae (Wainwright, 1967; LaJeunesse, 2020). As algas endossimbiontes fornecem uma proporção considerável de carbono fixado fotossinteticamente para o octocoral hospedeiro. Embora a autotrofia possa cobrir a necessidade de energia, ela não atende todas as necessidades nutricionais necessárias para os hospedeiros, já que nutrientes essenciais, como o nitrogênio e o fósforo, continuam dependendo da heterotrofia (Goldberg, 2018). Dessa maneira, os octocorais zooxantelados também são definidos como organismos mixotróficos (Coppari et al., 2019). Independentemente de sua origem, as entradas de carbono mantêm as atividades metabólicas essenciais dos octocorais, que são basicamente respiração, crescimento e reprodução (Fabricius et al., 1995).

Os octocorais são um dos organismos bênticos mais abundantes em vários ecossistemas, incluindo os costões rochosos do Atlântico ocidental e os recifes de coral do Caribe e Indo-Pacífico (Benayahu et al. 2019; Johnson and Hallock 2020). O acoplamento bento-pelágico, expresso por fluxos de energia, nutrientes e contaminantes, desempenha um papel significativo em ambientes costeiros e de plataforma. Os recursos alimentares pelágicos são consumidos pelos organismos bênticos suspensívoros, que por sua vez liberam matéria orgânica como muco e resíduos metabólicos (Leal et al. 2014b). O sequestro de carbono de suas atividades de alimentação atua como um sumidouro relevante no balanço de carbono azul (Coppari et al. 2019). Além disso, os octocorais desempenham um papel fundamental como engenheiros do ecossistema por meio do acúmulo de biomassa da alimentação heterotrófica e autotrófica. Eles transformam substratos bidimensionais em sistemas de incrustação tridimensionais biologicamente complexos, fornecendo habitat, alimento e proteção para vários organismos (Gili and Coma 1998). Suas estruturas atuam como "*baffles*", aumentando a turbulência e favorecendo a deposição de sedimento local, o que pode afetar o sucesso da fixação de larvas e a sucessão da estrutura do recife (Cerpovicz and Lasker 2021).

Relações simbióticas entre octocorais e ofiuroides

Várias espécies de ofiuroides são simbiontes epizóicos e sua relação com os hospedeiros é frequentemente considerada comensalística ou mutualística (Hendler 1984; Grange 1991; Mosher and Watling 2009; Girard et al. 2016). O uso de outros invertebrados como refúgios ou como mecanismos de dispersão está bem documentado (Hendler and Littman 1986; Ohtsuka et al. 2010; Mekhova et al. 2018). Alguns hospedeiros que se alimentam de suspensão podem se beneficiar da limpeza de suas superfícies inalantes, pois os ofiuroides se alimentam das partículas em seus corpos (Hendler 1984). O comportamento de limpeza também pode promover uma maior resiliência dos octocorais e antipatários contra eventos perturbadores, como derramamentos de óleo e deslizamentos de terra (Grange 1991; Girard et al. 2016).

Ao contrário da maioria dos casos de simbiose entre ofiuroides e hospedeiros, as altas densidades de colonização nos hospedeiros do ofiuroide *Ophiothela mirabilis* Verrill, 1867 reportadas no Atlântico ocidental podem indicar impactos negativos (Mantelatto et al. 2016). Sua presença pode obstruir o fluxo de água nas estruturas de alimentação do hospedeiro, restringir a extensão do pólipo ou induzir o hospedeiro a um maior arrasto (Mantelatto et al. 2016). Além disso, *O. mirabilis* também pode impactar outras espécies epizoicas associadas a octocorais, como ctenóforos e caprelídeos (Glynn et al., 2019). Por outro lado, estudos de campo e de laboratório não observaram marcas visuais de dano direto por *O. mirabilis* aos tecidos dos octocorais (Rich et al., 2020; Glynn et al., 2021). Experimentos de laboratório controlados também não indicaram nenhum dano substancial aos hospedeiros octocorais por *O. mirabilis* (Glynn et al., 2021). Mesmo assim, estudos *in situ* ainda são necessários para avaliar se as respostas do hospedeiro ao *O. mirabilis* são positivas, negativas ou neutras.

Efeitos negativos na alimentação suspensívora de *L. punicea* podem se refletir nos balanços de carbono de um sistema de costão rochoso no Atlântico ocidental. A avaliação das mudanças na biodiversidade e nos ecossistemas receptores permite avaliar a magnitude dos impactos de diferentes espécies não-nativas (Blackburn et al. 2011, 2014). Entre a grande variedade de métodos disponíveis na literatura, as câmaras de incubação *in situ* são uma abordagem de campo eficiente para avaliar a ecologia alimentar dos organismos bênticos suspensívoros (Ribes et al. 2000; Tsounis et al. 2006b; Coppari et al. 2016) e as respostas da biota aos distúrbios naturais e antrópicos (Roth et al. 2019). Além disso, as avaliações quantitativas do plâncton nos permitem entender melhor os ciclos biogeoquímicos, especialmente o acoplamento bento-pelágico dos sistemas costeiros e oceânicos (Lombard et al. 2019).

Mudanças de fase: a expansão dos octocorais e o declínio dos corais escleractíneos

Os recifes de coral são um dos ecossistemas mais diversos e produtivos do mundo (Connell 1978; Brandl et al. 2019). Além disso, fornecem bens e serviços importantes às populações costeiras, como pesca, turismo e proteção à tempestades (Cesar and van Beukering 2004). Apesar de seu relevante papel ecológico e econômico, os recifes de coral vêm sendo seriamente ameaçados por impactos (Richmond 1993), tais como mudanças climáticas (Hoegh-Guldberg and Bruno 2010), incluindo aumentos de temperatura (Heron et al. 2016), irradiações excessivas (Shick et al. 1996; Lesser 2011) e acidificação dos oceanos (Cornwall et al. 2021), além de surtos de predadores (Deaker et al. 2020), exposição a poluentes e eutrofização (Vollstedt et al. 2020; Zhao et al. 2021), e sedimentação (Baum et al. 2015). Eventos estressantes podem transformar sistemas estáveis em sistemas alternativos persistentes, que são caracterizados por um conjunto diferente de processos e funções do ecossistema (Schröder et al. 2005; Fung et al. 2011). Mudanças de fase de corais escleractíneos para outros organismos dominantes, como octocorais, coralimorfários, algas, esponjas, anêmonas e ascídias têm sido relatadas em muitos lugares do mundo, incluindo os oceanos Índico, Pacífico e Atlântico (Norström et al. 2009).

Ao contrário dos corais escleractíneos que têm diminuído sua distribuição em todo o mundo, os octocorais tem se tornado dominantes em diversos sistemas de recifes perturbados (Inoue et al., 2013; Lenz et al., 2015; Owen et al., 2020; Ruzicka et al., 2013). A resiliência relativa dos octocorais às mudanças nas condições ambientais talvez possa ser parcialmente explicada por diferenças na sua ecologia alimentar (Fabricius e Klumpp, 1995; Pupier et al., 2019; Tsounis et al., 2018). Além disso, outros fatores também podem contribuir para as mudanças de fase, como estratégias de reprodução (Lasker et al. 2020a), resistência à acidificação dos oceanos (Inoue et al. 2013), ou a produção de aleloquímicos para impedir o assentamento (Rodriguez et al. 2020). Nesse sentido, é possível que octocorais possuam vantagens competitivas de alimentação maiores do que os corais escleractíneos, o que explicaria parte das atuais mudanças de fase.

Estruturação da dissertação

O objetivo inicial desta dissertação se limitava à avaliação dos impactos de um ofiuroide não-nativo sobre a performance alimentar dos seus hospedeiros octocorais, através de experimentos manipulativos de campo. Embora houvesse suposições de impactos negativos na literatura, experimentos de campo avaliando os impactos ainda não haviam sido realizados. No entanto, a pesquisa foi paralisada em março de 2020, devido à pandemia do COVID-19. Para contornar este período incerto, sem perspectivas imediatas das saídas de campo e das atividades laboratoriais, optei por realizar um levantamento sistemático da ecologia alimentar de octocorais, tema que agregaria conhecimento ao objetivo inicial da dissertação e que ainda não havia sido objeto de qualquer revisão (Johnson and Hallock 2020). A adoção de rigorosos protocolos sanitários no início de 2021 permitiu a retomada do objetivo inicial do trabalho e a estruturação da dissertação em seu formato atual, com dois capítulos que se complementam e procuram responder a uma questão de interesse mais global, partindo de um experimento *in situ* associado com uma reavaliação sistemática da literatura.

Os dois capítulos da dissertação foram respectivamente formatados para a submissão aos periódicos científicos de língua inglesa *Biological Invasions* e *Marine Biology*. No primeiro capítulo, já submetido, buscamos avaliar os efeitos do ofiuroide não-nativo *Ophiothela mirabilis* Verrill, 1867 sobre a performance alimentar do octocoral azooxantelado *Leptogorgia punicea* (Milne Edwards & Haime, 1857). No segundo capítulo, realizamos uma revisão sistemática da ecologia alimentar da subclasse Octocorallia (Alcyonaria), buscando explicar as tendências de aumento de sua distribuição ao redor do mundo, ao contrário de seus parentes próximos, os corais escleractíneos, que estão diminuindo sua distribuição.

Todos os conjuntos de dados e os códigos R dessa dissertação estão disponíveis no repositório GitHub, https://github.com/pderviche/.

Capítulo I. The effects of the nonnative brittle star *Ophiothela mirabilis* Verrill, 1867 on the feeding performance of an octocoral host in a southwestern Atlantic rocky shore

Os efeitos do ofiuroide não-nativo *Ophiothela mirabilis* Verrill, 1867 no desempenho alimentar de um hospedeiro octocoral em um costão rochoso do Atlântico sul-ocidental

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Resumo

O ofiuroide epizóico do Pacífico *Ophiothela mirabilis* Verrill, 1867 tem se dispersado amplamente e colonizado hospedeiros em altas densidades ao longo do Atlântico ocidental. Avaliamos os impactos de *O. mirabilis* no desempenho alimentar do seu hospedeiro preferencial *Leptogorgia punicea* (Milne Edwards & Haime, 1857) por meio de experimentos *in situ* usando câmaras de incubação e estimamos seus efeitos putativos nos processos de acoplamento bento-pelágico de um sistema de costão rochosos. As taxas de alimentação e as entradas de carbono heterotrófico dos tratamentos de *L. punicea* com alta colonização por *O. mirabilis* (5,4 ± 0,6 indivíduos cm^{-2} de área do hospedeiro) foram comparados aos controles do hospedeiro naturalmente sem ofiuroides. Não foram observadas diferenças significativas no desempenho alimentar do hospedeiro entre o controle e os tratamentos. No geral, *L. punicea* ingeriu 3.047.118 ± 1.843.183 partículas g DW (peso seco) $^{-1}$ hora^{-1} (média ± desvio padrão), correspondendo a 116,1 ± 159,0 µg de carbono (C) g DW^{-1} hora^{-1}. Portanto, embora os octocorais hospedando *O. mirabilis* possam ter a abertura e a extensão do pólipo prejudicadas, seu desempenho alimentar permanece similar. Nesse sentido, o impacto de *O. mirabilis* no fluxo de carbono do sistema de costões rochosos impulsionado pela ingestão octocoral é mínimo. A taxa de pastejo de 49,9 ± 68,3 mg C m^{-2} dia^{-1} destaca o papel significativo de *L. punicea* em tais processos de acoplamento bento-pelágico. Mesmo assim, mais estudos experimentais de laboratório e de campo avaliando os efeitos nos taxa hospedeiros com características morfológicas e funcionais distintas são necessários para melhor compreender as respostas dos sistemas de fundo duro receptores ao longo do Atlântico ocidental às densidades crescentes de *O. mirabilis*.

Palavras-chave: Ecologia bêntica; Invasões biológicas; Acoplamento bento-pelágico; Alimentação em suspensão; Orçamento de carbono.

Abstract

The Pacific epizoic brittle star *Ophiothela mirabilis* Verrill, 1867 has widely spread and colonized hosts at high densities along the Western Atlantic. We assessed the impacts of *O. mirabilis* on the feeding performance of the preferred host *Leptogorgia punicea* (Milne Edwards & Haime, 1857) through *in situ* experiments using incubation chambers and estimated its putative effects on the benthic-pelagic coupling processes of a rocky shore system. The feeding rates and heterotrophic carbon inputs of *L. punicea* treatments with high colonization by *O. mirabilis* (5.4 ± 0.6 individuals cm^{-2} of host area; mean ± standard deviation) were compared to host controls naturally without brittle stars. No significant differences in host feeding performance were observed between the control and treatments. Overall, *L. punicea* ingested 3,047,118 ± 1,843,183 particles g DW (dry weight)$^{-1}$ hour^{-1}, corresponding to 116.1 ± 159.0 µg of carbon (C) g DW^{-1} hour^{-1}. Therefore, although octocorals hosting *O. mirabilis* may have impaired polyp opening and extension, their feeding performance remains similar. In this sense, the impact of *O. mirabilis* on the carbon flux of the rocky shore system driven by octocoral ingestion is minimal. The grazing rate of 49.9 ± 68.3 mg C m^{-2} day^{-1} highlights the significant role of *L. punicea* in such benthic-pelagic coupling processes. Notwithstanding, further laboratory and field experimental studies assessing the effects on host taxa with distinct morphological and functional features are needed to better understand the responses of the recipient hard-bottom systems along the Western Atlantic to increasing densities of *O. mirabilis.*

Key words: Benthic ecology; Biological invasions; Benthic-pelagic coupling; Suspension feeding; Carbon budget.

Declarations

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Conflicts of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data and code availability

The datasets and the R codes of the current study are available in the GitHub repository, https://github.com/pderviche/Ophiothela_mirabilis_Impacts.

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1 Introduction

Several brittle star species are epizoic symbionts, and their relationship with hosts is often considered commensalistic or mutualistic (Hendler 1984; Grange 1991; Mosher and Watling 2009; Girard et al. 2016). The use of other invertebrates as refuges or as dispersion mechanisms is well documented (Hendler and Littman 1986; Ohtsuka et al. 2010; Mekhova et al. 2018). Some suspension-feeding hosts may benefit from the cleaning of their inhalant surfaces as the brittle stars feed on the particles on their bodies (Hendler 1984). Cleaning behavior may also benefit the resilience of octocorals and antipatharians against disturbing events, such as oil spills and landslides (Grange 1991; Girard et al. 2016). In contrast, the increasing populations of the nonnative brittle star *Ophiothela mirabilis* Verrill, 1867 on hard-bottom systems along the Western Atlantic and the high colonization densities on hosts may produce negative impacts. Its presence may obstruct the water flow in the host's feeding structures, constrain polyp extension, or induce the host to higher drag (Mantelatto et al. 2016). Additionally, *O. mirabilis* may also impact other epizoic species associated with octocorals, such as ctenophores and caprellids (Glynn et al. 2019). Conversely, field and laboratory observations have observed no visual marks of direct damage by *O. mirabilis* to octocoral tissues (Rich et al. 2020; Glynn et al. 2021b). In fact, controlled laboratory experiments indicated no substantial harm to octocoral hosts by *O. mirabilis* (Glynn et al. 2021b). Notwithstanding, *in situ* studies are still needed to assess whether host responses to *O. mirabilis* are positive, negative or neutral.

Ophiothela mirabilis was originally limited to the Pacific until likely anthropic activity allowed its expansion to the Atlantic (Hendler et al. 2012). The first record in nonnative waters was at Ilha do Pai, Rio de Janeiro State (Southeastern Brazil) in 2000 (Hendler et al. 2012), spreading then to several sites from Santa Catarina State (South Brazil) to Southeast Florida (Lawley et al. 2018; Glynn et al. 2019). Ecological niche models have predicted that the species has the potential to spread further across the warm marine provinces of the Western Atlantic and establish dense populations (Derviche et al. 2021). Nonnative species that rapidly spread and increase their densities across several sites encompassing different systems can be considered invasive (Blackburn et al. 2011). The impacts of *O. mirabilis* are not as noticeable, and the effects on suspension feeder hosts have not yet been assessed in the field.

Epibionts can directly and indirectly affect hosts in subtle to most significant ways, depending on their number and size (Lane et al. 2018).

The measurement of changes in recipient biodiversity and ecosystems allows for assessing the magnitude of the impacts of different non-native species (Blackburn et al. 2011, 2014). Among the wide variety of methods in the literature, *in situ* incubation chambers are an efficient field approach to analyze benthic species' feeding ecology (Ribes et al. 2000; Tsounis et al. 2006; Coppari et al. 2016) and biota responses to natural and anthropic disturbances (Roth et al. 2019). In addition, quantitative measurements of plankton allow us to further understand biogeochemical cycles, especially benthic-pelagic coupling (Lombard et al. 2019).

Octocorals are the hosts most colonized by *O. mirabilis* both in the Pacific (Granja-Fernández et al. 2014) and in the Atlantic (Derviche et al. 2021). In the southwestern Atlantic, *O. mirabilis* may be present at densities as high as 3.6 ± 3.0 individuals per cm^{-2} on *Leptogorgia punicea* (mean ± standard deviation), one of the most populated hosts by the brittle star in this region (Derviche et al. 2021). *L. punicea* is an azooxanthellate octocoral that relies on passive suspension feeding to meet its metabolic demand. The generalist diet of the genus *Leptogorgia* comprises particles from 3.6 to 320 µm (Ribes et al. 2003; Rossi et al. 2004), whereas zooplankton prey range mainly between 80 and 200 µm (Rossi et al. 2004). Arm-waving behavior and morphological structures, as well as gut content analysis, indicate that *O. mirabilis* is a suspension feeder, feeding mainly on amorphous detritus and filamentous algae (Glynn et al. 2020). The habit of *O. mirabilis* to densely colonize and be near or in contact with host polyps has raised concern about potentially negative effects on host feeding capacity (Mantelatto et al. 2016; Araújo et al. 2018). Benthic suspension feeders may change their feeding behavior as a reaction against stressors in the environment (Martinez et al. 2019). Thus, regarding the hosts' feeding performance, the high densities of *O. mirabilis* observed in the Western Atlantic may be negative, as supposed in the literature, or even neutral or positive, as often observed for other brittle star species. A relationship presumed to be commensalistic or mutualistic will become structural parasitism if the hosts are negatively affected by the 'parasite' even without their nutrients or tissues exploited (Stevens 1987).

Although *O. mirabilis* has become rather common in rocky shore and coral reef systems along the Western Atlantic, its potential effects (or lack of) on recipient assemblages are still poorly understood. Herein, we assessed the impact of the nonnative brittle star *O. mirabilis* on the feeding performance of octocoral *L. punicea*, a prominent species and ecological engineer along the southwestern Atlantic, through *in situ* experiments using incubation chambers. We hypothesize that if the brittle star constitutes a structural parasite in octocorals, then it is expected that the feeding performance of the host will be significantly reduced. In addition, we estimated the putative effects of *O. mirabilis* on the benthic-pelagic coupling processes of a rocky shore system.

2 Materials and methods

2.1 Experimental design and sampling procedures

We performed *in situ* experiments at a depth of 3 meters in Marine National Park of the Currais Islands (-25.7368°, -48.3664°) in southern Brazil between February 14 and 15, 2021. Through a hierarchical experimental design (Fig. 1), experiments were conducted with *L. punicea* hosts under high natural colonization of *O. mirabilis* (treatment), which are colonies visibly and factually more colonized by the brittle stars compared to the overall population, hosts naturally without brittle star individuals (host control), and without hosts or brittle star individuals (sampling artifact control).

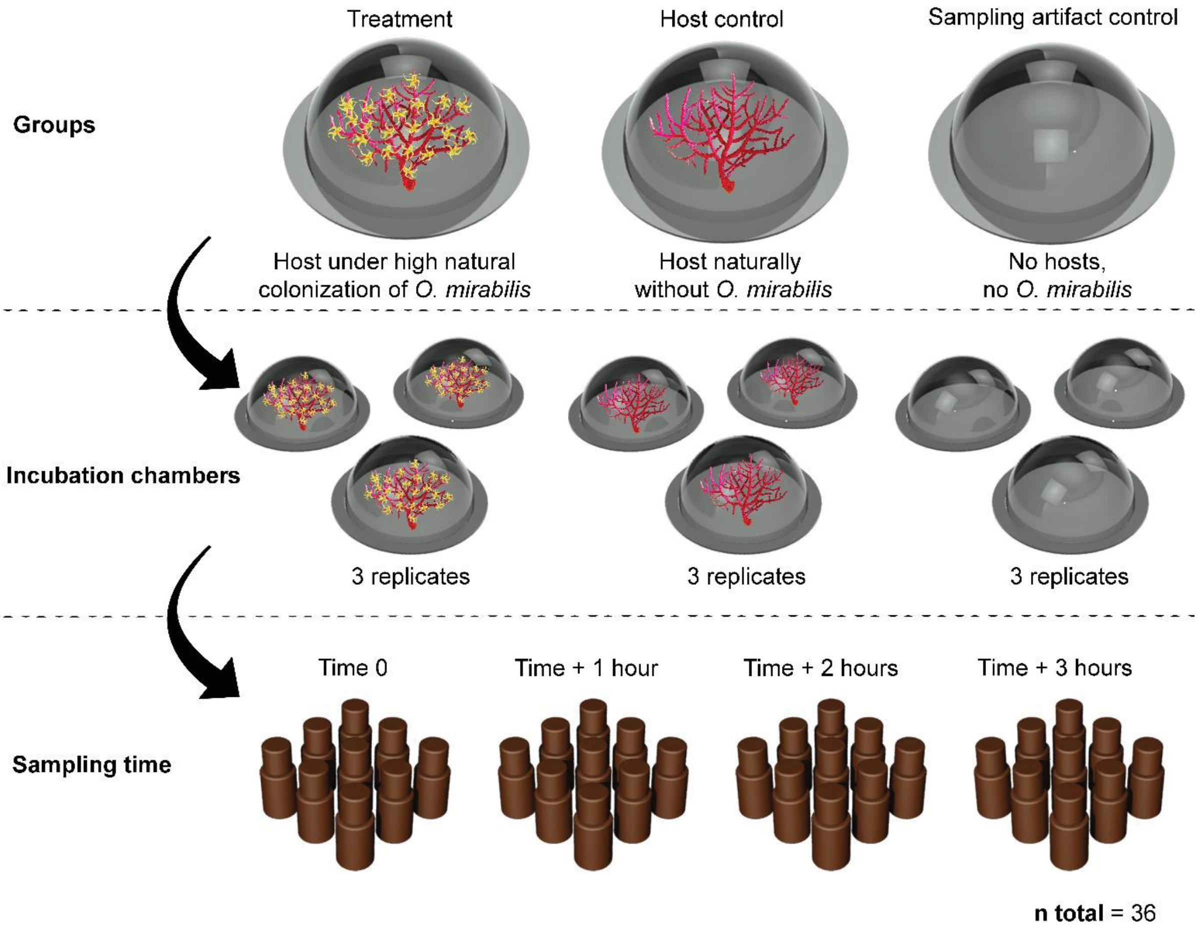

Fig. 1 The experimental design used in this study. Experiments were conducted with *Leptogorgia punicea* colonies under high natural colonization of *Ophiothela mirabilis* (treatment), hosts naturally without brittle star individuals (host control), and no host colonies or brittle star individuals (sampling artifact control). The experiments lasted for three hours, and 125 ml of seawater was sampled at the beginning (t_0) and every hour (t_1, t_2, and t_3) of the experiment

The experiments were performed using *in situ* incubation chambers (Fig. 2), adapted from Ribes et al. (2000). The system can alternate between open circulation, exchange between the seawater outside and the chamber's interior, and closed circulation, only with the seawater of its own chamber. The innovation of our system is the possibility of subaquatic sampling of seawater at specific times through a set of valves that traps seawater in polyethylene bottles. The water that circulates in each 2,590 ml acrylic chamber comes from the same sampling point during open circulation to avoid composition stochasticity in the planktonic community. A set of tubes allows for the individual water flow in each chamber, acting as replicates. A 120 $l.h^{-1}$ pump allows the turbulent flow of seawater and suspended particle maintenance within each chamber and in the bottles. A 6V 12Ah battery powers the nine circulation pumps.

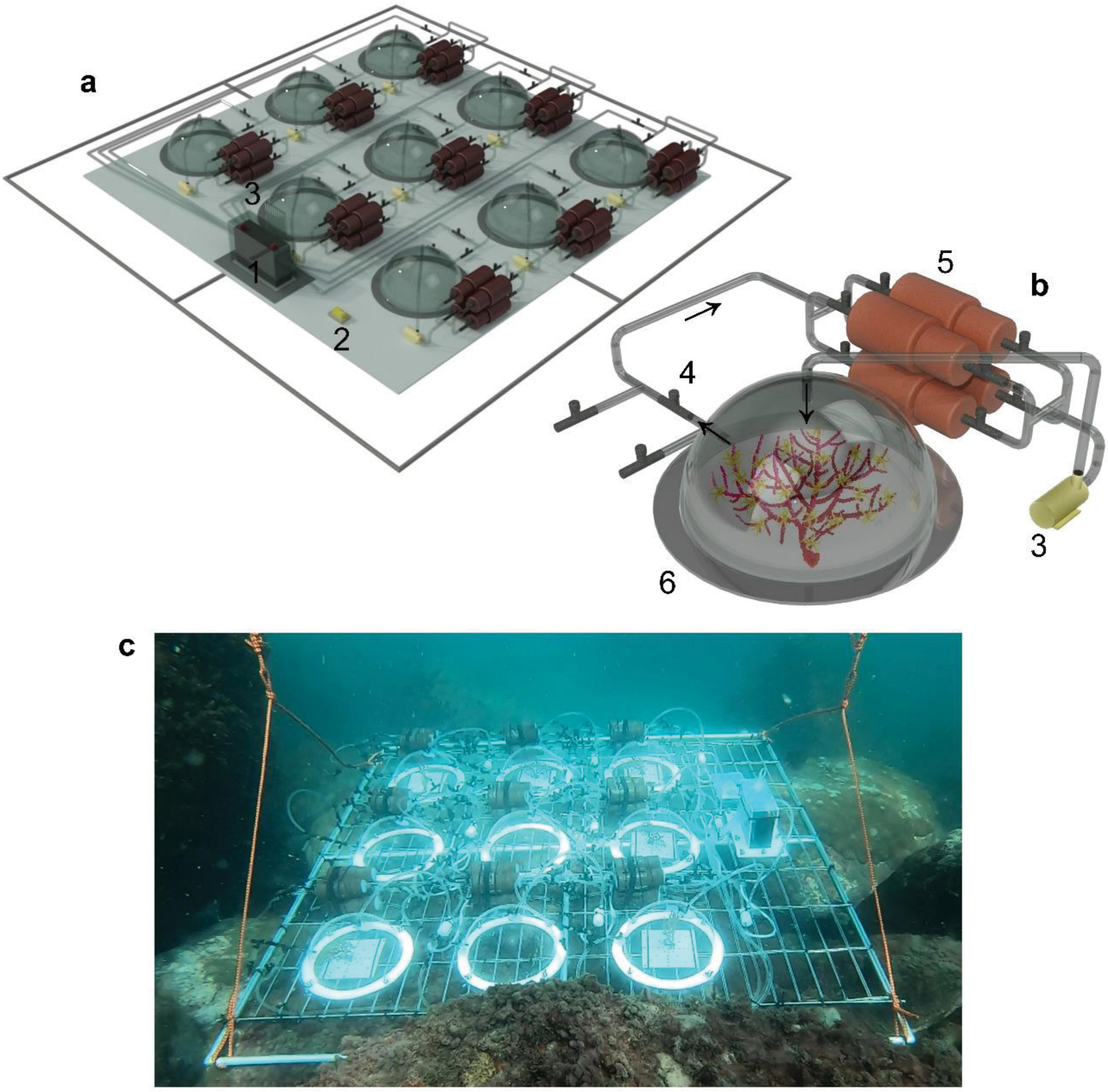

Fig. 2 a Image of an *in situ* incubation chamber system at 3 m depth. 6 V 12 Ah battery (1); on/off power switch (2); water sampling point that supplies chambers in open circulation (3); **b** view of an individual incubation chamber. 120 $l.h^{-1}$ circulation pump (3); plastic valve (4); 125 ml polyethylene bottle (5); and 2,090 ml acrylic dome (6). The arrows indicate the direction of the water flow; and **c** the real *in situ* incubation chamber system in the field

Colonies of *L. punicea* with similar biomass were selected at a depth of approximately 6 meters. We collected colonies under high natural colonization of *O.*

mirabilis and colonies naturally without individuals through SCUBA diving. In the study area, living brittle stars present coloration patterns that include yellow-orange, burgundy and yellow, and black with yellow details. Hybridization within different color patterns of individuals is also observed. *L. punicea* colony treatments that were dominated by yellow-orange *O. mirabilis* specimens were selected as treatments. The hosts colonized by *O. mirabilis* and hosts without brittle stars were carefully collected with the substrate's surface layer and transplanted to 144 cm^2 (12 × 12 cm) polyethylene supports. Then, we acclimatize the *O. mirabilis* individuals and octocorals under natural conditions on rocky shores at a depth of 6 meters for 24 hours to reduce the disturbance caused by its handling and removal from their original substrate. Healthy feeding colonies with open polyps were exposed to the experiment, conducted between 10:00 AM and 01:00 PM. *Ophiothela* treatments, host controls and sampling artifact controls were randomly assigned to the chambers. To acclimatize the organisms after handling and under experimental conditions, we kept the system working for 15 minutes in open circulation with the organisms before starting the experiment.

The experiment lasted three hours, and 125 ml of seawater was sampled at the beginning (t_0) and every hour (t_1, t_2, and t_3) of the experiment to monitor the swept clearing of seston by octocoral suspension feeding. Three hours is considered more than enough to measure changes in the chambers' seston composition by passive suspension feeding (Ribes et al. 2000). Moreover, the drop in dissolved oxygen during these three hours does not significantly affect the respiration rates and organisms' behavior (Ribes et al. 2000). Seawater samples were taken on board, fixed with 8 ml of glutaraldehyde Grade I (25% aqueous solution), and then stored in thermal coolers. After landing, the seawater samples were stored in a refrigerator (2–4 °C) and analyzed nine days later for two consecutive days. The organisms were also frozen until laboratory analysis.

2.2 Laboratory procedures for estimating variation in feeding rates

Numbers of *O. mirabilis* were counted within each octocoral colony using *Zeiss Stemi 2000, ZEISS ©*. The disk diameter of *O. mirabilis* was measured for 50 individuals within each of the three octocoral colonies using a stereomicroscope

SteREO Discovery. V12, ZEISS © to assess the population structure. The degree of body regeneration of *O. mirabilis* was assessed for 50 individuals within each of the three octocoral colonies into three categories: intact specimens with six arms of similar size; split discs or broken arms; and regenerating discs or arms. The colonies of *L. punicea* were photographed using a Canon Rebel T6i camera, and the images were analyzed using photoQuad © software (Trygonis and Sini 2012) to measure the colonies' height, width (in cm) and the total surface area (in cm^2). Octocoral polyp densities, expressed by the number of polyps per 1 cm^2 of area, were obtained by counting three sampling areas of the basal, central, and distal segments of the stem of the three octocoral colonies using a stereomicroscope *SteREO Discovery. V12, ZEISS* ©. *O. mirabilis* individuals and *L. punicea* colonies were dried at 60 °C for 90 hours and weighed separately to determine the relationship between the number of individuals and the dry weight (DW, in grams) of *O. mirabilis* and the relationship between the area (cm^2) and the DW of the host *L. punicea*.

The effect on feeding rates is the variable that can most directly assess the impacts of *O. mirabilis* on host feeding performance; therefore, we calculated the predation of particles between 3 and 120 µm in diameter. The water samples were previously filtered through 120 and 65 µm meshes. The number of particles was quantified with a *Z Coulter Counter* (*Beckman Coulter* © – USA) within the ranges of 3–8.99 µm, 9–19.99 µm, 20–59.99 µm and 60–120 µm. Cell biovolumes were estimated from the particle diameter, generalizing it as spherical, and then the carbon content was estimated. Using the conversion factors from the literature, we attributed particles < 19.99 µm to nanoeukaryotes, $\text{pg C cell}^{-1} = 0.433 \times (\mu m^3)^{0.863}$ (Verity et al. 1992), and particles > 20.00 µm to phytoplankton, $\text{pg C cell}^{-1} = 0.109 \times (\mu m^3)^{0.991}$ (Montagnes et al. 1994).

Feeding rates of the seston and heterotrophic carbon inputs by the octocoral *L. punicea* were calculated taking into account the exponential growth of the plankton during the experiment (Frost 1972; Saiz 1993; Ribes et al. 1998), an approach that is widely used in feeding studies of benthic suspension feeders (Ribes et al. 2003; Picciano and Ferrier-Pagès 2007; Coppari et al. 2016). The prey growth rate k (h^{-1}) was calculated as:

$$k = \ln(C_b / C_a) / (T_b - T_a)$$

where C_b and C_a are the prey and carbon concentrations in the chambers (particles mL^{-1} and estimated carbon content mL^{-1}) at previous time t_a to the consecutive time t_b. The clearance rate CR (particles swept clear DW^{-1} h^{-1} and estimated carbon content swept clear DW^{-1} h^{-1}) was calculated as:

$$CR = V\left(\frac{g}{b}\right)$$

where V is the volume of the chamber (in mL), b is the biomass of the octocoral colony (DW, in grams) and g is the grazing coefficient (h^{-1}), calculated as:

$$g = k_c - k_g$$

where k_c is the prey growth rate in the sampling artifact control, and k_g is the apparent growth in the chambers with animals. In cases where the values of k_c were higher than k_g, we arbitrarily disregarded the values in the statistical analysis. Then, we calculated the feeding rate and heterotrophic carbon input by:

$$\textit{Feeding rate} \text{ AND } \textit{Heterotrophic carbon input} = CR \times C$$

where C is the mean prey concentration of all chambers at the initial time. Finally, the feeding rate was expressed in terms of the number of particles consumed per unit of dry weight biomass per unit of time (*i.e.* particles g DW^{-1} h^{-1}), and the heterotrophic carbon inputs were expressed in terms of the mass of organic carbon consumed per unit of dry weight biomass per unit of time (*i.e.* µg C g DW^{-1} h^{-1}).

2.3 Hard-bottom system effects

Data from Derviche et al 2021 on the distribution and abundance pattern of *O. mirabilis* and *L. punicea* in the National Marine Park of Currais Islands were used to estimate the grazing rate of the octocoral population and the putative effects of the brittle star. In the study area, the density of *L. punicea* was 8.3 ± 10.4 colonies m^{-2}

(mean ± standard deviation), and the density of colonization by *O. mirabilis* on the octocoral species was 3.6 ± 3.0 inds. cm^{-2}. The morphological characteristics of the octocorals used in the present experiment were established as models for the overall population. The population grazing rate was then estimated taking into account this population structure and heterotrophic carbon inputs. The grazing rate was expressed in terms of the mass of organic carbon consumed per square meter per unit of time (*i.e.* mg C m^{-2} d^{-1}).

2.4 Data analysis

We investigated the relationship between octocoral feeding performance and high-density colonization of brittle stars (Dalgaard 2008). Assumptions of normality and homogeneity of variance were checked previously using *Shapiro-Wilk's* test and *Levene's* test, respectively. The heterotrophic carbon input did not assume normality and homogeneity of variance assumptions. So, we applied the transformation log10(x) to achieve it. In the case of swept clearing of the seston, that is, the difference between the particle concentration of the sample (particle. mL^{-1}) at consecutive times, we assigned together the *Ophiothela* treatments and the host controls to compare the differences to the chambers without animals, *i.e.*, the sampling artifact control. The swept clearing of the seston also did not assume normality and homogeneity of variance. Therefore, we applied the transformation sqrt(max(x+1) - x) to achieve it. Significant differences in the dependent variables feeding rates, heterotrophic carbon inputs and swept clearing of the seston were separately tested for groups (two levels, factor) and time (three levels, factor) using two-way ANOVA. Differences were further identified with *Tukey's post hoc* test. All statistical analyses and graphs were produced in the computational language R (R Core Team 2021).

3 Results

3.1 Specimens' characteristics

The density of *O. mirabilis* in the *L. punicea* treatments was 5.4 ± 0.6 inds. cm^{-2} (mean ± standard deviation), corresponding to a mean of 226 ± 50 brittle stars per colony. Although unnoticed in the field, we found that replicates 1 and 2 of the host control contained 3 and 1 individuals during the laboratory analysis, respectively. For the statistical analysis and the discussion, we disregarded this bias since the densities were lower than 0.1 inds. cm^{-2}. This highlighted the high incidence of infestation of *O. mirabilis* in the study area since almost all octocorals are colonized by it.

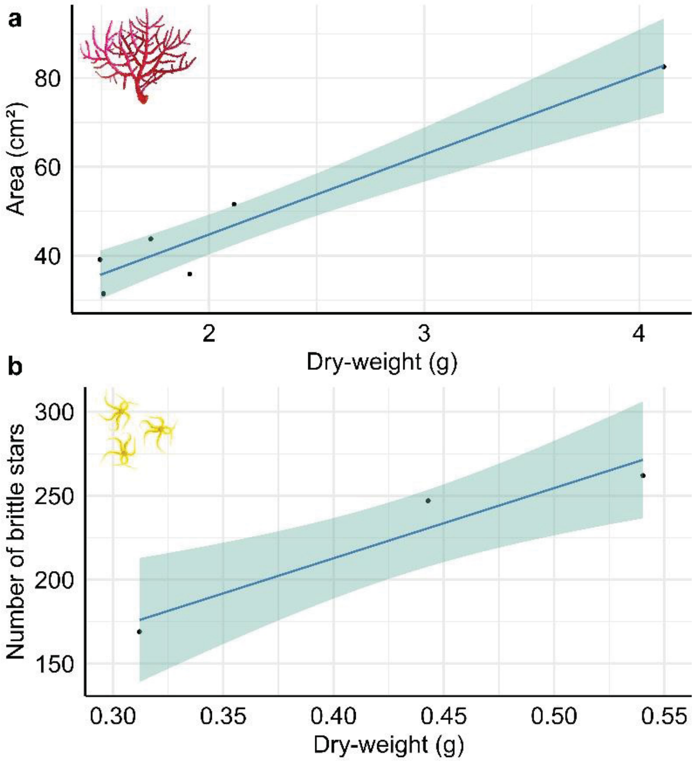

Fig. 3 Relationship between **a** the dry weight (g) and area (cm^2) of *Leptogorgia punicea* and between **b** the dry weight (g) and the number of individuals of *Ophiothela mirabilis.* Black dots are raw data, and lines and shaded areas represent GLM predictions ± standard error

Overall, regarding the degree of body regeneration of *O. mirabilis* specimens, 57.3% had split discs or broken arms, 29.3% had discs or arms regenerating, and 13.3% were intact. As expected, there was a trend of a linear increase in DW according to the number of brittle stars and the octocoral surface area (Fig. 3). The disc diameter of *O. mirabilis* averaged 1.540 ± 0.239 mm (Fig. 4), and the DW averaged 0.0019 ± 0.0001 g per brittle star individual.

The planar morphology of *L. punicea* colonies was 8.11 ± 1.54 cm in height and 13.10 ± 2.48 cm in width, comprising a mean density of 97.5 ± 39.7 polyps cm^{-2}. The DW of the octocoral species was 2.15 ± 0.99 g per colony.

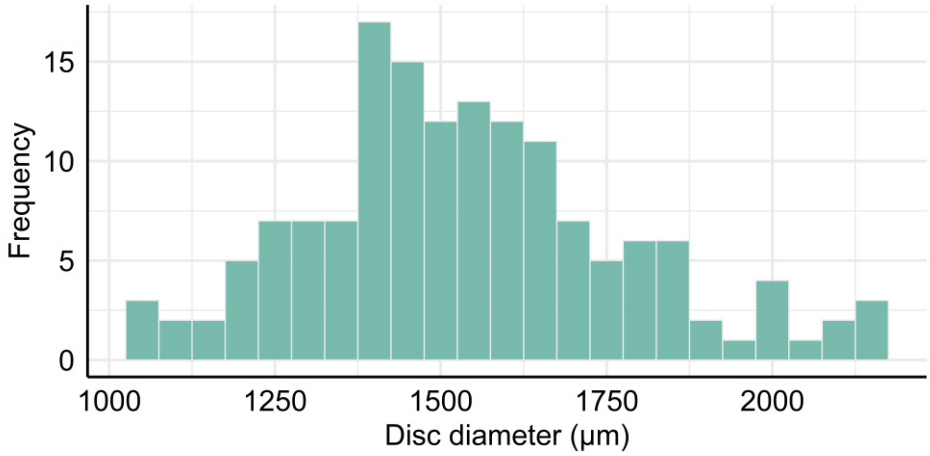

Fig. 4 Frequency histogram of the disc diameter (μm) of *Ophiothela mirabilis* in marine national park of the Currais Islands (S Brazil). The disc diameter was measured for 50 individuals within each of the three octocoral colonies

3.2 Effects on the host's feeding performance and the rocky shore system

No significant differences in host feeding performance were observed between the *L. punicea* colonized by *O. mirabilis* and those without the brittle star (Fig. 5, Table 1). Overall, *L. punicea* ingested 3,047,118 ± 1,843,183 particles g DW^{-1} h^{-1} (mean ± standard deviation), corresponding to 116.1 ± 159.0 μg C g DW^{-1} h^{-1}, regardless of the colonization or not of the brittle star. There was a linear relationship between the increase in the number of particles (particle mL^{-1}) and the increase in the estimated carbon content (μg C mL^{-1}) of the seawater samples (Fig. 6).

The feeding rates and heterotrophic carbon inputs of the *Ophiothela* treatments were 3,029,699 ± 1,730,106 particles g DW^{-1} h^{-1} (mean ± standard deviation) and 163.0 ± 214.7 μg C g DW^{-1} h^{-1}, respectively, whereas those of the host controls were 3,062,049 ± 2,073,571 particles g DW^{-1} h^{-1} and 69.2 ± 72.7 μg C g DW^{-1} h^{-1}, respectively. These feeding rates and heterotrophic carbon inputs remained constant throughout the experiment (Fig. 7, Table 1). During the experiments, we did not observe *O. mirabilis* armwaving, which could indicate predation of the seston within the chambers.

There was a clear trend of seston consumption within the *Ophiothela* treatment and host control chambers, while the artifact control chambers remained relatively constant, with a slight increase after 3 hours (Fig. 8; Table 1). The concentration of particles at time zero within groups was not significantly different (*p* value = 0.2643; one-way ANOVA).

Overall, *L. punicea* grazed 49.9 ± 68.3 mg C m^{-2} day^{-1}. The grazing rates of the *Ophiothela* treatments were 70.1 ± 92.3 mg C m^{-2} day^{-1}, while those of the host controls were 29.7 ± 31.2 mg C m^{-2} day^{-1}. The differences between the grazing rate of the *Ophiothela* treatments and the host controls were likely due to *O. mirabilis* grazing.

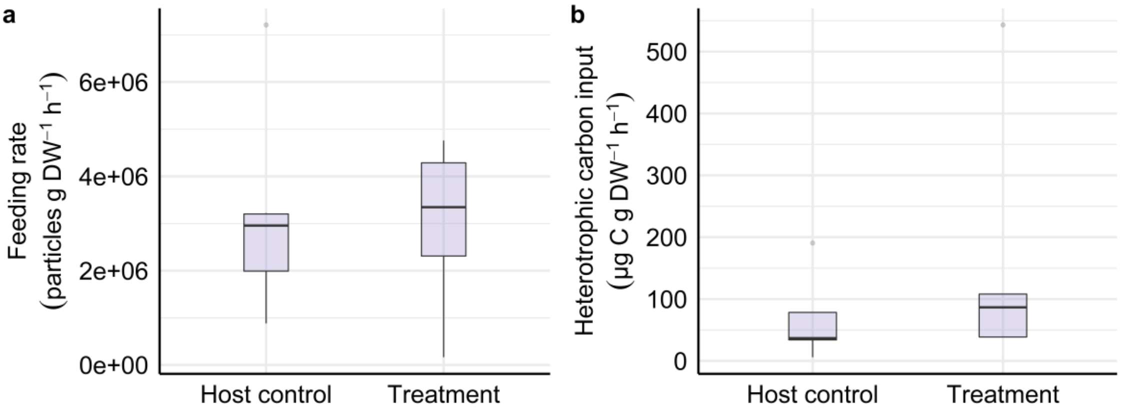

Fig. 5 Comparison of **a** the feeding rate (particles g DW^{-1} h^{-1}) and **b** the heterotrophic carbon input (µg C g DW^{-1} h^{-1}) of the octocoral *Leptogorgia punicea* under high natural colonization of *Ophiothela mirabilis* (treatment) and the octocoral naturally without brittle star individuals (host control)

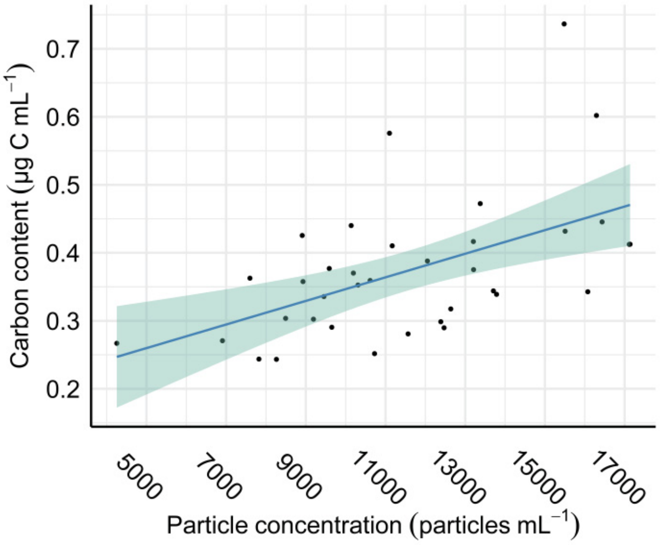

Fig. 6 Relationship between the particle concentration (particle mL^{-1}) and the estimated carbon content (µg C mL^{-1}) of the seawater samples. Black dots are raw data, and lines and shaded areas represent GLM predictions ± standard error

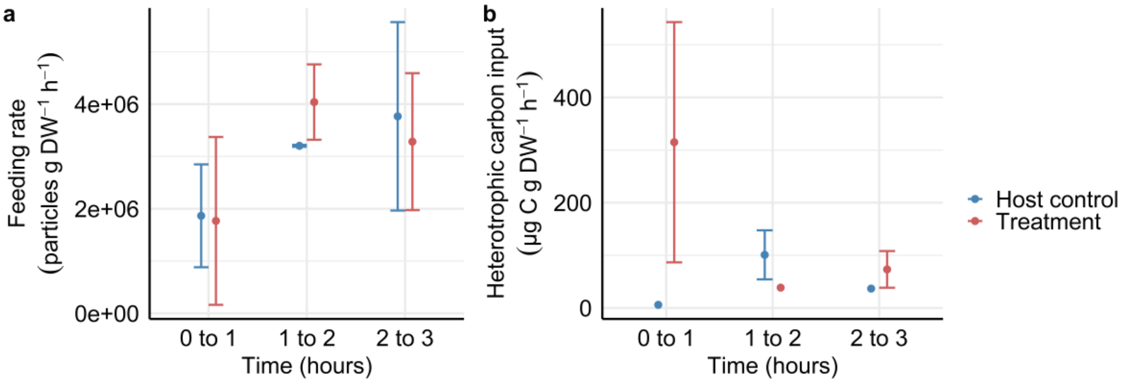

Fig. 7 Comparison of **a** the feeding rate (particles g DW^{-1} h^{-1}; means ± standard error) and **b** the heterotrophic carbon input (µg C g DW^{-1} h^{-1}) of the *Leptogorgia punicea* hosts under high natural colonization of *Ophiothela mirabilis* (treatment) and the hosts naturally without brittle star individuals (host control) over time

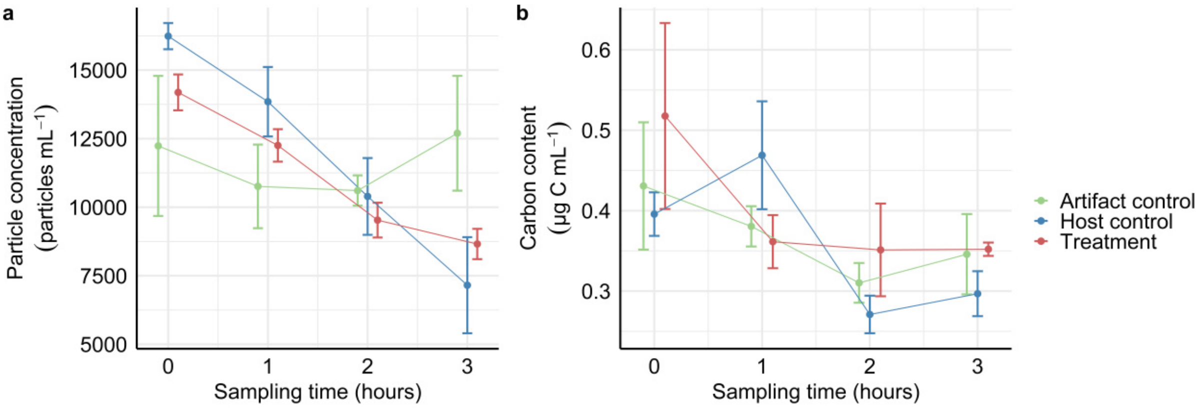

Fig. 8 Comparison of **a** the number of particles (particles mL^{-1}; means ± standard error) and **b** the carbon content (µg C mL^{-1}) within the chambers with *Leptogorgia punicea* hosts under high natural colonization of *Ophiothela mirabilis* (treatment), hosts naturally without brittle star individuals (host control), and no hosts or brittle stars (sampling artifact control) over time

Table 1 Two-way analysis of variance (ANOVA) of the feeding rate, the heterotrophic carbon input and swept clearing of the seston according to groups (two levels, factor) and time (three levels, factor)

Model	Predictors	Df	Sum Sq	Mean Sq	F value	Pr (>f)
Feeding rate ~ group + time + group * time						
	Group	1	3.381e+09	3.381e+09	0.001	0.979
	Time	2	8.762e+12	4.381e+12	0.989	0.419
	Group : Time	2	9.828e+11	4.914e+11	0.111	0.897
	Residual	7	3.102e+13	4.431e+12		
Heterotrophic carbon input ~ group + time + group * time						
	Group	1	0.3346	0.3346	1.916	0.239
	Time	2	0.1311	0.0655	0.375	0.709
	Group : Time	2	1.2880	0.6440	3.688	0.124
	Residual	4	0.6986	0.1746		
Swept clearing of the seston ~ group + time + group * time						
	Group	1	2324	2324.4	7.282	**0.0135 ***
	Time	2	793	396.3	1.242	0.3093
	Group : Time	2	659	329.7	1.033	0.3734
	Residual	21	6703	319.2		

Significant differences are in bold. Significance code: * *p* value < 0.05

4 Discussion

4.1 Effects on the host's feeding performance

Our field study indicated no significant negative impacts on the feeding performance of *L. punicea* caused by high densities of *O. mirabilis*. Initially, it was supposed that the brittle star presence could occlude water flow or restrict polyp opening, consequently hindering prey capture and impairing the efficient feeding of octocoral hosts. Although octocorals hosting *O. mirabilis* may have impaired polyp opening and extension, the overall feeding performance remains comparatively similar (Fig. 5; Table 1). Additionally, there is no evidence that the performance of the octocoral would be improved, as reported in other epizoic brittle star species relationships (Hendler 1984; Girard et al. 2016). Efficient suspension feeding is crucial to overcome the unpredictability of food availability in the water column. The carbon inputs provided by feeding activity maintain the essential metabolic activities of the octocoral, which are basically respiration, growth, and reproduction (Fabricius et al. 1995). These activities are energy-costly processes, and it is supposed that there is a trade-off in energy resource allocation, especially among growth and reproduction (Rinkevich 1996; Tsounis et al. 2012). Recent laboratory studies with octocorals highly colonized by *O. mirabilis* have indicated that they acquire sufficient energy to grow, as evidenced by the expansion of the coenenchyme around its stem bases in just over two months of study (Glynn et al. 2021b).

The morphology of feeding structures of host species, including the polyp diameter, polyp height, calyx shape, tentacle length, number of pinnules, and pinnule spacing, may determine the lesser or greater susceptibility to negative impacts of *O. mirabilis*. Species with smaller feeding structures are likely more affected by *O. mirabilis* individuals. The physical presence of a disk diameter of 1.54 ± 0.24 mm could impair the particle encounter by the polyp or prevent polyp opening and extension, which consequently hides efficient feeding. *O. mirabilis* individuals tend to be attached to the stems of *L. punicea*; however, it is not uncommon to observe polyps blocked in the field. The polyps of *L. punicea* were between 0.08 and 0.16 mm tall (Castro et al. 2010) and had a density of 97.51 ± 39.73 polyps cm^{-2}. In laboratory experiments, the octocoral *Eunicea flexuosa*, which comparatively has a lower polyp density (83.8 ± 15.2 polyps cm^{-2}), did not exhibit negative impacts of reduced extended polyp areas by increasing the *O. mirabilis* density as opposed to *Muricea elongate,* which was slightly affected (139.0 ± 37.0 polyps cm^{-2}; Glynn et al. 2021b). In the Caribbean, field surveys have observed retract polyps where *O. mirabilis* was attached in several octocoral species, including *Pterogorgia anceps*, *Muriceopsis flavida*, *Gorgonia ventalina*, *Muriceopsis sulphurea*, *Antillogorgia acerosa* and *Eunicea flexuosa* (Ferry et al. 2020). In contrast, the relatively higher length and distinct shape of the calyxes prevent contact between polyps and brittle stars in the octocoral species *Eunicea laxispica* and *Muricea muricata* (Ferry et al. 2020).

Several host species of *O. mirabilis* have symbiotic interactions with zooxanthellae, which are photosynthetic dinoflagellates mainly within the family Symbiodiniaceae (LaJeunesse 2020). This mutualism results in lower rates of host feeding since endosymbiont algae contribute a significant portion of photosynthetic carbon (Goldberg 2018). Although this issue was not addressed in our study, high population densities of *O. mirabilis* on zooxanthellate species may significantly reduce areas of exposure to light and consequently cause lower photosynthetic carbon assimilation. Since most *Symbiodinium* cells are concentrated in the polyps, it is likely that the brittle star colonizes the host (*i.e.* attached to polyps, stalks or rods) and may affect photosynthetic rates. A potential reduction in photosynthetic rates may also have consequences for the carbon budgets of hard-bottom systems, especially in biogeographic realms characterized by oligotrophic waters where this mutualism is more frequent.

The study area is characterized by eutrophic and high-nutrient water conditions. Even though *L. punicea* colonies preyed on a considerable amount of particles, a significant portion remained after 3 h (Fig. 8). In contrast, there are records of *O. mirabilis* in biogeographic realms characterized by oligotrophic waters and prey scarcity, such as the Caribbean Sea (Ferry et al. 2020; Rich et al. 2020). In these areas, octocorals species commonly possess mutualism with zooxanthellae (Schubert et al. 2016), and their grazing rates are expected to be considerably lower than those reported in this study. In this sense, further studies on the effects of brittle stars on hosts in environments with prey scarcity are still needed.

Octocorals act as ecological engineers for hard-bottom systems, as they increase the complexity of habitats for several organisms (Jones et al. 1994). In Florida, the ctenophore *Coeloplana waltoni* is an octocoral epizoite that has been declining and, in some sites, even disappearing (Glynn et al. 2021a). Field and laboratory observations suggest that *O. mirabilis* negatively affects ctenophore species by interference competition (Glynn et al. 2021a). These observations highlight that the potential impacts of brittle stars are carried out not only on hosts but also in species that occupy the same ecological niche.

The fidelity between brittle stars and hosts throughout life, from maturation to senescence, is known (Mosher and Watling 2009). In contrast, host switching by brittle stars is observed between the same or within distinct host species (Girard et al. 2016; Mekhova et al. 2018) and the transition from a symbiont to a free-living mode (Hendler et al. 1999). Laboratory observations of *O. mirabilis* individuals occasionally outside the hosts (Glynn et al. 2021b) may indicate that the species migrates similarly to nearby hosts. Although host switching of *O. mirabilis* is not quantified or documented, it would affect the colonization abundances. There is evidence that some brittle star species settle directly on hosts (Hendler et al. 1999; Mosher and Watling 2009; Girard et al. 2016). However, larval recruitment and direct settlement to hosts are unlikely for *O. mirabilis*, since individuals with small sizes are not observed (Fig. 4; Tavares et al. 2019).

4.2 Effects on the hard-bottom systems

Several studies assessed the role of benthic suspension feeder predation on seston taking into account population structure and density, including octocorals (Coppari et al. 2019), sponges (Pile et al. 1996; Pile and Young 2006; Kahn et al. 2015; Coppari et al. 2016), ascidians (Coppari et al. 2014), and hydroids (Coma et al. 1995). The total ingestion of C by *L. punicea* (49.9 ± 68.3 mg C m^{-2} d^{-1}) is comparable to that of other octocorals, such as *Paramuricea clavata* (150 ± 130 mg C m^{-2} d^{-1}), *Eunicella singularis* (100 ± 110 mg C m^{-2} d^{-1}), and *Leptogorgia sarmentosa* (2 ± 1 mg C m^{-2} d^{-1}; Coppari et al. 2019). These rates depend substantially on the population characteristics and species performance. Passive suspension feeders tend to have lower ingestion rates than active feeders since they have lower metabolic costs (Gili and Coma 1998). The studied *L. punicea* populations are located in a marine protected area, which theoretically protects them from fishing threats, such as gill nets and trawling. By-caught reduces the abundance, consequently affecting the octocoral contribution to benthic-pelagic coupling processes (Tsounis et al. 2012; Coppari et al. 2019).

Our results reflect a snapshot of the environment, which does not allow us to determine seasonal variations. To obtain more reliable data about feeding performance, relevant factors should be incorporated into models, such as the prey digestion time, polyp expansion activity, and stochasticity of available food (Rossi et al. 2020). In addition, the heterotrophic carbon input was calculated by generalizing the diameter of particles to the spherical shape and taking into account that the carbon content of the particles is proportional to the size using nanoeukaryotes and phytoplankton conversion factors from the literature (Verity et al. 1992; Montagnes et al. 1994). However, in the real-life world, a significant part of the seston is composed of nonliving particles. Since plankton are a very heterogeneous group, the amount of carbon varies according to the particle characteristics. In addition, colonization by bacteria and microorganisms also interferes with nutrient quality. Values may also differ if a considerable number of particles in the samples do not have the spherical format or if the carbon content differs significantly from those in the study area. As such, our data can be used as a preliminary *in situ* assessment of the effects on a non-native species on the feeding performance of hosts and on the ecosystem's carbon budget.

Octocorals are prevalent in Western Atlantic rocky shores and Caribbean coral reefs (Johnson and Hallock 2020). Carbon sequestration from octocoral feeding activities acts as a relevant sink in the blue carbon budget (Coppari et al. 2019). Negative impacts on key species could reflect harmful cascading effects on hard-bottom systems and affect the carbon budget from benthic-pelagic coupling. The similar feeding performance between octocorals colonized by the brittle star and octocorals without brittle stars indicates that there are no negative putative effects on the carbon flux driven by the ingestion of *L. punicea*. Therefore, according to a classification of alien species impacts (Blackburn et al. 2014), the impacts of *O. mirabilis* through structural parasitism to hosts and the impacts on the benthic-pelagic coupling of the ecosystem through host feeding performance may be considered minimal. However, the responses of hosts with distinct morphological and functional features and the potential consequences to hard-bottom systems may differ and are still worthwhile to be studied.

5 Conclusion

The high densities previously reported for the nonnative brittle star *O. mirabilis* on octocoral hosts along the Western Atlantic have raised concerns about potentially negative effects. Herein, we assessed whether the relationship between brittle stars and *L. punicea* hosts could be considered structural parasitism through field experiments. However, no significant impacts on the feeding performance of the azooxanthellate suspension feeder *L. punicea* caused by the brittle star were observed. Notwithstanding, we are aware that the responses of potential hosts to feeding performance from increasing brittle star densities may differ depending on their morphological and functional features.

Benthic suspension feeders play a significant role in the benthic-pelagic coupling processes of rocky shore and coral reef systems. Therefore, negative effects on key or engineer-species could affect their structure and functioning. The lack of fitness reduction of *L. punicea*, a rather common species in the southwestern Atlantic rocky shores, may imply that the carbon flux driven by this passive suspension feeder is also not affected by heavy colonization of *O. mirabilis*. Notwithstanding, further laboratory and field experimental studies assessing the effects on host taxa with distinct morphological and functional features are needed to better understand the responses of the recipient biodiversity and ecosystem of the Western Atlantic to increasing densities of *O. mirabilis.*

References

Araújo JT, Oliveira MO, Matthews-Cascon H, Correia FAC (2018) The invasive brittle star *Ophiothela mirabilis* Verrill, 1867 (Echinodermata, Ophiuroidea) in the southwestern Atlantic: filling gaps of distribution, with comments on an octocoral host. Lat Am J Aquat Res 46:1123–1127. https://doi.org/10.3856/vol46-issue5-fulltext-25

Blackburn TM, Essl F, Evans T, et al (2014) A unified classification of alien species based on the magnitude of their environmental impacts. PLoS Biol 12:e1001850. https://doi.org/10.1371/journal.pbio.1001850

Blackburn TM, Pyšek P, Bacher S, et al (2011) A proposed unified framework for biological invasions. Trends Ecol Evol 26:333–339. https://doi.org/10.1016/j.tree.2011.03.023

Castro CB, Medeiros MS, Loiola LL (2010) Octocorallia (Cnidaria: Anthozoa) from Brazilian reefs. J Nat Hist 44:763–827. https://doi.org/10.1080/00222930903441160

Coppari M, Gori A, Rossi S (2014) Size, spatial, and bathymetrical distribution of the ascidian *Halocynthia papillosa* in Mediterranean coastal bottoms: benthic–pelagic coupling implications. Mar Biol 161:2079–2095. https://doi.org/10.1007/s00227-014-2488-5

Coppari M, Gori A, Viladrich N, et al (2016) The role of Mediterranean sponges in benthic-pelagic coupling processes: *Aplysina aerophoba* and *Axinella polypoides* case studies. J Exp Mar Bio Ecol 477:57–68. https://doi.org/10.1016/j.jembe.2016.01.004

Coppari M, Zanella C, Rossi S (2019) The importance of coastal gorgonians in the blue carbon budget. Sci Rep 9:13550. https://doi.org/10.1038/s41598-019-49797-4

Dalgaard P (2008). Introductory Statistics with R. Springer, New York, NY. https://doi.org/10.1007/978-0-387-79054-1

Derviche P, Saucsen A, Spier D, Lana P (2021) Distribution patterns and habitat suitability of the non-native brittle star *Ophiothela mirabilis* Verrill, 1867 along the Western Atlantic. J Sea Res 168:101994. https://doi.org/10.1016/j.seares.2020.101994

Ferry R, Hubert L, Philippot V, Priam F, Smith J (2020) First record of the non-indigenous brittle star species *Ophiothela mirabilis* Verrill, 1867 (Echinodermata:

Ophiuroidea), off Martinique Island, French Lesser Antilles. BioInvasions Rec. 9:228–238. https://doi.org/10.3391/bir.2020.9.2.08

Frost B (1972) Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. Limnol Oceanogr 17:805–815. https://doi.org/10.4319/lo.1972.17.6.0805

Gili JM, Coma R (1998) Benthic suspension feeders: their paramount role in littoral marine food webs. Trends Ecol Evol 13:316–321. https://doi.org/10.1016/S0169-5347(98)01365-2

Girard F, Fu B, Fisher CR (2016) Mutualistic symbiosis with ophiuroids limited the impact of the Deepwater Horizon oil spill on deep-sea octocorals. Mar Ecol Prog Ser 549:89–98. https://doi.org/10.3354/meps11697

Glynn PW, Coffman B, Dettloff K, et al (2021a) Non-native brittle star interactions with native octocoral epizoites: an endemic benthic ctenophore in peril? Mar Biol 168:1–12. https://doi.org/10.1007/s00227-021-03927-7

Glynn PW, Alitto R, Dominguez J, et al (2020) A tropical eastern Pacific invasive brittle star species (Echinodermata: Ophiuroidea) reaches southeastern Florida. Adv Mar Biol 87:443–472. https://doi.org/10.1016/bs.amb.2020.08.010

Glynn PW, Coffman B, Primov K, et al (2019) Benthic ctenophore (Order Platyctenida) reproduction, recruitment, and seasonality in south Florida. Invertebr Biol 138:e12256. https://doi.org/10.1111/ivb.12256

Glynn PW, Gillette PR, Dettloff K, et al (2021b) Experimental evidence of minimal effects on octocoral hosts caused by the introduced ophiuroid *Ophiothela mirabilis*. Coral Reefs. https://doi.org/10.1007/s00338-021-02067-0

Goldberg WM (2018) Coral food, feeding, nutrition, and secretion: a review. In: Marine organisms as model systems in biology and medicine. Springer, Cham, pp 377–421

Grange KR (1991) Mutualism between the antipatharian *Antipathes fiordensis* and the ophiuroid *Astrobrachion constrictum* in New Zealand fjords. Hydrobiologia 216–217:297–303. https://doi.org/10.1007/BF00026478

Granja-Fernández R, Herrero-Pérezrul MD, López-Pérez RA, et al (2014) Ophiuroidea (Echinodermata) from coral reefs in the Mexican Pacific. Zookeys 406:101–145. https://doi.org/10.3897/zookeys.406.6306

Hendler G (1984) The association of *Ophiothrix lineata* and *Callyspongia vaginalis*: a brittlestar-sponge cleaning symbiosis? Mar Ecol 5:9–27. https://doi.org/10.1111/j.1439-0485.1984.tb00304.x

Hendler G, Grygier MJ, Maldonado E, Denton J (1999) Babysitting brittle stars: heterospecific symbiosis between ophiuroids (Echinodermata). Invertebr Biol 118:190–201. https://doi.org/10.2307/3227060

Hendler G, Littman BS (1986) The ploys of sex: relationships among the mode of reproduction, body size and habitats of coral-reef brittlestars. Coral Reefs 5:31–42. https://doi.org/10.1007/BF00302169

Hendler G, Migotto AE, Ventura CRR, Wilk L (2012) Epizoic *Ophiothela* brittle stars have invaded the Atlantic. Coral Reefs 31:1005–1005. https://doi.org/10.1007/s00338-012-0936-6

Johnson SK, Hallock P (2020) A review of symbiotic gorgonian research in the western Atlantic and Caribbean with recommendations for future work. Coral Reefs 39:239–258. https://doi.org/10.1007/s00338-020-01891-0

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386. https://doi.org/10.2307/3545850

Kahn AS, Yahel G, Chu JWF, et al (2015) Benthic grazing and carbon sequestration by deep-water glass sponge reefs. Limnol Oceanogr 60:78–88. https://doi.org/10.1002/lno.10002

LaJeunesse TC (2020) Zooxanthellae. Curr Biol 30:PR1110–R1113. https://doi.org/10.1016/j.cub.2020.03.058

Lane SJ, Tobalske BW, Moran AL, et al (2018) Costs of epibionts on Antarctic sea spiders. Mar Biol 165:1–8. https://doi.org/10.1007/s00227-018-3389-9

Lawley JW, Fonseca AC, Faria Júnior E, Lindner A (2018) Occurrence of the non-indigenous brittle star *Ophiothela* cf. *mirabilis* Verrill, 1867 (Echinodermata, Ophiuroidea) in natural and anthropogenic habitats off Santa Catarina, Brazil. Check List 14:453–459. https://doi.org/10.15560/14.2.453

Lombard F, Boss E, Waite AM, et al (2019) Globally consistent quantitative observations of planktonic ecosystems. Front Mar Sci 6:. https://doi.org/10.3389/fmars.2019.00196

Mantelatto MC, Vidon LF, Silveira RB, et al (2016) Host species of the non-indigenous brittle star *Ophiothela mirabilis* (Echinodermata: Ophiuroidea): an invasive generalist in Brazil? Mar Biodivers Rec 9:1–7. https://doi.org/10.1186/s41200-016-0013-x

Martinez AS, Mayer-pinto M, Christofoletti RA (2019) Functional responses of filter feeders increase with elevated metal contamination: Are these good or bad signs of environmental health? Mar Pollut Bull 149:110571. https://doi.org/10.1016/j.marpolbul.2019.110571

Mekhova ES, Martynov A V., Britayev TA (2018) Host selection and host switching in *Gymnolophus obscura* – a symbiotic ophiuroid associated with feather stars (Crinoidea: Comatulida). Symbiosis 76:313–320. https://doi.org/10.1007/s13199-018-0566-z

Montagnes, DJS, Berges, JA, Harrison, PJ, Taylor, FJR (1994). Estimating carbon, nitrogen, protein, and chlorophyll a from volume in marine phytoplankton. Limnol. Oceanogr. 39, 1044–1060. https://doi.org/10.4319/lo.1994.39.5.1044

Mosher CV, Watling L (2009) Partners for life: A brittle star and its octocoral host. Mar Ecol Prog Ser 397:81–88. https://doi.org/10.3354/meps08113

Ohtsuka S, Kondo Y, Sakai Y, et al (2010) *In-situ* observations of symbionts on medusae occurring in Japan, Thailand, Indonesia and Malaysia. Bull Hiroshima Univ Museum 2:9–18. http://doi.org/10.15027/32060

Picciano M, Ferrier-Pagès C (2007). Ingestion of pico- and nanoplankton by the Mediterranean red coral *Corallium rubrum*. Mar. Biol. 150:773–782. https://doi.org/10.1007/s00227-006-0415-0

Pile A, Patterson M, Witman J (1996) In situ grazing on plankton less than 10 micrometer by the boreal sponge *Mycale lingua*. Mar Ecol Prog Ser 141:95–102. https://doi.org/10.3354/meps141095

Pile AJ, Young CM (2006) The natural diet of a hexactinellid sponge: benthic-pelagic coupling in a deep-sea microbial food web. Deep Res Part I Oceanogr Res Pap 53:1148–1156. https://doi.org/10.1016/j.dsr.2006.03.008

R Development Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Ribes M, Coma R, Gili JM, et al (2000) A “semi-closed” recirculating system for the *in situ* study of feeding and respiration of benthic suspension feeders. Sci Mar 64:265–275. https://doi.org/10.3989/scimar.2000.64s1265

Ribes M, Coma R, Gili JM (1998) Seasonal variation of *in situ* feeding rates by the temperate ascidian *Halocynthia papillosa*. Mar Ecol Prog Ser 175:201–213. https://doi.org/10.3354/meps175201

Ribes M, Coma R, Rossi S (2003) Natural feeding of the temperate asymbiotic octocoral-gorgonian *Leptogorgia sarmentosa* (Cnidaria: Octocorallia). Mar Ecol Prog Ser 254:141–150. https://doi.org/10.3354/meps254141

Rich L-P, Dennis MM, Freeman MA (2020) New record of the non-native *Ophiothela mirabilis* (Verrill 1867) in St. Kitts, West Indies. Adv Oceanogr Mar Biol 2:2–6. https://doi.org/10.33552/AOMB.2020.02.000526

Rinkevich B (1996) Do reproduction and regeneration in damaged corals compete for energy allocation? Mar Ecol Prog Ser 143:297–302. https://doi.org/10.3354/meps143297

Rossi S, Ribes M, Coma R, Gili JM (2004) Temporal variability in zooplankton prey capture rate of the passive suspension feeder *Leptogorgia sarmentosa* (Cnidaria: Octocorallia), a case study. Mar Biol 144:89–99. https://doi.org/10.1007/s00227-003-1168-7

Rossi S, Schubert N, Brown D, et al (2020) Trophic ecology of Caribbean octocorals: autotrophic and heterotrophic seasonal trends. Coral Reefs 39:433–449. https://doi.org/10.1007/s00338-020-01906-w

Roth F, Wild C, Carvalho S, et al (2019) An *in situ* approach for measuring biogeochemical fluxes in structurally complex benthic communities. Methods Ecol Evol 10:712–725. https://doi.org/10.1111/2041-210X.13151

Saiz E (1993) Sources of variability in zooplankton feeding experiments: The importance of accurate determination of algal growth rates. Sci Mar 57:23–29

Schubert N, Brown D, Rossi S (2016) Symbiotic versus non-symbiotic octocorals: physiological and ecological implications. In: Rossi S, Bramanti L, Gori A, Orejas C (eds) Marine Animal Forests. Springer, Cham. https://doi.org/10.1007/978-3-319-17001-5_54-1

Stevens GC (1987) Lianas as structural parasites: The *Bursera simaruba* example. Ecol Soc Am 68:77–81. https://doi.org/10.2307/1938806

Tavares MR, Costa PAS, Ventura CRR (2019) Population size structure, asexual reproduction, and somatic growth estimates of the non-indigenous brittle star

Ophiothela mirabilis (Echinodermata: Ophiuroidea) on the southeastern coast of Brazil. Mar Biodivers 49:1713–1725. https://doi.org/10.1007/s12526-019-00938-y

Trygonis V, Sini M (2012) PhotoQuad: a dedicated seabed image processing software, and a comparative error analysis of four photoquadrat methods. J Exp Mar Bio Ecol 424–425:99–108. https://doi.org/10.1016/j.jembe.2012.04.018

Tsounis G, Martinez L, Bramanti L, et al (2012) Anthropogenic effects on reproductive effort and allocation of energy reserves in the Mediterranean octocoral *Paramuricea clavata*. Mar Ecol Prog Ser 449:161–172. https://doi.org/10.3354/meps09521

Tsounis G, Rossi S, Laudien J, et al (2006) Diet and seasonal prey capture rates in the Mediterranean red coral (*Corallium rubrum* L.). Mar Biol 149:313–325. https://doi.org/10.1007/s00227-005-0220-1

Verity, P.G., Robertson, C.Y., Tronzo, C.R., Andrews, M.G., Nelson, J.R., Sieracki, M.E., 1992. Relationships between cell volume and the carbon and nitrogen content of marine photosynthetic nanoplankton. Limnol. Oceanogr. 37, 1434–1446. https://doi.org/10.4319/lo.1992.37.7.1434

Supplementary material

In situ incubation chambers system' description

Suspension feeding is one of the most common feeding strategies in hard-bottom benthic communities. Enclosure experiments are often used to assess variables related to suspension-feeding in underwater habitats, but due to logistical restrictions they often lack adequate sampling design and sampling effort. To overcome these challenges, we have developed an innovative incubation chambers system to assess variations in feeding rates, diet composition, and clearance rates of benthic suspension feeders in a reliable and repeatable way.

The system, operated by two SCUBA divers, consists of nine connected 2,590 ml incubation chambers. Each chamber is composed of a 2,090 ml transparent acrylic dome, 20 cm in diameter and 2 cm flaps, coupled with four 125 ml polyethylene bottles. The chambers are uniformly arranged on a 120 x 120 cm, 5 mm acrylic plate coupled with a galvanized metal grid frame to provide support. The chamber is fastened using four thumbscrews on the acrylic plate with a silicone rubber between them. The animals are fixed to perforated polyethylene plates using Hellermann cable ties and then positioned inside the chambers using elastics that held the plates.

Seawater flows independently in each chamber, which may be treated as replicates for experimental designs. The system may be switched from open (continuous entry of seawater from outside) to closed circulation (seawater only inside the chamber) by a set of valves. To avoid an uneven input of suspended particles among the chambers during the open circulation operation, seawater entry is restricted to a single point, nearby the battery, in which all the chambers are supplied through 2 mm tubes.

Nine 120 $l.h^{-1}$ pumps powered by a sealed 6V 12Ah battery allows for turbulent flow and the maintenance of suspended particles within each chamber. The battery's waterproof case consists of a 3 mm acrylic case, with dimensions 17 x 7 x 12 cm and 2 cm flaps. The waterproof case are fastened using thumbscrews on the acrylic plate with a silicone rubber between them. There is a sealed switch to turn all pumps on and off. Besides that, cables for lifting the system are attached to the edges, and there is a buoyancy buoy marking its position.

Underwater sampling can occur at varying times, depending on the research problems and hypotheses being tested, through a set of valves that traps the seawater in the bottles. Feeding rates and variations in the density or abundance of preys may be calculated from the decrease in the number and nature of particles from the initial to the final samples. Our system provides consistent estimates of the feeding performance of benthic suspension feeders under natural or experimental conditions. As such, it can be widely applied to experimental ecology, allowing for a better understanding of ecological relationships between benthic species, bentho-pelagic coupling, and the biogeochemical cycles of shallow benthic marine habitats. Although some values of the dimensions of the system were changed, images of the functioning of the incubation chamber system are available at: https://youtu.be/8kp2gbg_MUE.

Capítulo II. Current worldwide trends in the expansion of octocorals may be related to their feeding ecology: a literature review and data reassessment

As tendências mundiais atuais na expansão dos octocorais podem estar relacionadas à sua ecologia alimentar: uma revisão da literatura e reavaliação dos dados

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Resumo

Embora os octocorais sejam um componente chave em vários sistemas marinhos de fundo duro e o acoplamento bento-pelágico possa ser moldado em grande parte por sua ecologia trófica, seu desempenho alimentar ainda é pouco compreendido. Diferentemente dos seus parentes próximos, os corais escleractíneos, os octocorais estão mantendo e até aumentando sua distribuição e abundância em vários sistemas marinhos, o que pode ser parcialmente explicado por diferenças na ecologia alimentar. Portanto, a compreensão da sua ecologia alimentar é essencial para modelar o acoplamento bento-pelágico, para estimar o balanço de carbono e para prever respostas potenciais às mudanças ambientais. Aqui, realizamos uma reavaliação geral de dados e uma revisão da ecologia alimentar de octocorais por meio de uma pesquisa sistemática e abrangente da literatura revisada por pares publicada entre 1960 e 2020. Além disso, descrevemos os orçamentos de carbono da alimentação em suspensão e autotrofia em octocorais. A alimentação em suspensão é responsável por 191 ± 200% das necessidades metabólicas em octocorais azooxantelados e 29 ± 32% em octocorais zooxantelados. Em compensação, a autotrofia é responsável por 146 ± 107% da contribuição do carbono adquirido autotroficamente para os octocorais zooxantelados. A dieta dos octocorais engloba fontes alimentares heterogêneas, desde a fração fina até a grosseira do séston, em que a seletividade das presas varia principalmente de acordo com a morfologia do octocoral. Duas hipóteses principais foram identificadas em relação às vantagens das estratégias de alimentação dos octocorais em comparação com os escleractíneos, incluindo a sua capacidade de diminuir os gastos de energia para superar eventos de estresse e a sua menor dependência da autotrofia.

Abstract

Although octocorals are a key component of marine hard-bottom systems, their feeding performance is still poorly understood. In contrast to their counterpart scleractinian corals, octocorals are maintaining and even increasing their distribution and abundance worldwide, which may be partly explained by differences in feeding strategies. Therefore, understanding such trends looks essential to assess octocorals' role in the benthic-pelagic coupling, to estimate their carbon budget and to predict their responses to environmental changes. Herein, we provide an overall data reassessment and a review of the feeding ecology of octocorals through a systematic and comprehensive search of peer-reviewed literature published between 1960 and 2020. We describe the carbon budgets of suspension feeding and autotrophy in octocorals and identify potential mechanisms that may contribute to their worldwide expansion trends. Overall, suspension feeding accounts for 186 ± 208% of the metabolic requirements in azooxanthellate octocorals and 29 ± 32% in zooxanthellate octocorals. In compensation, autotrophy is responsible for 149 ± 113% of the contribution of autotrophically acquired carbon to zooxanthellate octocorals. We suggest that octocorals' present advantages in relation to scleractinians derive from their ability to decrease energy expenses to overcome stress events, and their lower dependency on autotrophy. We also indicate that scleractinians which display plasticity in increase heterotrophy to compensate for reduced autotrophy are expected to be more resilient.

Keywords: Octocoral expansion; Autotrophy; Heterotrophy; Feeding ecology; Trophic ecology; Benthic-pelagic coupling.

Declarations

Acknowledgments

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Data availability

The datasets and the R codes of the current study are available in the GitHub repository, https://github.com/pderviche/Octocorals_review.

Author contributions

Both authors contributed to the review concept, data interpretation, and the writing of the manuscript. PD performed the literature search and statistical analysis. Both authors contributed intellectually to this study.

Conflict of interest

The authors declare that they have no conflict of interest.

Ethical approval

This review article does not contain any studies with human participants performed by any of the authors. This review article does not contain any studies with animals performed by any of the authors.

Consent for publication

All authors have contributed to the preparation and editing of this manuscript and have approved it for publication in its current form.

1 Introduction

Several octocorals display symbiotic interactions with zooxanthellae, which are photosynthetic dinoflagellates mainly within the family Symbiodiniaceae (Kanwisher and Wainwright 1967; LaJeunesse 2020). Algal endosymbionts often provide a considerable proportion of photosynthetically fixed carbon to the octocoral host. Besides autotrophy, zooxanthellate octocorals also perform heterotrophy, which defines them as mixotrophic organisms (Coppari et al. 2019). Alternatively, azooxanthellate octocorals rely only on heterotrophy to meet their energetic needs. In general, the diet of octocorals encompasses heterogeneous food sources, from the fine fraction of seston, such as dissolved organic matter (Schlichter et al. 1983) and pico-, nano- and microplankton (Coppari et al. 2019), to detrital particulate matter (Tsounis et al. 2006) and mesoplankton prey (Coma et al. 2001).

Octocorals are one of the most abundant benthic organisms in several marine ecosystems, such as the Western Atlantic rocky shores, the Caribbean and Indo-Pacific coral reefs (Benayahu et al. 2019; Johnson and Hallock 2020). Although the benthic-pelagic coupling in oceanic and coastal hard-bottom systems may be shaped to a large extent by the trophic ecology of octocorals, their feeding performance is still poorly understood and has received less attention than that of scleractinian corals (Houlbrèque and Ferrier-Pagès 2009; Johnson and Hallock 2020). Octocorals and scleractinian corals respond differently to environmental changes. Overall, scleractinian corals have been declining, while octocorals have become dominant within disturbed reef systems (Done 1992; Norström et al. 2009; Ruzicka et al. 2013; Inoue et al. 2013; Lenz et al. 2015; Owen et al. 2020). Besides phase shifts from scleractinian coral-dominated reefs to octocoral-dominated reefs, other plants and animals, such as macroalgae, corallimorpharians, sponges and urchins, may also become dominant (Norström et al. 2009). The relative resilience of octocorals to changing environmental conditions may be partly explained by their feeding characteristics (Fabricius and Klumpp 1995; Tsounis et al. 2018; Pupier et al. 2019). Since the feeding performance of octocorals is a key factor shaping several marine systems and partly explains their success under changing environmental conditions, studies of their feeding ecology are essential to predict the responses of coastal marine systems to climate change.

Benthic-pelagic coupling, expressed by fluxes of energy, nutrients, and contaminants, plays a significant role in coastal and shelf environments. In short, pelagic food resources are consumed by suspension feeders, which in turn release organic matter as mucus and metabolic wastes (Leal et al. 2014a). Carbon sequestration from feeding activities acts as a relevant sink in the blue carbon budget (Coppari et al. 2019). Additionally, octocorals play a key role as ecosystem engineers through the accumulation of biomass from heterotrophic and autotrophic feeding. They transform two-dimensional substrates into biologically complex three-dimensional fouling systems, providing habitat, food, and protection for several organisms (Gili and Coma 1998). Their structures baffle increasing turbulence and local sediment deposition, which ultimately affect the success of larval settlement and reef succession (Cerpovicz and Lasker 2021).

Herein, we present a review of suspension feeding and autotrophy of octocorals through a systematic and comprehensive search of peer-reviewed literature over sixty years. We reassessed literature data on octocoral feeding ecology to explain their current expansion trends worldwide. We revisited the main hypothesis proposed to explain the phase shifts, discussed overall differences in the feeding ecology between octocorals and scleractinians, and assessed their energetic responses to environmental changes. For this, data on the carbon budgets of suspension feeding, autotrophy and metabolic demands of octocorals were compiled and re-assessed. We have also identified the biogeographic ecoregions with the highest research efforts, the octocoral taxa studied, and reassessed the main questions, hypotheses and inferences related to octocoral distribution in the current literature.

2 Methods

2.1 Literature search

We performed a systematic and comprehensive search of peer-reviewed literature by selecting studies focusing on the feeding ecology of octocorals, including field surveys and laboratory experiments. We attempted to select all studies with primary data related to suspension feeding and autotrophy of octocorals. We used the keywords "octocoral*" OR "gorgonian*" OR "soft coral*" AND "feeding*" OR "trophic ecology*" OR "diet*" OR "heterotrophy*" OR "autotrophy*" to retrieve papers from the Web of Science, Google Scholar, and the Scientific Electronic Library Online (SciELO). We inspected the first 99 pages (10 results by page) of the listed search results from Google Scholar and the whole results from Web of Science and SciELO. In addition, we tracked additional studies extracted from the references of the retrieved papers that met our selection criteria but had not been retrieved by the search machines (*i.e.* snowball search). Our searches were limited to peer-reviewed publications in English published from 1960 to December 6, 2020.

We implemented an adapted checklist of the Preferred Reporting Items for Systematic Review and Meta-Analysis (PRISMA) Statement (Moher et al. 2009). The PRISMA protocol identified 994 studies whose titles and abstracts were scanned to identify studies suitable for systematic review. Then, 174 papers were fully screened through the reading and assessment of methodological and discussion sections. Finally, we identified 135 peer-reviewed studies that met our selection criteria. All these studies were used for qualitative analyses, and 30 for quantitative analyses (Fig. 1).

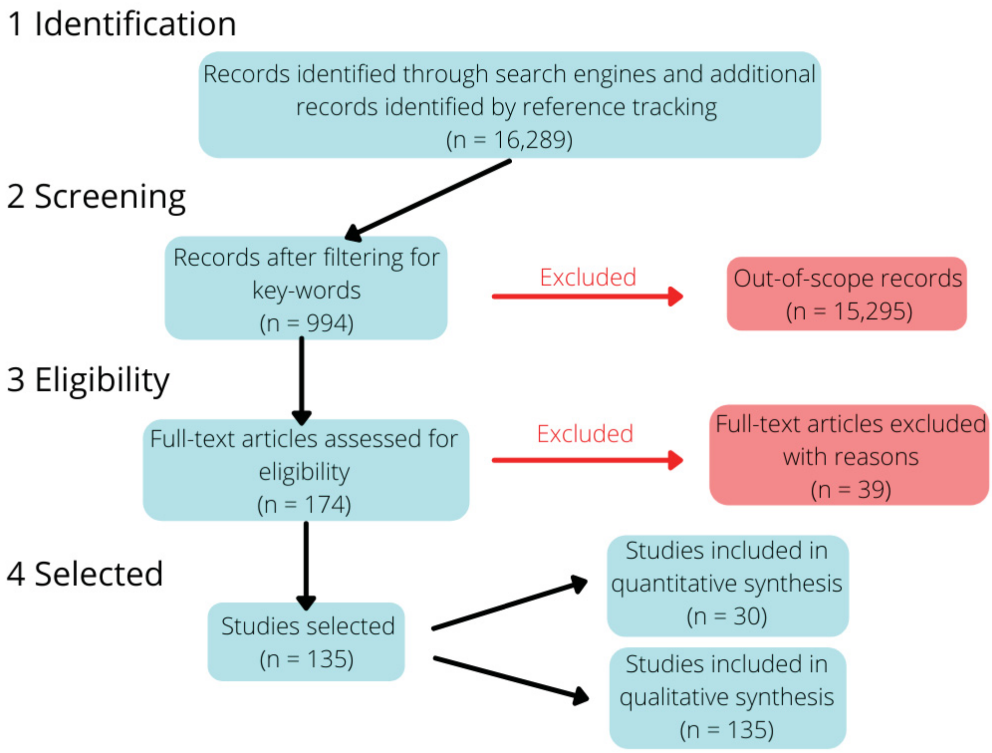

Fig. 1 PRISMA flow diagram showing the procedure used for the selection of studies for our systematic review, based on Moher et al. (2009)

2.2 Approaches and literature analysis

Taxa names followed the World Register of Marine Species (WoRMS). Information for each taxon was entered in a database, which included the taxonomic groups based on Bayer (1961), author(s) names, publication year, and the additional fields detailed below:

- Biogeographic ecoregions and realms

We categorized data into marine ecoregions and realms of the world according to Spalding et al. (2007). Realms are large spatial units that share high levels of endemicity because of evolutionary history and historical isolation (Spalding et al. 2007). Ecoregions are sufficiently extensive areas within biogeographic realms that encompass distinct species compositions and are based mainly on environmental forces (Spalding et al. 2007), although such ecological units do not have significant levels of endemicity (Costello et al. 2017).

- Study type and research problem

The studies were classified as *descriptive field studies*, those that were performed under natural conditions or through direct samplings in the field; *experimental field studies*, those that were performed in the field using experimental approaches; and *laboratory studies*, those that were performed in a laboratory. Some studies encompassed more than one approach and were assigned more than once to the database.

The research problems or main themes of the studies, defined as the compilation of main ideas, questions, assumptions and hypotheses within a study, were categorized as (1) natural diet description, (2) experimental diet description, (3) prey selectivity, (4) role of autotrophy, (5) feeding responses to environmental forces, (6) feeding activity rhythms, (7) seasonal variability, (8) food web description, (9) record of environmental changes, (10) bleaching, and (11) other subjects. Again, some studies also encompassed more than one research problem and were assigned more than once to the database.

- Heterotrophic, photosynthetic, and respiration rates

Data on heterotrophic carbon input (H_C), photosynthetic carbon input (P_C), and respiratory carbon demand (R_C) were extracted wherever available. We extracted the mean, and when possible, also the standard deviation for each variable. In cases where data were presented in graphs, Data Thief III software was used to extract the values (Tummers 2006). To standardize the normalization metric for all variables, we used values that only allowed for conversions in terms of the mass of organic carbon by the unit of ash-free dry weight biomass by the unit of time (µg C g $AFDW^{-1}$ $hour^{-1}$). Ash-free dry weight biomass is a suitable metric to compare soft coral data with distinct morphologies (Lasker et al. 1983; Pupier et al. 2018). H_C covers all kinds of heterotrophic prey sources, including zooplankton, phytoplankton, particulate organic carbon (POC), and dissolved organic carbon (DOC). Not all studies assessed all prey types but were also considered in the statistical analysis. Values of P_C or R_C originally represented in units of oxygen were converted into units of carbon by using a conversion factor of 0.281, based on McCloskey et al. (1978).

- Source of acquired carbon to animal respiration and scope for growth and reproduction

Whenever data on H_C, P_C, and R_C were available, we assessed the contribution of heterotrophically acquired carbon to octocoral respiration (CHAR = H_C: R_C × 100%) based on Grottoli et al. (2006) and the contribution of autotrophically acquired carbon to octocoral respiration (CZAR = P_C: R_C × 100%) based on Muscatine et al. (1981). Papers that did not provide H_C, P, and R_C but still had data on the CZAR or CHAR, were also used. We also estimated the scope for growth, which is the carbon budget available for growth and reproduction (SfG = $H_C + P_C - R_C$), based on Anthony and Fabricius (2000). SfG values above 100% indicate the capability of the organism to self-maintenance., Data Thief III software was also used to extract the values in cases where data were present in graphs (Tummers 2006).

- Prey types

To determine the prey selectivity of different octocoral taxa, the heterotrophic prey sources in terms of abundance and carbon sources were estimated in percentages. We categorized them in terms of abundance into zooplankton, phytoplankton, particulate organic carbon (POC), dissolved organic carbon (DOC), and in terms of carbon source into zooplankton, phytoplankton, and particulate organic matter (POM).

2.3 Data analysis

We used general linear regression models (GLMs) to investigate the relationship between biological and environmental features (Zuur et al. 2007). The assessment of the significance of the dependent variables CHAR, CZAR, H_C, P_C, and R_C was performed by applying GLMs with a negative binomial probability distribution family, adjusting each one separately to biogeographic realms and taxonomic groups. The assessment of the significance of the dependent variable SfG was performed by applying GLMs with the Gaussian probability distribution family due to presenting negative values, adjusting to biogeographic realms and taxonomic groups. The assessment of the significance of the dependent P_C and CZAR was also adjusted to the algal endosymbiont clade.

The models were then compared using the Akaike information criterion (AIC). Significant differences were further identified with the *post hoc* test of general linear hypotheses (GLHT). All statistical analyses, graphs, and figures were performed using the R programming language (R Core Team, 2020).

3 Feeding ecology of Octocorallia: survey results and general trends

In the last twenty years, studies on octocoral feeding ecology have become more popular, representing 68% of the total number of studies since 1960 (Fig. 2). Although a considerable high diversity of taxa was assessed and several ecoregions studied, most target species inhabit shallow and warm-water systems (*e.g.*, coral reefs and coralligenous systems). Not all taxonomic groups and biogeographic ecoregions have received the same research efforts. All CHAR, H_C, and R_C data came from tropical or temperate shallow-water systems, as well as CZAR and P_C, as expected.

Our findings below provide innovative and relevant insights to octocoral feeding ecology, especially regarding the increasing trends in their distribution and abundance in several marine systems. However, available data should be interpreted with caution due to the expected variation in sampling methods and time surveys

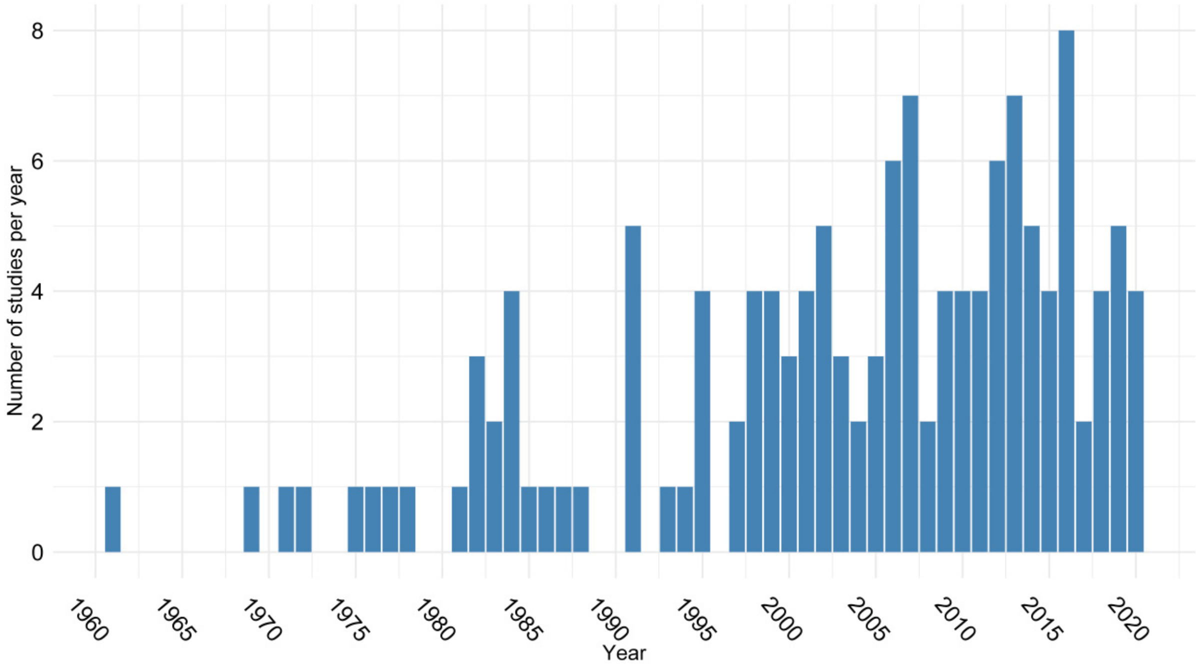

Fig. 2 Variation trends in the total number of indexed, peer-reviewed studies on octocoral feeding ecology per year.

3.1 Biogeographic ecoregions and realms

Phase shifts from scleractinian coral-dominated reefs to octocoral-dominated reefs are restricted to tropical regions, as already reported by Schubert et al. (2017) and Norström et al. (2009), including the realms of the Western Tropical Atlantic, Western Indo-Pacific and Central Indo-Pacific (Fig. 3). Surprisingly, many records are found precisely in the biogeographic province of the Red Sea and the Gulf of Aden. The likely disturbing factors related to such changes encompass mass coral bleaching (Stobart et al. 2005; Ruzicka et al. 2013; Villamizar et al. 2013), cyclones (Wakeford et al. 2008; Coles et al. 2015), outbreaks of crown-of-thorns (Bruckner and Dempsey 2015), eutrophication (Baum et al. 2015; Vollstedt et al. 2020), pollution (Al-Zibdah et al. 2007), blast fishing (Fox et al. 2003; Wood and Dipper 2008) and tourism (Hoffman 2002).

Most of the studies about the feeding ecology of octocorals are concentrated in the Temperate Northern Atlantic, comprising 41 studies (Fig. 3). Within this realm, the coralligenous system of the Western Mediterranean is the most studied biogeographic ecoregion. This system has markable seasonal variability in primary production, with blooms occurring in winter and spring and low carbon production in the rest of the year (Coma et al. 2000; Ribes et al. 2003). To compensate for the scarce production period during summer, benthic suspension feeders decrease their metabolic activity, an event known as summer dormancy (Coma and Ribes 2003). In this ecoregion, there is only one zooxanthellate octocoral species, *Eunicella singularis*, in which algae endosymbiosis occurs just in shallow-water zones, while in deep waters, this relationship is absent (Gori et al. 2012). Recently, the Indo-Pacific octocoral *Melithaea erythraea* has spread across the Southeast Mediterranean Sea as a consequence of the increase of environment suitable habitats due to rising temperatures (Grossowicz et al. 2020). In contrast, the mass mortality events of native octocorals, including *Paramuricea clavata* and *Eunicella cavolini*, related to thermal anomalies have been also reported (Aurelle et al. 2020). These processes indicate the ‘‘tropicalization’’ of the Mediterranean Sea ecoregion driven by climate change (Grossowicz et al. 2020).

The feeding ecology of octocorals within the biogeographic realms of the Tropical Atlantic, the Western Indo-Pacific, and the Central Indo-Pacific has also been substantially studied, comprising 33, 22, and 19 studies, respectively. These biogeographic realms are characterized by coral reefs that constantly face nutrient limitations and are efficient recyclers of organic matter (Hatcher 1990). To overcome nutrient constraints, which affect food supply, several benthic species benefit from mutualism with algal endosymbionts (Kinzie 1973). In such realms, phase shifts from hard corals to octocorals have been most common and reported (Fig. 3). This striking phenomenon is characterized by a decline in the abundance of scleractinian corals and an increase in the abundance of octocorals (Tsounis and Edmunds 2017; Lasker et al. 2020a; Rodriguez et al. 2020). Naturally, the suborders Alcyoniina and Stolonifera are more abundant in the Central Indo-Pacific, while Calcaxonia, Holaxonia, and Scleraxonia are more common in the Tropical Atlantic (Johnson and Hallock 2020), a pattern that is also reflected in the number of research efforts on their feeding ecology.

Considerable efforts have been made in the polar ecoregions of the Southern Ocean and Arctic, comprising 8 and 2 studies, respectively. The general focus consists mainly of deep-water coral ecosystems, formed by gravel or pebbles on soft bottoms, often dominated by Pennatulaceans and Calcaxonia. Most colonies of these taxonomic groups are supported by an internal skeletal rod of non-scleritic calcite, which allows them to live in zones where the calcium carbonate compensation depth may constrain the distribution of scleractinians (Guinotte et al. 2006). These realms face a prolonged period of almost no productivity in winter, during which suspension feeders rely on sediment resuspension and lateral advection and have developed strategies to use the seston fine fraction and to increase efficiency in food assimilation (Gili et al. 2001; Orejas et al. 2002; Elias-Piera et al. 2013). In fact, it has been suggested that octocorals have a relevant ecological role in recycling organic matter in such systems (Orejas et al. 2001). In recent years, although local glaciers have been retreating due to climate change, the pennatulid *Malacobelemnon daytoni* has increased in abundance and distribution range, likely related to increased sedimentation (Servetto et al. 2017).

Few efforts have been made in the temperate Northern Pacific (10 studies), Temperate Australasia (2 studies), Temperate South America (1 study) and Tropical Eastern Pacific (1 study). In fact, there are several ecoregions worldwide where the feeding ecology of octocorals is largely unknown; gaps occur in the realms of Eastern Indo-Pacific and Temperate Southern Africa.

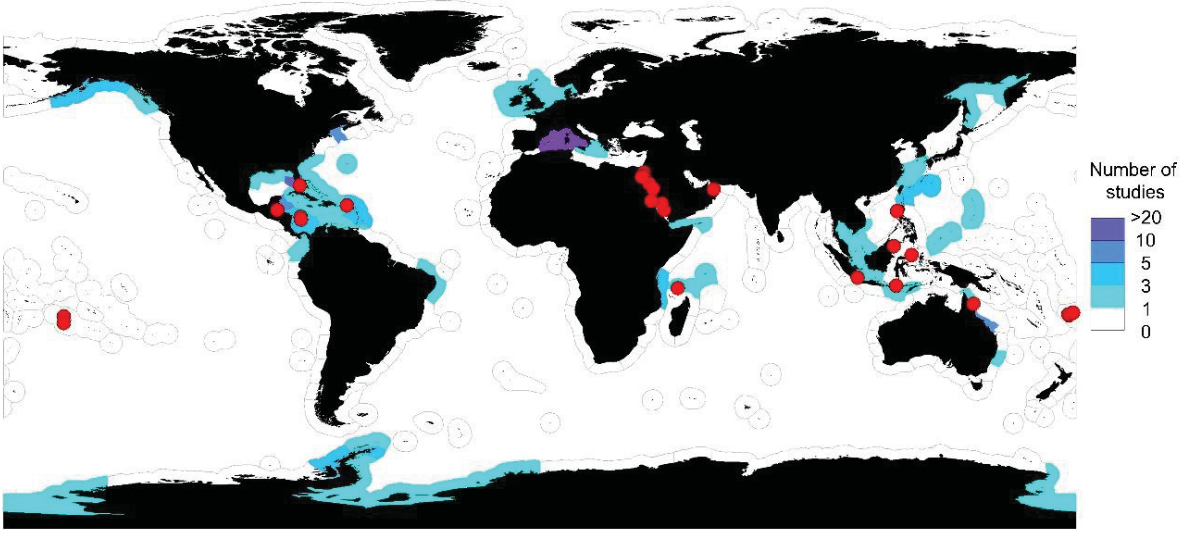

Fig. 3 Distribution of studies on octocoral feeding ecology worldwide taken from 135 papers published between 1961 and 2020. Biogeographic ecoregions are defined according to Spalding et al. (2007). Red circles indicate where there are phase shift reports of scleractinians decline and octocorals expansion

3.2 Taxonomic groups

The feeding ecology of 172 octocoral taxa distributed in 7 taxonomic groups and 25 families was investigated (Fig. 4). Most studies used only descriptive field (46%) or laboratory approaches (32%), followed by studies that included both approaches (15%), studies that used only experimental field approaches (6%), and other studies that used experimental field and descriptive field or laboratory approaches (2%).

Among the families studied, Alcyoniidae, Plexauridae, and Nephtheidae were the most common, representing 57% of all taxonomic groups. Only one taxon was studied in the case of several families, namely Anthoptilidae, Coralliidae, Halipteridae, Helioporidae, Keroeididae, Kophobelemnidae, Paragorgiidae, Spongiodermidae, Tubiporidae, and Veretillidae.

If we consider that the subclass Octocorallia is a monophyletic group that encompasses approximately 3,200 species (Daly et al. 2007), the current amount of only 172 studied taxa indicates that significant gaps still exist. Currently, Octocorallia is divided into three orders based on Bayer (1981). Most feeding ecology studies have focused on the order Alcyonacea (164 taxa studied), distributed in five groups (Alcyoniina, Calcaxonia, Holaxonia, Scleraxonia and Stolonifera). Comparatively fewer efforts have been made in the orders Pennatulacea (eight taxa studied) and Helioporacea (one taxon studied).

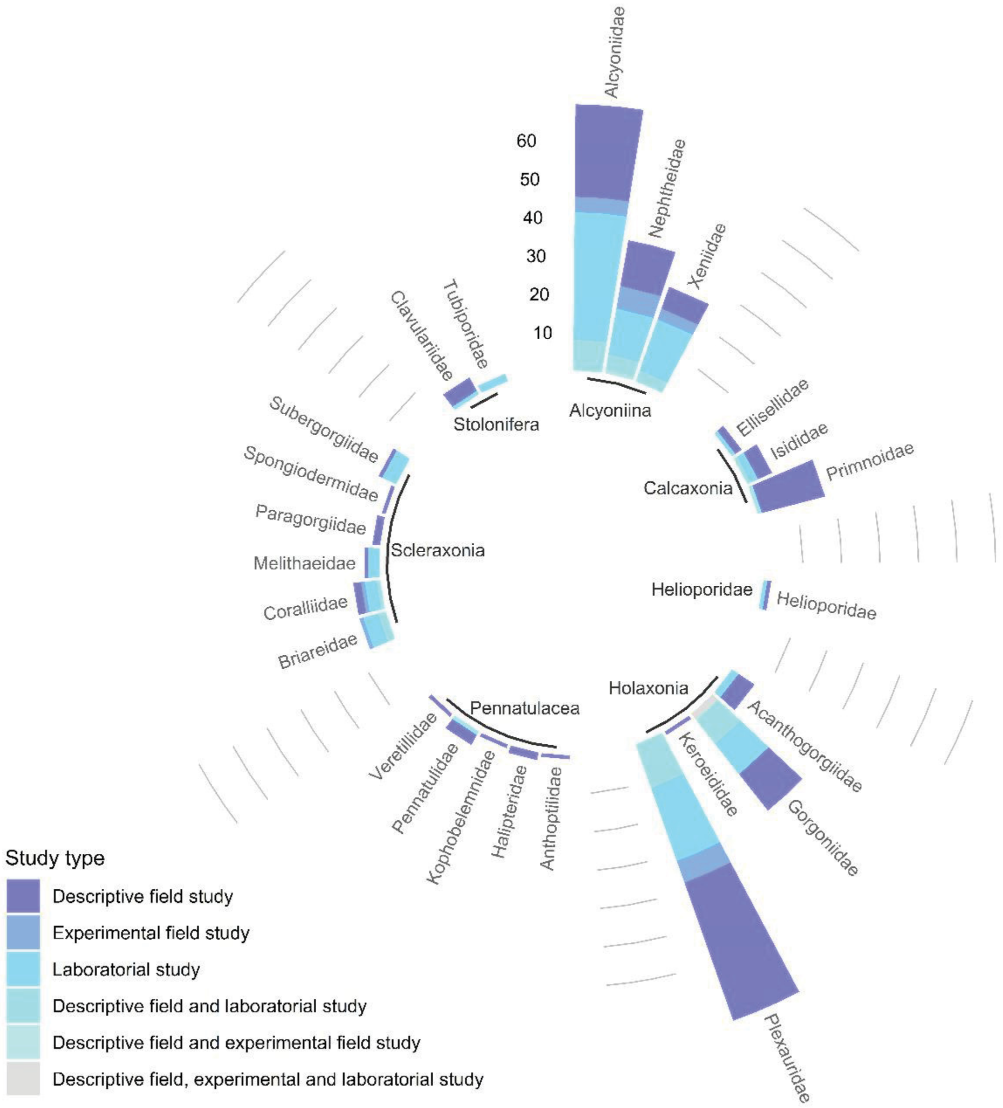

Fig. 4 Circular barplot of literature efforts by studied taxonomic groups and by study type (number of studies)

There is evidence that the three current subordinate designations of Octocorallia are polyphyletic (McFadden et al. 2006). Molecular data support that Octocorallia phylogenetically encompasses three distinct clades: Holaxonia – Alcyoniina, Calcaxonia – Pennatulacea, and *Anthomastus* – *Corallium*. Most of the octocoral taxa belong to the two first clades, and few taxa belong to the latter. Studies of prevailing feeding strategies are congruent with this pattern, with higher efforts on the clade

Holaxonia – Alcyoniina (70%), followed by Calcaxonia – Pennatulacea (10%) and *Anthomastus* – *Corallium* (2%), while 17% of the taxa did not have phylogenetic data.

3.3 Investigated research problems or main research themes

Studies of octocoral feeding ecology usually encompass more than one research problem. Natural diet description was the most common focus, followed by descriptions of experimental diet (Fig. 5). Such studies are essential to identify trends in the feeding ecology of octocorals and may serve as a basis for the formulation of hypotheses and guide experiments. Gastrovascular analysis is a method widely employed in natural diet descriptions. This is a method that requires highly skilled researchers to identify the composition of gastrovascular content. However, the appearance of the content is highly affected by the digestion time and the prey type, and advanced stages of digestion lead to prey items not being identifiable. Phytoplankton tends to be easier to digest than crustacean fragments and copepod carapaces (Rossi et al. 2004; Coma et al. 2015). Octocoral species have different digestion times that generally increase as the temperature decreases (Coma et al. 2015). Moreover, gastrovascular analysis is unable to identify prey items of the fine fraction of seston, such as pico- and nanoplankton.

Isotope ratios have also been largely applied to octocorals to assess their feeding ecology (Cocito et al. 2013; Rossi et al. 2020), to identify food web structural properties (Sherwood et al. 2008), and to record natural and anthropic environmental changes (Heikoop et al. 2002; Conlan et al. 2006). Most octocorals are primary or secondary consumers. Moreover, the use of isotope ratios has demonstrated the coupling between octocorals and surface water processes, such as biological productivity and nutrient inputs (Sherwood et al. 2005a), as well as anthropic impacts (Williams et al. 2007; Sherwood et al. 2010). Most octocorals used as a proxy for palaeoceanographic reconstructions inhabit deep-water environments, although some efforts using shallow-water octocorals have already been made (Williams and Grottoli 2010). Deep-water octocorals are excellent candidates for recording oceanographic changes since they are long-lived animals capable of reaching hundreds of years (Heikoop et al. 2002; Sherwood et al. 2005b; Williams et al. 2007). Commonly, $\delta^{15}N$ and $\delta^{13}C$ are the most widespread isotopes used. Higher values of $\delta^{15}N$ tend to indicate higher heterotrophic carbon inputs, while lower values indicate autotrophic carbon inputs since zooplankton have higher values than their prey, phytoplankton (Sherwood et al. 2008). However, $\delta^{15}N$ can also be used to assess anthropic pollution as eutrophication since polluted environments have higher values than natural ones (Ward-Paige et al. 2005; Conlan et al. 2006; Baker et al. 2010, 2011; Sherwood et al. 2010; Fujii et al. 2020). Likewise, $\delta^{13}C$ can also indicate the trophic level, with high values indicating predation of zooplankton and phytoplankton and low values indicating autotrophy (Rossi et al. 2020). Moreover, $\delta^{13}C$ indicates the feeding type, whose low values are usually linked to pelagic sources, while high values are linked to benthic sources (Sherwood et al. 2008). In this way, $\delta^{15}N$ and $\delta^{13}C$ values vary across habitats and biogeographic realms, as prey composition and nutrient availability are important factors controlling its values.

Bleaching is the breakdown of the host-algal endosymbiont relationship, in which zooxanthellae are expelled, causing the hosts to pale in color. The main factors driving this event are excessively high sea surface temperature, high ultraviolet radiation, and exposure to dissolved inorganic nitrogen and carbon dioxide partial pressure enrichment (Wooldridge 2010; Lesser 2011; Slattery et al. 2019). Although bleaching of corals has been reported since 1870, the intensity and frequency have accelerated since the 1970s (Glynn 1993; Donner et al. 2005). Therefore, the bleaching of octocorals has gained notoriety in recent years, and suspension feeding has been a factor that may explain their greater or lesser vulnerability (Baker et al. 2015).

As expected, due to logistical and financial resource constraints, most of the studies are carried out in shallow waters down to SCUBA diving depths. Data on CHAR, CZAR, H_C, and R_C are thus currently limited to forty meters of depth. Although benthic-pelagic coupling may lose strength as depth increases, relevant ecological functions between octocorals and planktonic communities continue to occur in the first layers upon the seabed of deep-water systems. Even so, efforts to better understand the communities of mesophotic and deep-water systems have increased considerably in recent times. Most studies that encompass these depths use isotope ratios and biochemical analysis as methodological approaches. In addition, access to deep-water systems (*e.g.,* abyssal plains, seamounts, and ocean ridges) requires specialized equipment and, consequently, heavy funding.

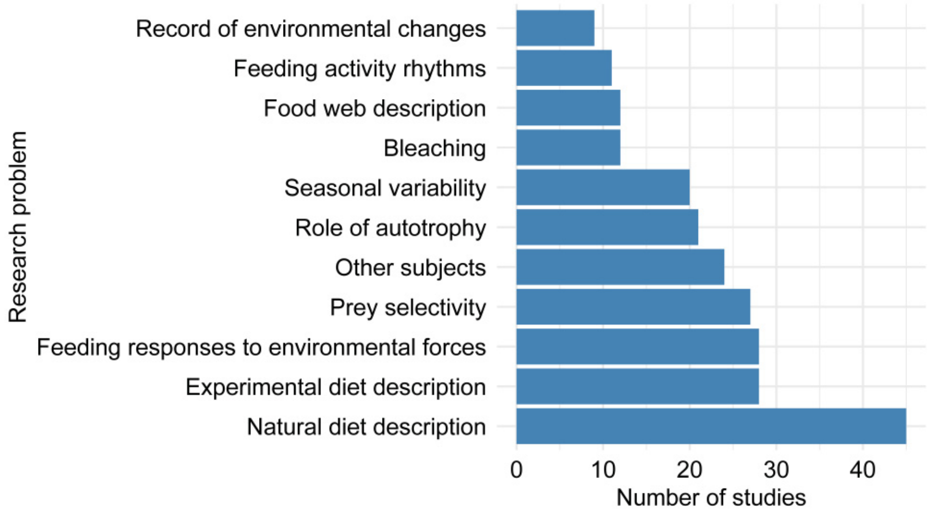

Fig. 5 Main research problems investigated of the peer-reviewed literature on octocorals' feeding ecology

3.4 Metabolic demands in octocorals

Overall, the R_C of octocorals is 207.2 ± 199.2 µg C g AFDW^{-1} hour^{-1} (mean ± standard deviation) (Fig. 6). Although R_C among zooxanthellate octocorals encompassing values from host and algal endosymbionts are expected to present higher values than azooxanthellate octocorals, the differences were not statistically significant (one-way ANOVA, *p* value = 0.22). These values are comparatively lower than those of scleractinians (Fabricius and Klumpp 1995). The metabolic demand of octocorals varies within the same species and is strongly affected by the quantity of energy available in their living habitats. Colonies more exposed to light or in optimum water flow regimes, which ultimately is related to food availability, tend to have higher energy costs than those located in shaded areas or stable waters (Sebens 1984). The diffusion rate of oxygen is also a factor influencing the R_C of octocorals, which is directly influenced by the thickness of the diffusion-limiting boundary layer in octocoral tissue (Patterson and Sebens 1989). Thick layers are related to habitats with low water flow, while thin layers are related to habitats with high water flow (Nakamura and Van Woesik 2001).

The variation in R_C among taxa is related to organic biomass per surface, influencing gas exchange and, in the case of zooxanthellate octocorals, the light exposure of *Symbiodinium* (Rossi et al. 2020). R_C tends to be higher in tropical and temperate realms than in polar realms (Table 1; Fig. S1). This trend was expected since the metabolic rates of the organisms, as well as the oxygen consumption, increase as the temperature increases (Breitburg et al. 2018). Our results also indicated that Acyoniina, Holaxonia, and Scleraxonia require quantitively higher values of R_C than Calcaxonia and Stolonifera (Table 1; Fig. S2). Higher R_C is expected in sea fan and plume colonies since they have a higher polyp density and smaller polyps (Lewis and Post 1982; Rossi et al. 2018).

The R_C of octocorals exhibits significant seasonal variations in temperate biogeographic realms (Coma et al. 2002). The R_C is driven by water temperature, increasing simultaneously until reaching a species-specific threshold in which oxygen consumption decreases. For instance, the respiration rates and polyp activity of Mediterranean octocorals (*Paramuricea clavata*, *Eunicella singularis*, *Eunicella cavolinii* and *Corallium rubrum*) are usually higher at temperatures ranging between 18 and 20 °C (Previati et al. 2010). The ability to overcome excessive temperatures varies according to each species, with different responses in polyp activity, necrotic tissues, and time of regeneration (Sammarco and Strychar 2013).

In this sense, the higher resilience of octocorals compared to scleractinians may be related to their capacity to decrease respiration rates to withstand thermal stress events. Autotrophic performance is negatively impacted by high temperatures, and to compensate for the decrease in P_C, they reduce their energy expenses, especially R_C (Ferrier-Pagès et al. 2009; Previati et al. 2010; Ezzat et al. 2013). In such species, heterotrophy remains constant and is not capable of meeting all energy requirements or preventing bleaching (Khalesi et al. 2011; Ezzat et al. 2013). During periods of high temperatures, octocorals reduce energetic expenses, including oxygen consumption and polyp activity (Previati et al. 2010; Ezzat et al. 2013). In contrast, experiments with the Caribbean scleractinian *Orbicella faveolata* revealed that high temperatures increased holobiont respiration (Baker et al. 2018).

Although polyp expansion is related to feeding efficiency, it provides a greater area for gas diffusion, increasing the consumption of oxygen by organisms. Contracted polyps reduce approximately 50% of the R_C compared with expanded polyps (Coma et al. 2002), although slight differences in this rate may be related to the polyp size (Schubert et al. 2017). In this way, the energy costs in feeding have to be worthwhile to supply the energy losses of respiration. As a response to high temperatures, polyps tend to become inactive and reduce the R_C. The thermotolerance of octocoral species may define the distribution in natural habitats, with species more tolerant to high temperatures occupying shallow waters and less tolerant distributed in deep waters (Previati et al. 2010). Moreover, octocoral species that demonstrate higher tolerance towards high temperatures may be favored in future scenarios of higher temperatures. Another factor influencing R_C is the synthesis of new tissue, which in the Mediterranean octocoral *Paramuricea clavata* can increase by 40% (Coma et al. 2002).

Severe hypoxia events can naturally occur in reef ecosystems, affecting their structures and functioning due to coral mortality (Simpson et al. 1993; Nelson and Altieri 2019). However, anthropic activities have caused a sharp decline in oxygen in marine and coastal systems because of rising temperatures and increasing nutrient discharge, causing serious biological implications, such as phase shifts (Altieri et al. 2017; Breitburg et al. 2018). Although hypoxia events influence coral bleaching and mass mortality, coral species are less vulnerable to low oxygen levels, leading to shifts in more stress-tolerant communities (Altieri et al. 2017). Oxygen minimum zones (OMZs) have expanded worldwide and the global oceanic oxygen content has decreased more than two percent since 1960, varying within biogeographic realms and depths (Stramma et al. 2010; Schmidtko et al. 2017). OMZs in Northeast Pacific seamounts were related to mortality and declines in the abundance of the bamboo gorgonian *Isidella tentaculum* (Ross et al. 2020). Therefore, since OMZs have been expanding recently and causing significant ecological damage, studies assessing the effects of low dissolved oxygen on octocoral feeding performance are essential to predict future changes within disturbed systems. Not only hypoxia, but also hyperoxia can reduce photosynthetic rates among corals (Nelson and Altieri 2019).

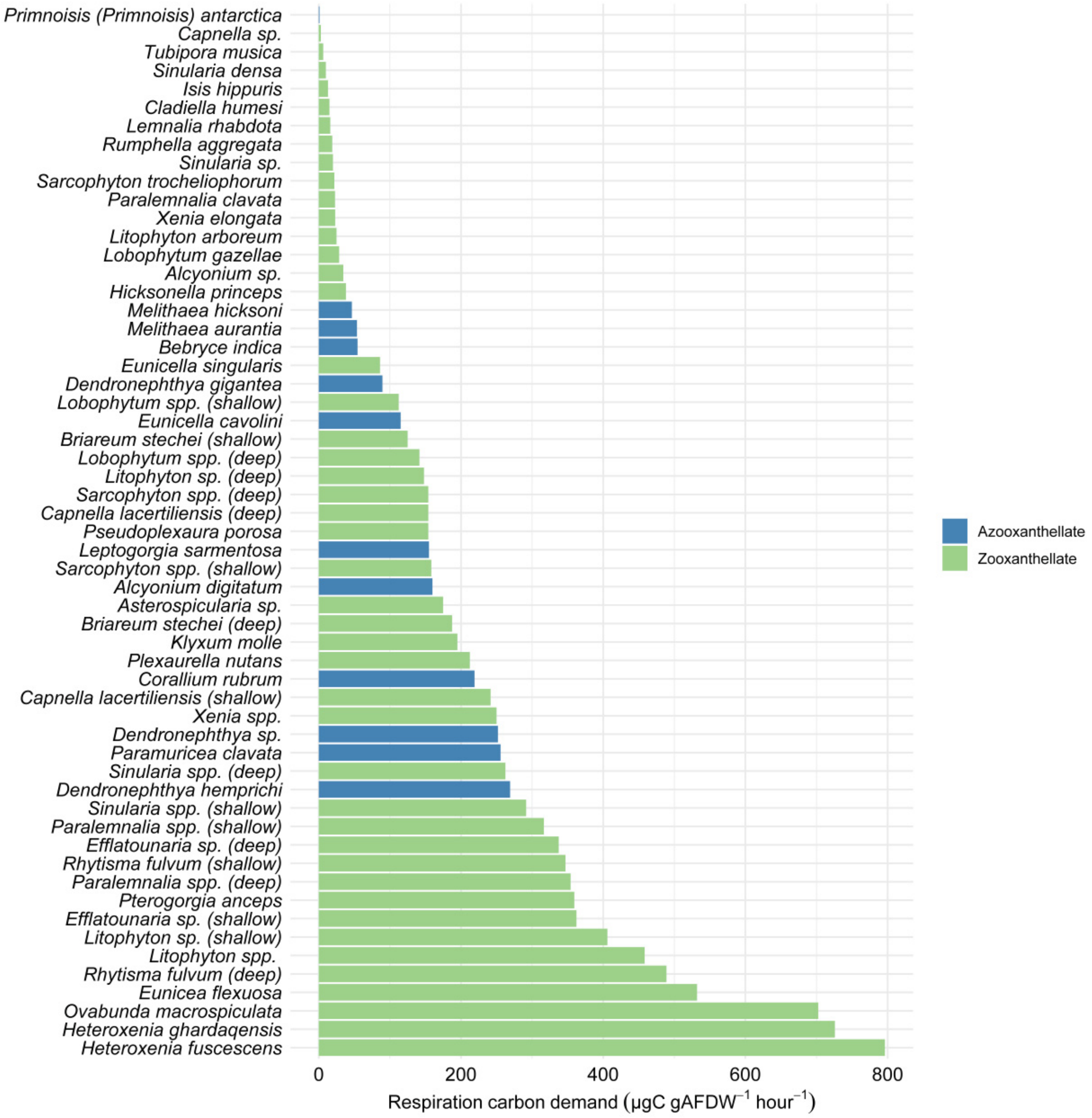

Fig. 6 Respiratory carbon demand – R_C (µg C g AFDW^{-1} hour^{-1}) of zooxanthellate and azooxanthellate octocoral taxa.

3.5 Suspension-feeding in octocorals

The presence or absence of algal endosymbionts is the main driver shaping suspension feeding of octocorals. The H_C in azooxanthellate octocorals of 300.6 ± 493.9 µg C g AFDW^{-1} hour^{-1} is comparatively higher than that in zooxanthellate octocorals of 19.1 ± 40.2 µg C g AFDW^{-1} hour^{-1} (Fig. 7). Azooxanthellate species are forced to meet their carbon metabolic demands by heterotrophy; otherwise, the depletion of the energy reserve would cause the organism to perish. In this way, azooxanthellate octocorals have a CHAR of 185.7 ± 208.0% (Fig. 8). In contrast, the heterotrophy of the zooxanthellate species does not meet the metabolic demand, presenting a CHAR of 28.7 ± 32.3% (Fig. 8). Thus, to meet their carbon metabolic demand, another source of carbon is required, which is carbon assimilation from the algal endosymbiont. The values of zooxanthellate octocorals are comparable to tropical scleractinian corals, in which heterotrophy accounts for between 15 and 35% of the metabolism in healthy corals (Houlbrèque and Ferrier-Pagès 2009). Laboratory experiments have shown that feeding rates of octocorals are influenced by their satiation, although the prey availability tested is comparatively higher than that in the natural environment (Lin et al. 2002).

Knowledge about the feeding ecology of octocorals, combined with patterns of distribution and abundance data, allows for the assessment of the role of these benthic suspension feeders on carbon fluxes and budgets (Rossi et al. 2004; Coppari et al. 2019). The H_C combined with abundance and distribution data allows the estimation of the grazing rate. These data have shown that octocorals act as significant carbon sinks, having an important implication for benthic-pelagic coupling. In near-shore Great Barrier Reef systems, octocoral assemblages sequester an amount of carbon equivalent to 2.5 ± 1.1 g C m^{-2} d^{-1} (Fabricius and Dommisse 2000). The total amount of carbon accumulated by the growth of three octocoral species (*Paramuricea clavata*, *Eunicella singularis,* and *Leptogorgia sarmentosa*) is estimated to be 1.15×10^{-2} t C ha^{-1} $year^{-1}$ in the Cap de Creus, NW Mediterranean (Coppari et al. 2019).

The food type captured by octocoral species is mainly driven by their morphology, such as polyp diameter, polyp height, tentacle length, number of pinnules, and pinnule spacing (Leversee 1976; Porter 1976; Lasker et al. 1983). Within the same colony, differences in prey capture occur, in which apical and peripheral branches have higher values than those located in the center or base of the colony (Coma et al. 1994). The feeding capacity varies according to the food availability and the feeding activity rhythm (*i.e.* open polyps). In turn, the polyp rhythm is related to exogenous stimuli, including food availability, water flow, and temperature (Roushdy and Hansen 1961; Picciano and Ferrier-Pagès 2007; Rossi et al. 2019b). The stimulus to food availability is a saving energy strategy developed to overcome the heterogeneity of the seston that often has significant diel and seasonal variations, especially in shallow-water habitats. In this way, octocorals from ecoregions characterized by inconsistent periodicities of food supply may rely on food pulses (Rossi et al., 2019). Conversely, deep-water octocoral species usually experience stable food availability (Grinyó et al. 2018).

The optimal spectrum flow varies among species and is mainly related to colony morphology. The increase in water flow simultaneously increases the particle encounter to the polyps until reaching a threshold in which polyp deformation occurs, reducing prey capture efficiency (Patterson 1984; Best 1988). Under excessive flow conditions, species with flexible skeletons minimize the drag forces on polyps by decreasing the colony area (Dai and Lin 1993). The flexibility of the colony, combined with polyp flexion, increases the suitable range of water flow for feeding (Sponaugle 1991). On the other hand, rigid skeletons have a broader range of optimal flow conditions for feeding (Rossi et al. 2019b). The branch rigidity is related to sclerite content and refractory content (Shirur et al. 2014).

There is no consensus on the diel cycle in polyp opening and contraction (Garrabou and Wainwright 1999). The contraction of polyps during daylight periods among azooxanthellate octocorals could be considered a predator avoidance strategy, especially against fishes (Bell et al. 2006). However, polyp opening occurs in periods of high current flow, which indicates that feeding outweighs protection at these moments (Bell et al. 2006).

Anthozoans have significant phenotypic plasticity (Todd 2008), that is, the shaping of distinct morphologies as a response to environmental forces. Planar morphology species grow to a position perpendicular to water flow (Grigg 1972; Russo 1985) and may bend and twist throughout their lives, seeking to improve particle encounters (Wainwright and Dillon 1969). Water flow is also considered the most important environmental driver of the ramification of colonies (Weinbauer and Velmirov 1995). The number of branches increases as the flow increases until a limit and then decreases again at high water flow velocities (Khalesi et al. 2007). Curiously, branching patterns, such as reticulation, pinnation, and candelabra, likely evolved independently along the phylogenetic tree, *i.e.*, a convergent evolution (Sánchez 2004). The morphological plasticity among specimens of the same species influences the carbon inputs from suspension feeding and autotrophy, as well as the metabolic demand. For instance, the octocoral *Briareum asbestinum* exhibits encrusting and branching morphologies in the same habitat, influencing the carbon budgets, with the first shape having a CZAR above 100% and the latter below 100% (Ramsby and Goulet 2019).

Anthropogenic disturbances negatively affect the feeding ability of octocorals. Organic eutrophication in coastal systems has negatively affected scleractinian corals, decreasing P_C values (Haas et al. 2009), and in chronic events causing mortality (Kuntz et al. 2005). Although eutrophication may improve the nutritional status of scleractinian corals, it may also act as an additional stress factor, impairing their physiology and survival (Fabricius et al. 2013). On the other hand, octocorals generally do not present negative responses to eutrophication, and may benefit from using a higher amount of organic matter as an energy source (Vollstedt et al. 2020). However, they may present negative physiological responses to heavy metal-contaminated waters, such as excessive mucus secretion, tissue necrosis and reduced polyp activity (Chan et al. 2012).

Excessive sedimentation negatively affects octocoral survival, and azooxanthellate octocorals are thought to be more tolerant than zooxanthellate octocorals (Williamson et al. 2011). Some octocoral species, such as *Leptogorgia punicea*, in the Gulf of Mexico, are tolerant to high sediment loads and adapted to euryhaline conditions (Williamson et al. 2011). Although anthozoans can clean themselves by mucus production and ciliary currents, excessive chronic sedimentation shades the colony surface, decreasing the feeding performance provided by zooxanthellae (Richmond 1993; Tseng et al. 2011). A suitable spectrum of water flow helps in the removal of sediments and metabolic wastes. Sedimentation events caused a decline in chlorophyll content of up to 22%, a proxy for endosymbiotic algal density, in the scleractinian *Orbicella annularis* (Dallmeyer et al. 1982). Sedimentation may also interfere with feeding structures, reducing heterotrophic energy inputs (Riegl and Branch 1995). Consequently, the increases in the energy demand due to the cleaning effort may increase the R_C by 30% in both octocorals and scleractinians (Riegl and Branch 1995). Interestingly, there are mutualistic associations in which brittle star species clean the surface of octocorals as they feed, enhancing the prey capture efficiency of the host (Hendler 1984; Girard et al. 2016). In fact, mutualistic associations could even enhance the hosts' resilience, as indicated by the faster recovery of anthozoans with the epizoic partners after disturbing events, including oil spills (Girard et al. 2016) and landslides (Grange 1991).

Some scleractinian species compensate for periods of low photosynthetic inputs by increasing heterotrophy under thermal stress events, which can exceed 100% of the CHAR (Anthony and Fabricius 2000; Grottoli et al. 2006; Houlbrèque and Ferrier-Pagès 2009). Bleaching events significantly reduce P_C by 67 to 90% and CZAR by up to 60% in scleractinians (Rodrigues and Grottoli, 2007). In compensation, some scleractinian species, including *Montipora capitata*, can increase their H_C to reach CHAR values above 100%, while other species, such as *Porites compressa* and *P. lobata*, cannot (Grottoli et al., 2006). Species that present this capacity in autotrophy and heterotrophy balance are expected to be more resilient to bleaching events (Anthony and Fabricius 2000; Grottoli et al. 2006). To the best of our knowledge, heterotrophy-autotrophy plasticity has not been reported in octocorals. Notwithstanding, more studies of the balance between suspension feeding and autotrophy of octocorals are needed to better understand their physiological responses under stressful periods.

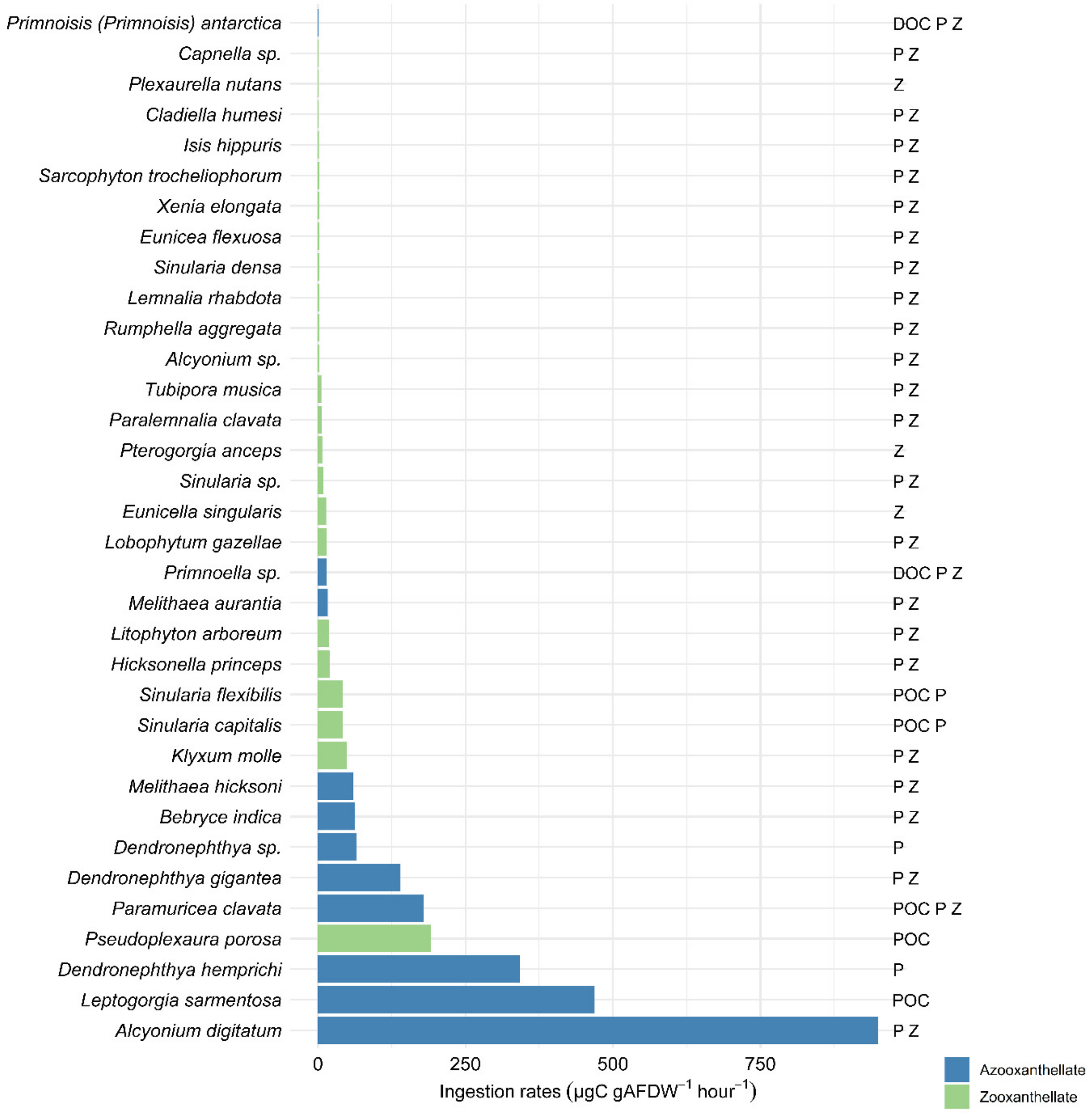

Fig. 7 Heterotrophic carbon input – H_C (μg C g AFDW^{-1} hour^{-1}) of the zooxanthellate and azooxanthellate octocoral taxa. Letters indicate the carbon sources that were assessed for each taxon: DOC (dissolved organic carbon); POC (particulate organic carbon); P (phytoplankton); Z (zooplankton)

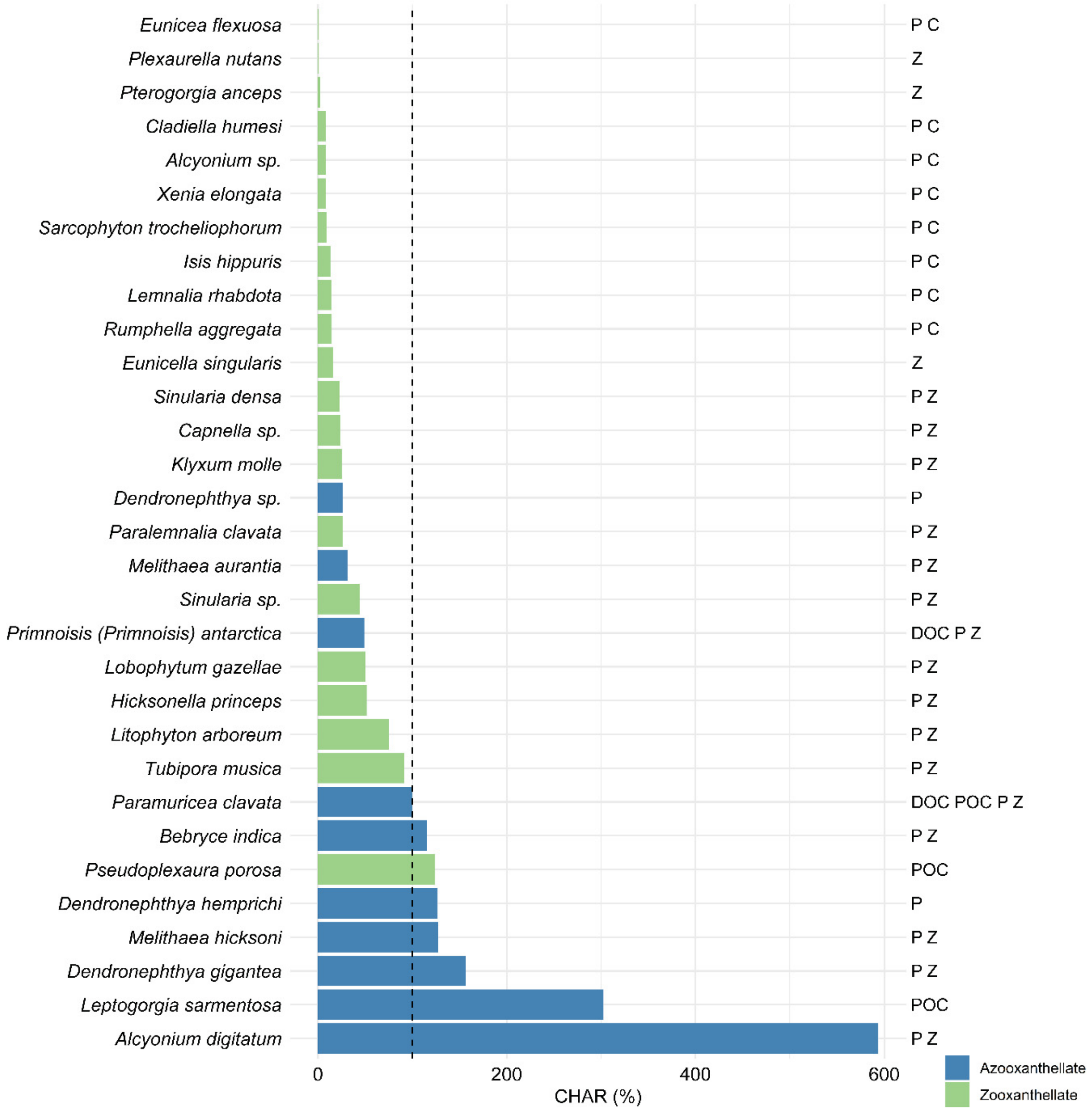

Fig. 8 Contribution of heterotrophically acquired carbon to animal respiration (CHAR = H_C: R_C × 100%) in zooxanthellate and azooxanthellate octocoral species in percentages. The black dashed line indicates the threshold at which Hc meets Rc. Letters indicate the carbon sources that were assessed for each taxon: DOC (dissolved organic carbon); POC (particulate organic carbon); P (phytoplankton); Z (zooplankton)

3.6 Autotrophy in octocorals

The metabolic demand of zooxanthellate octocorals is supplied by the P_C, contributing 303.9 ± 298.6 µg C g AFDW^{-1} hour^{-1} (Fig. 9), and is responsible for 148.7

± 112.7 of CZAR (Fig. 10). These values are in fact lower than those of overall scleractinian corals, which range from 200 to 400% (Mergner and Svoboda 1977; Fabricius and Klumpp 1995). This mutualism is fundamental in tropical oligotrophic waters since prey are relatively scarce (Kinzie, 1973). Species that acquire energy above 100% of CZAR can be considered net autotrophs.

Zooxanthellate octocorals tend to inhabit shallow and less turbid environments where light is available (Schubert et al. 2017), and a shift from mixotrophic to heterotrophic assemblages occurs as the depth increases (Fabricius and De'ath 2008; Schubert et al. 2017). The P_C of octocorals remains relatively constant from shallow to mesophotic habitats due to photolimited and photoacclimatized mechanisms that they possess (Mergner and Svoboda 1977; Pupier et al. 2019). On the other hand, most scleractinians experience a significant decrease in P_C as depth increases (Lesser et al. 2010; Einbinder et al. 2016; Ezzat et al. 2017). Lower light levels tend to increase the zooxanthellae densities in octocorals, increasing their photobiological performance, an adaptation to compensate for the depth (Rocha et al. 2013; Pupier et al. 2019).

Although autotrophy can cover the energy requirement (*i.e.* CZAR > 100%), it does not meet all the nutritional requirements needed by host species, and nutrients such as nitrogen and phosphorus rely on heterotrophy (Goldberg 2018). Additionally, the host provides derived substrates to algal endosymbionts, including carbon dioxide and ammonium (Wooldridge 2010). Experimental studies have indicated that octocoral colonies cultivated in aquaculture systems without food supply grew slowly and even had lower pigmentation compared to the colonies that were fed, which was likely related to nutrition limitation (Chang et al. 2020). In addition, one of the mechanisms by which the host acquires algal endosymbionts from the environment (*i.e.* vertical transmission) occurs through ingestion from the environment by suspension feeding (Fitt 1984).

Traits in the feeding ecology of anthozoans may be related to colony morphology, specifically, the ratio of surface area to volume (SA:V), in which higher ratios would exhibit higher CZAR (Porter 1976; Baker et al. 2015; Rossi et al. 2018). The contribution of autotrophy is related to colony morphology, in which branched colonies are expected to have higher CZAR than encrusting and unbranched colonies (Porter 1976). The reason for this is because the algal endosymbiont density and light exposure would be increased (Baker et al. 2015). Planar morphology, such as reticulate and candelabra branching, may reduce self-shading and maximize the surface area under light exposure (Baker et al. 2015). On the other hand, sea rods with whip-like branching may be more efficient in capturing prey in the water column by generating eddies close to the branches (Baker et al. 2015). The general trend is that photosynthetic performance is enhanced by thin branches and small polyps, corroborating the idea that species with this morphology rely more on autotrophy (Pupier et al. 2019). In Caribbean coral reefs, sea rods tend to be more dependent on heterotrophy than sea fans and sea plumes, which achieve energy to meet the metabolic demand only considering autotrophy (Baker et al. 2015). The polyp density can cause self-shading, and the host tissue thickness can constrain gas exchange (Kaniewska et al. 2011). Additionally, octocorals with higher *Symbiodinium* and chlorophyll densities often have higher photosynthetic efficiencies, such as the case of *Pseudoplexaura porosa* and *Pseudoplexaura wagenaari* (Ramsby et al. 2014). However, these octocorals present low photosynthetic rates per *Symbiodinium* cell and per chlorophyll compared to other species such as *Pterogorgia anceps* and *Eunicea tourneforti* (Ramsby et al. 2014).

Most *Symbiodinium* cells are concentrated in polyps and in lower quantities embedded in the upper layers of the coenenchyme, and for this reason, the expansion and contraction of polyps strongly influence P_C. Contracted polyps can decrease the P_C by up to 60% and, consequently, lead to CZAR values below 100% (Fabricius and Klumpp 1995). Although the observations have often been divergent, it has been suggested that the diurnal behavior of open polyps is predominant in zooxanthellate octocorals, while nocturnal behavior predominates in azooxanthellate octocorals (Schubert et al. 2017). Another factor that may also affect the *Symbiodinium* densities is the skeletal composition of the colony, which includes the sclerites and refractory material, as it influences the availability of host cells to house the algal endosymbiont (Shirur et al. 2014).

The capacity of algal symbionts to transfer photosynthetic carbon to the host is species-specific and varies greatly among octocoral species, algal endosymbiont clades, and habitat conditions (Stat et al. 2008). In the Gulf of Eilat, the translocation of photosynthates to the host ranges from 35 to 60% on the soft coral *Litophyton* sp. according to depths of 8 and 30 meters, respectively, while on the soft coral *Rhytisma* *fulvum* remains relatively constant at 80% independent of depth (Pupier et al. 2019). In the Caribbean, the sea rod *Pterogorgia anceps* seem to be more mutualistic, with algal endosymbionts transferring higher portions of photosynthetic carbon to the host, in contrast to the sea rods *Eunicea mammosa* and *Eunicea succinea*, which exhibit a less mutualistic relationship (Baker et al. 2015). Interestingly, the relationship between the octocoral host and the algal endosymbiont is not necessarily mutualistic, but in some interactions, it can be considered commensalism, as in the case of Caribbean *Plexaurella fusifera*, *Plexaurella nutans*, or *Briareum asbestinum*, in which there was no translocation of photosynthates by *Symbiodinium* cells to the octocoral host (Baker et al. 2015). Eutrophication may negatively affect the symbiotic association because the increased nitrogen levels allow the algal endosymbiont to use in higher quantity the products of their carbon fixation to their own growth and consequently decrease the translocation of carbon metabolites to the host (Muscatine et al. 1989; Stambler et al. 1991; Fleury et al. 2000). In fact, experiments with the scleractinian *Orbicella faveolate* exposed to elevated temperatures and excess nitrogen indicated that the relationship between the host and the algal endosymbiont was inclined to parasitize by increasing the respiratory demands of the holobiont and limiting the transfer of resources to the coral (Baker et al. 2018).

Zooxanthellae are genetically diverse and are classified into eight major lineages, from clades A to H, in which each clade possesses several subclade genotypes. The specificity of zooxanthellae clades tends to remain relatively constant over time and in biogeographic realms (Goulet 2006), and octocorals are reported to harbor algal endosymbiont clades A to D (Goulet et al. 2008) and G (Van Oppen et al. 2005). As in both scleractinians and octocorals, clade C dominates the Indo-Pacific scleractinian hosts, and clade B dominates the Atlantic-Caribbean hosts (LaJeunesse 2005), while clade A is seldom reported among scleractinian hosts (Stat et al. 2008). A study comparing the symbioses between the coral host *Acropora cytherea* and its symbionts indicated that clade A provides less carbon to the host than C (Stat et al. 2008). It is generally accepted that mutualism between host and algal endosymbiont likely evolved from what was initially parasitism (Lesser et al. 2013; LaJeunesse 2020). This is in agreement with the phylogeny of the algal endosymbiont clades since the oldest clade is A (Lesser et al. 2013). However, our analysis did not indicate significant differences between zooxanthellae clades A, C and D, which generally presented a positive CZAR.

On the other hand, B showed CZAR values that ranged close and B&C below 100% (Table 2; Fig. S4). Therefore, the dominance of the algal endosymbiont clade and the relationship between less or greater dependency on autotrophy remain unclear. More studies addressing algal endosymbiont composition and potential host fitness are needed to better understand the role of autotrophy.

Cnidarian host cells are more tolerant to increased temperature than their algae endosymbionts (Sammarco and Strychar 2009, 2013). In several cases, increased temperatures do not directly cause host mortality, but the expulsion of endosymbiont algae causes considerable host mortality (Sammarco and Strychar 2009). Additionally, the sensitivity to high seawater temperatures may depend not only on the algal endosymbiont but also on the whole holobiont. Experiments with the octocorals *Sinularia lochmodes* and *Sarcophyton ehrenbergi* have indicated different responses even harboring the same clade of zooxanthellae C (Sammarco and Strychar 2013). Possibly, one species may harbor a subclade of C that is more temperature tolerant, or the way spicules are organized may provide more efficient insulation to short-term temperature disturbances (Sammarco and Strychar 2013).

The hypothesis of scleractinians and octocorals changing algal endosymbiont clades to face environmental changes is controversial and has been widely debated (Goulet 2006; Baker and Romanski 2007; LaJeunesse 2020). While it has been argued that only a few coral species (<10%) change their algal endosymbiont clades, and their survival depends on the performance of the holobiont to deal with environmental change (Goulet 2006), in contrast, it has been suggested that most coral species (>50%) are able to change their algal endosymbiont clades and that flexibility has a role in withstanding changing environmental conditions (Baker and Romanski 2007). Some octocoral species have long temporal and spatial stability regarding the zooxanthellae clade (Goulet and Coffroth 2003). This symbiont diversity might explain the variability of the contribution between autotrophic and heterotrophic sources to octocoral metabolic demand (Baker et al. 2015). Octocorals are less flexible in changing algal endosymbiont clades than scleractinians (Baker and Romanski 2007). Such characteristics in algal endosymbiont flexibility may be related to the general trend of octocorals being more dependent on heterotrophy than scleractinians (Fabricius and Klumpp 1995). It is argued that octocorals that maintain obligate and specialized algae symbiont clades are more dependent on autotrophy and more resistant to bleaching, while facultative and generalist octocorals are more vulnerable (Baker et al. 2015).

Data on CHAR and CZAR come mostly from octocorals of the clade Holaxonia – Alcyoniina, with only one octocoral genus of the clade Calcaxonia – Pennatulacea, which has information only on CZAR, and no data of the clade *Anthomastus* – *Corallium*. Since common ancestry could share traits that prevailed over evolutionary time, including feeding features, the research efforts focused only on one clade could lead to bias in interpreting the feeding performance of octocorals from a general perspective. Xeniid octocorals stand out among their counterparts by exhibiting a unique rhythmic pulsation of their tentacles (Kremien et al. 2013). Although pulsation increases R_C, it is a strategy of surplus energy that enhances P_C by 56% since it allows oxygen efflux of the colony surface (Kremien et al. 2013), which may explain the expressive CZAR values (Fig. 10). Pulsation also helps to avoid water reflow by neighboring polyps, likely improving the uptake of nutrients and suspended particles and the excretion of metabolic wastes (Kremien et al. 2013).

P_C contributes to the sustained metabolic activities of zooxanthellate octocorals and is critically threatened by environmental changes. The structure and functioning of hard-bottom ecosystems have undergone critical effects of climate change (Hoegh-Guldberg and Bruno 2010; Rossi et al. 2019a). Bleaching events have been observed in several locations around the globe and are often associated with increased surface sea temperatures and high irradiation (Lesser 2011; Hughes et al. 2018). In addition to the decreased incorporation of energy, larvae from bleached octocorals are also affected by reduced fitness and fewer chances of achieving maturity (Michalek-Wagner and Willis 2001).

The responses of octocorals to thermal stress vary according to algal endosymbiont communities and host species (Slattery et al. 2019). There is evidence that octocorals are more resilient to stressful events, including excessive ultraviolet radiation and high temperatures than scleractinians (Goulet et al. 2017; McCauley et al. 2018). The bleaching susceptibility can change over time and is related to the composition of the dominant symbiotic algae and the host's intrinsic characteristics (Slattery et al., 2019). Octocoral species that are more dependent on autotrophy and are characterized by small polyps are expected to be more vulnerable to bleaching (Rossi et al. 2018). The higher diversity of algal endosymbiont clades of the Pacific soft coral *Sinularia polydactyla* was probably the main factor explaining its greater resilience to thermal stress and prospering in communities, while the counterpart's populations of *Sinularia maxima* and the hybrid *S. maxima* x *polydactyla* declined during a given moment in bleaching events (Slattery et al., 2019). In contrast, specialized and obligate interaction symbioses demonstrated more resilience to coral bleaching events than generalist facultative symbioses in Caribbean coral reefs (Baker et al. 2015). Populations that experience a higher range in annual seawater temperature tend to have a higher thermal tolerance (Kemp et al. 2006). The susceptibility to bleaching varies among populations, as indicated by shallow populations being more impacted by high temperatures than deep populations because shallow populations host a higher quantity of algal endosymbiont (Ferrier-Pagès et al. 2009) and inhabit the upper limit of thermal tolerance. Additionally, populations that bleached during thermal anomalies that could be adapted and acclimatized to environmental conditions tend to increase their thermal tolerance (Guest et al. 2012).

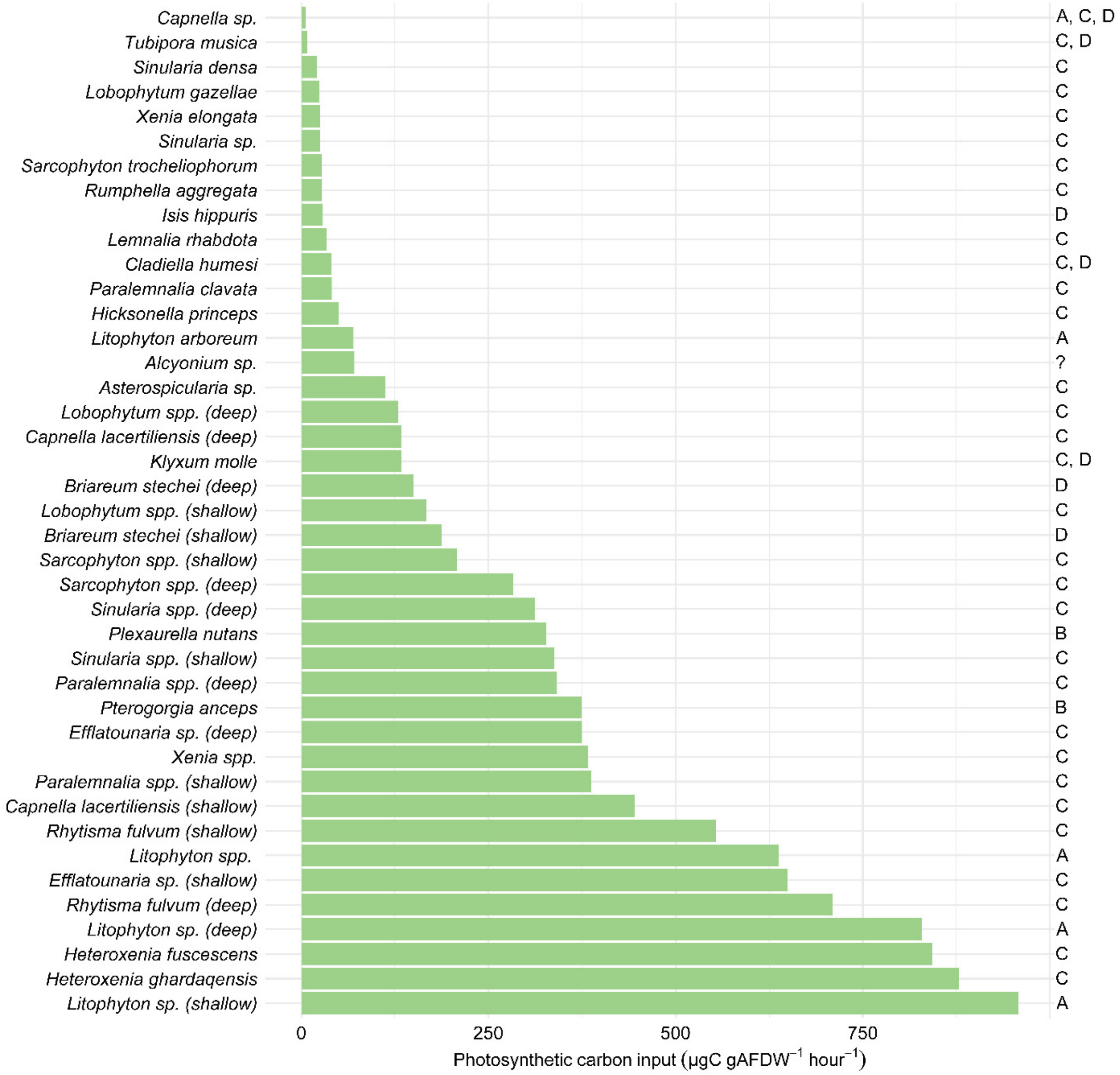

Fig. 9 Photosynthetic carbon input – P_C (μg C g AFDW^{-1} hour^{-1}) of octocoral taxa. Letters indicate the *Symbiodinium* clade based on Goulet et al. (2008).

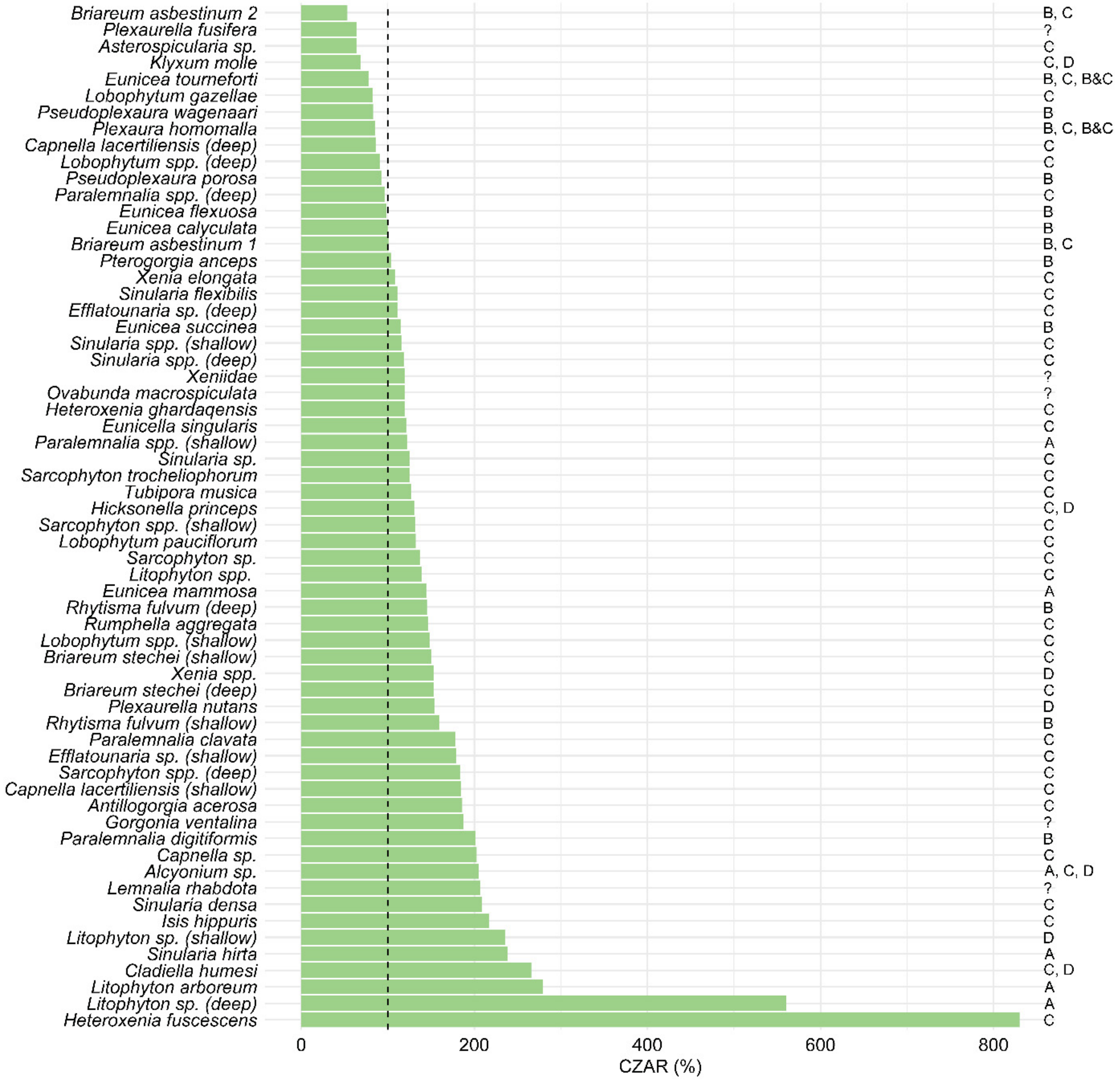

Fig. 10 Contribution of zooxanthellae to animal respiration (CZAR = P_C: R_C × 100%) in zooxanthellate octocoral species in percentage. The black dashed line indicates the threshold at which *Pc* meets *Rc*. Letters indicate the *Symbiodinium* clade based on Goulet et al. (2008).

3.7 Carbon available for growth and reproduction

The leftover carbon acquired by autotrophy and/or heterotrophy (*i.e.* SfG) is directed to the growth, reproduction, and production of metabolic wastes. Overall, azooxanthellate octocorals have a comparatively higher SfG (152.6 ± 305.9 µg C g AFDW^{-1} hour^{-1}) than zooxanthellate octocorals (23.2 ± 28.2 µg C g AFDW^{-1} hour^{-1}; Fig.

11). It is important to emphasize that the carbon acquired in zooxanthellate octocorals is not used only by the host but by the entire holobiont. Resource availability directly affects the physiology of octocorals, including growth and reproduction. These activities are ‘energy costly’ processes, and it is supposed that there is a trade-off in energy resource allocation among them (Rinkevich 1996). Injured octocorals are able to allocate resources from reproduction for the recovery of tissues (Tsounis et al. 2012). Octocorals may have distinct resource allocation strategies during feeding, efficiently storing carbon inputs and minimizing losses, or capturing large quantities of carbon even with losses occurring (Rakka et al. 2021). Additionally, scleractinian specimens inhabiting different light regimes experience contrasting SfG. Specimens in shaded areas are capable of maintaining respiration costs and minimal growth, while specimens in open areas maintain high productivity rates (Anthony and Hoegh-Guldberg 2003).

As it is natural to assume, the peaks in growth rates occur in periods of higher food availability (Garrabou and Wainwright 1999) until they stabilize with age when the colony reaches an optimal size (Garrabou and Wainwright 1999; Cordes et al. 2001). Additionally, the increased number of embryos is related to the seasonal periods of high energetic content of the octocorals, which is the result of the increase in nutrient levels and the raised light levels (Ben-David-Zaslow and Benayahu 1999; Ben-David-Zaslow et al. 1999). Under periods of starvation, octocorals use mainly protein, lipids and carbohydrates as energy reserve materials (Rossi et al. 2006). Starved female colonies of the surface brooder *Paramuricea clavata* tend to produce smaller oocytes than fed ones, while starved male colonies produce fewer spermaries per polyp than fed ones (Gori et al. 2013). Differences in reproductive performance and energy storage between octocoral populations have been associated with spatial variability of prey quality and availability (Gori et al. 2007, 2013).

The amount of surplus energy invested in organisms’ metabolic activities (*e.g.,* growth and reproduction) varies with the species. The reproductive strategy of *Paramuricea clavata*, a surface brooder that invests a significant amount of energy in reproductive activity, is different from that of *Corallium rubrum*, an internal brooder that invests comparatively less energy into spawning (Viladrich et al. 2016). Species that invest less in reproduction may have a wider thermal resistance (Viladrich et al. 2016), although they may have a lower recovery capacity after disturbing events (Santangelo et al. 2015). Moreover, disturbed colonies have to reallocate energy resources in the recovery of injured tissue, investing less energy in reproduction than undisturbed and healthy colonies (Tsounis et al. 2012).

The surplus of energy can have minor to strong seasonal oscillations depending on the biogeographic realm. Among the biogeographic realms assessed, the Temperate Northern Atlantic has the highest SfG (Fig. S1), although we have to take into account that the benthic suspension feeders of this realm face marked seasonal constraints in food availability (Coma et al., 2000), which strongly affects the surplus of energy. For instance, *Eunicella singularis* maintains a CHAR ranging between 6 and 30%, except in spring, which accounts for 110% (Coma et al. 2015). In contrast, shallow-water colonies have CZAR values above 100% and positive SfG during the whole year (Ferrier-Pagès et al. 2015). Deep-water colonies that do not possess symbiotic interactions with *Symbiodinium* algae (Gori et al. 2012) may face restrictions of the surplus of energy. Different octocoral species within the same biogeographic regions can also face distinct changes in the carbon budget. In the Western Caribbean, the gorgonian *Plexaurella nutans* has a positive SfG that is relatively constant throughout the year, with a mean of 112.5 μg C AFDW g^{-1} $hour^{-1}$, while *Pterogorgia anceps*, which have a higher annual mean of 154.17 μg C AFDW g^{-1} $hour^{-1}$, has a sharp decrease in spring to only 1.67 μg C AFDW g^{-1} $hour^{-1}$, a trend that is likely related to different reproduction strategies between the species (Rossi et al. 2020).

SfG is likely related to the resistance to environmental changes. Evidence has suggested that the higher capacity of octocoral *Heliopora coerulea* to store carbon than other scleractinian species in South Kuroshio may be responsible for the higher tolerance to heat stress and higher survival rates during bleaching events (Fujii et al. 2020).

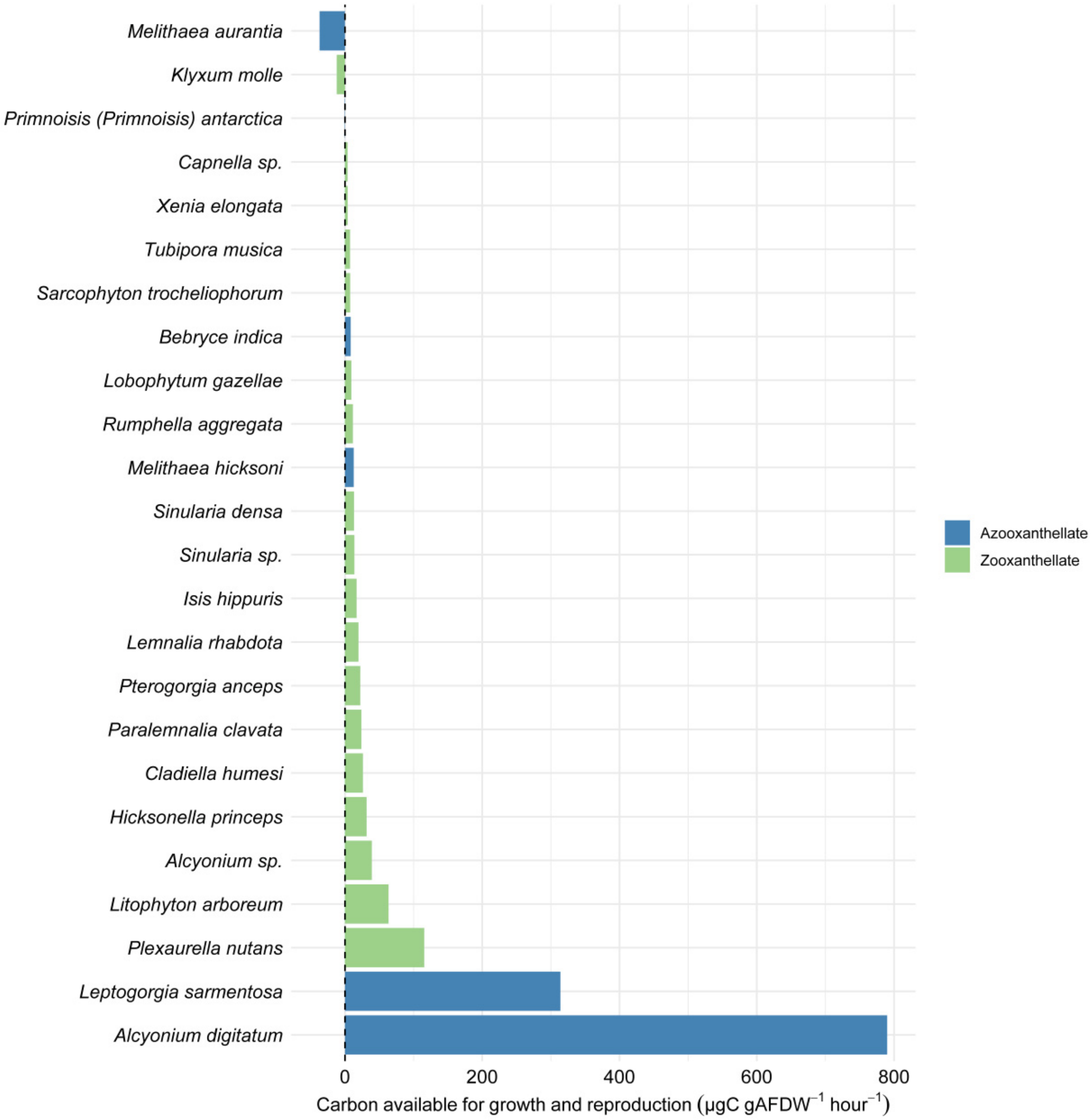

Fig. 11 Carbon available for growth and reproduction (SfG = $H_C + P_C - R_C$), expressed in µg C g AFDW^{-1} hour^{-1}, of zooxanthellate and azooxanthellate octocoral taxa.

3.8 Preys of octocorals

Octocorals are passive suspension feeders that rely on suspended particles carried by the water flow, a strategy that is an ecological success in terms of saving energy, as the metabolic expense is almost zero (Gili and Coma 1998). Even so, *Gersemia antarctica* is a benthic deposit feeder that bends towards the substrate to capture its prey, which is a unique strategy among octocorals and likely evolved to complement planktonic food (Slattery et al. 1997). For many years, the diet of octocorals was thought to be exclusive zooplanktivory (Muscatine 1973; Lewis 1982). Nevertheless, the employment of new methodological approaches has provided evidence that their diet is much more complex than previously thought and that they are also important grazers of phytoplankton. The recent use of novel technical and multidisciplinary approaches has provided clearer evidence than conventional observational methods and may prevent hasty conclusions (Fabricius et al. 1998; Piccinetti et al. 2016).

Octocorals, in general, have a broad spectrum of prey types and sizes, from the fine to the coarse fraction of seston, such as dissolved organic matter (Schlichter et al. 1983; Bednarz et al. 2012), pico-, nano- and microplankton (Coppari et al. 2019), detrital particulate matter (Ribes et al. 2003; Tsounis et al. 2006), and mesoplankton prey (Coma et al. 2001). Dissolved CO_2 and HCO_3^- are used as a source of carbon in the formation of sclerites in the octocoral skeleton (Lucas and Knapp 1997). Dissolved organic matter is the main heterotrophic nutritional source for octocoral taxa such as *Heteroxenia fuscescens* (Schlichter 1982) and *Xenia* spp. (Bednarz et al. 2012). Preys with high avoidance ability are hardly captured by passive suspension feeding. Zooplankton prey are characterized by being of low motile, such as eggs and invertebrate larvae, since octocorals, in general, have low nematocyst densities that would paralyze prey (Chester 1913; Lasker 1981; Orejas et al. 2003; Rossi et al. 2004). Curiously, it is not only the octocoral that preys but also *Symbiodinium* cells that are able to feed on heterotrophic bacteria, cyanobacteria (*Synechococcus* spp.) and small microalgae, in addition to obtaining energy through photosynthesis (Jeong et al. 2012). Moreover, anthozoan hosts may occasionally digest algae endosymbiotic partners seeking to regulate symbiont abundance (Jones and Yellowlees 1997; Gateño et al. 1998). In this sense, the gastrovascular system has a significant influence on the bleaching process of octocorals since large portions of endosymbiont algae are expelled through the mouth (Gateño et al. 1998).

There are reports of octocorals feeding on prey larger than themselves, as in the case of *Anthomastus bathyproctus* feeding on salps (Mehrotra et al. 2016). Interestingly, salps may play the role of middleman, feeding directly on phytoplankton in the top layers of the ocean and then transferring fresh prey to octocoral colonies, indicating wide benthic-pelagic coupling (Gili et al. 2006). In contrast, the majority of plankton predated by the zooplanktivory octocoral *Alcyonium siderium* are associated with the substrate, characterized by mero-plankton and demersal prey, while holoplanktonic animals are quantitatively less predated. This pattern indicates tight benthic-pelagic coupling by this species (Sebens and Koehl 1984). Therefore, the diet of octocoral species may determine the extent of its influence on benthic-pelagic coupling.

The reports of modified thread-like tentacles in some octocoral species, characterized by a higher concentration of nematocysts located at the tips than normal tentacles, may indicate a strategy involved in prey capture, as well as for defense competition between other benthic organisms (López-Gonzalez et al. 2018). The Cold Temperate Northeast Pacific octocoral *Alcyonium* sp. performs fissiparity as it grows, forming several small colony aggregations, which is likely a strategy to maximize the prey capture per polyp (McFadden 1986). *In situ* experiments with octocorals in a linear array exposed to a predominant flow have indicated that resource competition has a significant role in suspension feeding, with octocorals in the front positions and more exposed to the water flow with higher growth rates than those in the rear positions (Kim and Lasker 1997).

Octocorals are opportunistic regarding their prey type and size, a strategy likely developed to overcome the stochasticity of food availability. However, there is slight selectivity, which is strongly related to colony morphology and prey size (Lasker et al. 1983; Gomes et al. 2012). Moreover, distinct feeding activity rhythms may be related to the type of prey captured (Porter 1976). It is assumed that feeding structures and feeding behavior have an important influence on resource partitioning between species (Grossowicz and Benayahu 2012) and other benthic suspension feeders within communities (Porter 1976; Gili and Coma 1998; Corry et al. 2018). Resource partitioning by different octocoral species avoids competition in the same ecological niche (Imbs et al. 2016; Rakka et al. 2021). For instance, the diet of species belonging to Primnoidae differs from that of other cold-water soft coral families (Nephtheidae, Paragorgiidae, and Acanthogorgiidae) in the Sea of Okhotsk, a characteristic that likely allows them to occupy the same habitat (Imbs et al. 2016). The dependency on different food sources in the same habitat is also reported in the Northwest Atlantic among three Pennatulacean species (Baillon et al. 2016). On the other hand, to address the scarcity of food in autumn-winter in Antarctic ecosystems, the pennatulacean *Malacobelemnon daytoni* exhibits an omnivorous diet and opportunistic feeding strategy (Servetto et al. 2017). An alternative hypothesis of prey selectivity is based on palatability, explaining that preys that are absent in the natural environment could be considered artificial and less preyed, although feeding octocorals with, for instance, *Artemia* cysts and nauplii has been widely effective (Leal et al. 2014b).

Heterotrophic sources vary greatly among octocoral species, and they can be considered a species-specific feature (Fig. 12). For instance, the Red Sea soft-coral *Dendronephthya hemprichi* relies almost exclusively on phytoplankton, accounting for up to 97.3% of its carbon inputs (Fabricius and Klumpp 1995), while its counterpart, the Seychelles soft-coral *Dendronephthya gigantea,* relies on zooplankton, which is responsible for 92.8% (Sorokin 1991). This trend could be related to the food type that is available at that moment for predation. On the other hand, an experimental feeding test on the soft coral *Alcyonium digitatum* indicated a preference for zooplankton instead of phytoplankton (Migné and Davoult 2002).

Additional impacts to octocorals are microplastics, typically defined as plastic debris < 5 mm, whose concentrations have dramatically grown in the past few years. Microplastics have been found on the surface of the deep-water octocorals of the Indian Ocean (Woodall et al. 2014; Taylor et al. 2016). Although their effects may also be species-specific, the Indo-Pacific octocoral *Heliopora coerulea* displayed a negative response in growth when exposed to microplastics, probably because of increasing the metabolic demand (Reichert et al. 2019). In addition, experiments showed that microplastic effects on *H. coerulea* were less harmful than those on scleractinian organisms (Reichert et al. 2019), which may also explain the increasing prevalence of octocorals within disturbed reef systems. In this way, more studies addressing the impacts of microplastics on biodiversity may add greatly to the knowledge of the feeding ecology of octocorals and, consequently, to the benthic-pelagic coupling and on the effects of carbon budgets of marine systems.

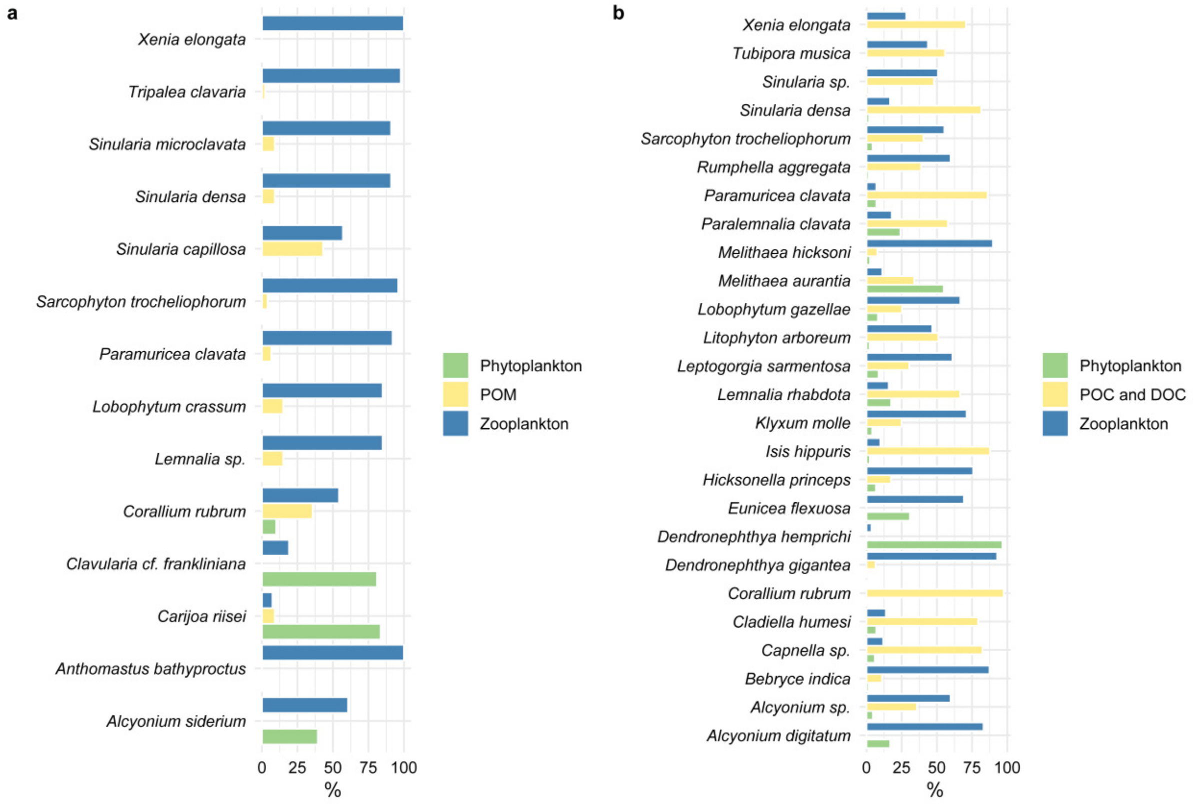

Fig. 12 Percentages of heterotrophic prey sources in terms of abundance (a) and in terms of carbon (b) according to each octocoral taxon.

Table 1. GLMs of dependent variables CHAR, CZAR, P_C, H_C, R_C, and SfG according to biogeographic realms and taxonomic group.

Model	Predictors	Df	Deviance residuals	AIC	Pr (>Chi)
CHAR ~ Realm + Group + Realm * Group (n = 35)					
	Realm	4	19.7	373.89	**0.0005756** ***
	Group	4	0.0	385.86	1.0000000
	Realm * Group	1	3871.1	374.53	**2.2e-16** ***
CZAR ~ Realm + Group + Realm * Group (n = 66)					
	Realm	3	18.6422	748.74	**0.0003242** ***
	Group	4	1.7518	801.97	0.7812838
	Realm * Group	1	0.7253	756.31	0.3944175
H_C ~ Realm + Group + Realm * Group (n = 37)					
	Realm	4	42.882	366.13	**1.095e-08** ***
	Group	4	0.080	386.79	0.99921
	Realm * Group	1	6.153	370.25	**0.01312** *
P_C ~ Realm + Group + Realm * Group (n = 43)					
	Realm	2	18.540	571.48	**9.421e-05** ***
	Group	4	12.857	579.88	**0.012** *
	Realm * Group	0	0.000	567.94	
R_C ~ Realm + Group + Realm * Group (n = 62)					
	Realm	5	27.8367	770.64	**3.917e-05** ***
	Group	4	12.6222	773.15	**0.01328** *
	Realm * Group	3	4.1096	769.50	0.24987
R_C ~ Realm + Group + Realm * Group (n = 62)					
	Realm	4	29.6596	776.07	**5.741e-06** ***
	Group	4	15.2051	814.15	**0.004294** **
	Realm * Group	2	1.8143	772.70	0.403666
SfG ~ Realm + Group + Realm * Group (n = 25)					
	Realm	4	318671	320.96	
	Group	4	60525	336.57	
	Realm * Group	1	215972	289.30	

*** *p* value < 0.001; ** *p* value; < 0.01 * *p* value < 0.05 . *p* value < 0.1

Table 2. GLMs of dependent variables CZAR and P_C according to algal endosymbiont clade.

Variable	Predictors	Df	Deviance residuals	AIC	Pr (>Chi)
CZAR ~ Clade (n = 65)					
	Clade	8	16.582	750.19	**0.03476 ***
P_C ~ Clade (n = 44)					
	Clade	5	17.507	580.082	0.003632 **

*** p value < 0.001; ** p value; < 0.01 * p value < 0.05.

4 Conclusion

We carried out a systematic and comprehensive review of the feeding ecology of octocorals, trying to provide a better understanding of the balance between autotrophic and heterotrophic inputs to meet their metabolic demands. We reassessed carbon budgets driven by the feeding ecology of octocorals from literature data, including heterotrophic and autotrophic inputs and metabolic demands. We identified the octocoral taxa and biogeographic ecoregions for which more efforts are needed, characterized their main food sources, and further identified the main current research problems that may be of interest to future researchers.

The suspension feeding of octocorals is relevant to understanding benthic-pelagic coupling, since their extensive formations may act as significant blue carbon sinks. Octocorals can use a wide variety of food types and sizes, including dissolved organic matter, particulate organic matter, phytoplankton, and zooplankton prey. Alternatively, some species have symbiont zooxanthellae, which provide a significant portion of carbon to the host most of the time. In this way, zooxanthellate octocorals tend to have lower ingestion rates than azooxanthellate octocorals. Autotrophy is an adaptive strategy to overcome the scarcity of food in biogeographic realms characterized by oligotrophic waters and large light availability throughout the year. Such evolutionary strategies in recycling explain the high production in nutrient-poor waters. The amount of carbon provided by autotrophy among zooxanthellate octocorals is quantitively comparable to suspension feeding among azooxanthellate octocorals, which alone is often able to meet their energetic demands. However, such symbiotic relations between octocorals and algal endosymbionts are not always characterized by mutualism and may exhibit commensalism or parasitic features in some cases.

Two main hypotheses may explain the phase shifts from scleractinian to octocoral-dominated communities considering their feeding ecology. First, octocorals may possess the ability to decrease polyp activity under stress, such as elevated temperatures. Second, zooxanthellate octocorals are apparently less dependent on autotrophy than scleractinians. In addition, not all scleractinians are vulnerable to environmental changes, and those that have plasticity in heterotrophy to compensate for the reduced autotrophy are expected to be more resilient. Such particularities in feeding ecology may be an advantage in the face of environmental stressors, which consequently might partially shape the communities. However, other factors not addressed in this study may certainly contribute to the current trend of expansion among octocorals and decline among scleractinians in tropical and subtropical waters, including varying reproduction strategies (Lasker et al. 2020b), lesser or larger resistance to ocean acidification (Inoue et al. 2013), the production of allelochemicals to deter settlement (Rodriguez et al. 2020) or toxic and unpalatable substances to deter predation (Garra et al. 2020).

In contrast to scleractinian corals, octocorals are maintaining and even increasing their distribution and abundance in several marine systems, which may be partly explained by differences in the functioning of feeding ecology. In the face of environmental change, it seems that octocorals are becoming winners, whereas scleractinians are the current losers. Octocorals may possess higher feeding competitive advantages than scleractinian corals, which, combined with other behavioral and physiological factors (*e.g.*, reproduction, settlement, thermal tolerance), might explain the observed phase shifts in tropical areas. In this sense, understanding the suspension feeding and autotrophy of octocorals is essential to better model benthic-pelagic coupling, estimate carbon budgets and predict potential responses to environmental changes.

References

Al-Zibdah MK, Damhoureyeh SA, Badran MI (2007) Temporal variations in coral reef health at a coastal industrial site on the Gulf of Aqaba Red Sea. Oceanologia 49:565–578

Altieri AH, Harrison SB, Seemann J, et al (2017) Tropical dead zones and mass mortalities on coral reefs. PNAS 114:3660–3665. https://doi.org/10.1073/pnas.1621517114

Anthony KRN, Fabricius KE (2000) Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. J Exp Mar Bio Ecol 252:221–253. https://doi.org/10.1016/S0022-0981(00)00237-9

Anthony KRN, Hoegh-Guldberg O (2003) Variation in coral photosynthesis, respiration and growth characteristics in contrasting light microhabitats: An analogue to plants in forest gaps and understoreys? Funct Ecol 17:246–259. https://doi.org/10.1046/j.1365-2435.2003.00731.x

Aurelle D, Tariel J, Zuberer F, et al (2020) Genetic insights into recolonization processes of Mediterranean octocorals. Mar Biol 167:1–14. https://doi.org/10.1007/s00227-020-03684-z

Baillon S, English M, Hamel JF, Mercier A (2016) Comparative biometry and isotopy of three dominant pennatulacean corals in the Northwest Atlantic. Acta Zool 97:475–493. https://doi.org/10.1111/azo.12141

Baker AC, Romanski AM (2007) Multiple symbiotic partnerships are common in scleractinian corals, but not in octocorals: Comment on Goulet (2006). Mar Ecol Prog Ser 335:237–242. https://doi.org/10.3354/meps335237

Baker DM, Freeman CJ, Knowlton N, et al (2015) Productivity links morphology, symbiont specificity and bleaching in the evolution of Caribbean octocoral symbioses. ISME J 9:2620–2629. https://doi.org/10.1038/ismej.2015.71

Baker DM, Freeman CJ, Wong JCY, et al (2018) Climate change promotes parasitism in a coral symbiosis. ISME J 12:921–930. https://doi.org/10.1038/s41396-018-0046-8

Baker DM, Kim K, Andras JP, Sparks JP (2011) Light-mediated ^{15}N fractionation in Caribbean gorgonian octocorals: Implications for pollution monitoring. Coral Reefs 30:709–717. https://doi.org/10.1007/s00338-011-0759-x

Baker DM, Webster KL, Kim K (2010) Caribbean octocorals record changing carbon and nitrogen sources from 1862 to 2005. Glob Chang Biol 16:2701–2710. https://doi.org/10.1111/j.1365-2486.2010.02167.x

Baum G, Januar HI, Ferse SCA, Kunzmann A (2015) Local and regional impacts of pollution on coral reefs along the thousand islands north of the megacity Jakarta, Indonesia. PLoS One 10:1–26. https://doi.org/10.1371/journal.pone.0138271

Bednarz VN, Naumann MS, Niggl W, Wild C (2012) Inorganic nutrient availability affects organic matter fluxes and metabolic activity in the soft coral genus *Xenia*. J Exp Biol 215:3672–3679. https://doi.org/10.1242/jeb.072884

Bell JJ, Shaw C, Turner JR (2006) Factors controlling the tentacle and polyp expansion behaviour of selected temperate Anthozoa. J Mar Biol Assoc United Kingdom 86:977–992. https://doi.org/10.1017/S0025315406013956

Ben-David-Zaslow R, Benayahu Y (1999) Temporal variation in lipid, protein and carbohydrate content in the Red Sea soft coral *Heteroxenia fuscescens*. J Mar Biol Assoc United Kingdom 79:1001–1006. https://doi.org/10.1017/S002531549900123X

Ben-David-Zaslow R, Henning G, Hofmann DK, Benayahu Y (1999) Reproduction in the Red Sea soft coral *Heteroxenia fuscescens*: Seasonality and long-term record (1991 to 1997). Mar Biol 133:553–559. https://doi.org/10.1007/s002270050495

Benayahu Y, Bridge TCL, Colin PL, et al (2019) Octocorals of the Indo-Pacific. In: Mesophotic Coral Ecosystems. Springer. Springer, Cham, pp 709–728. https://doi.org/10.1007/978-3-319-92735-0_38

Best BA (1988) Passive suspension feeding in a sea pen: Effects of ambient flow on volume flow rate and filtering efficiency. Biol Bull 175:332–342. https://doi.org/10.2307/1541723

Breitburg D, Levin LA, Oschlies A, et al (2018) Declining oxygen in the global ocean and coastal waters. Science 359:eaam7240. https://doi.org/10.1126/science.aam7240

Bruckner AW, Dempsey AC (2015) The Status, Threats, and Resilience of Reef-Building Corals of the Saudi Arabian Red Sea. In: Rasul NMA, Stewart ICF (eds) The Red Sea, Springer E. Springer-Verlag Berlin Heidelberg, pp 471–486

Cerpovicz AF, Lasker HR (2021) Canopy effects of octocoral communities on sedimentation: modern baffles on the shallow-water reefs of St. John, USVI. Coral Reefs 40:295–303. https://doi.org/10.1007/s00338-021-02053-6

Chan I, Tseng LC, Kâ S, et al (2012) An experimental study of the response of the gorgonian coral *Subergorgia suberosa* to polluted seawater from a former coastal mining site in Taiwan. Zool Stud 51:27–37

Chang TC, Mayfield AB, Fan TY (2020) Culture systems influence the physiological performance of the soft coral *Sarcophyton glaucum*. Sci Rep 10:1–10. https://doi.org/10.1038/s41598-020-77071-5

Chester WM (1913) The Structure of the Gorgonian Coral *Pseudoplexaura Crassa* Wright and Studer. Proc Am Acad Arts Sci 48:737–774. https://doi.org/10.2307/20022876

Cocito S, Ferrier-Pagès C, Cupido R, et al (2013) Nutrient acquisition in four Mediterranean gorgonian species. Mar Ecol Prog Ser 473:179–188. https://doi.org/10.3354/meps10037

Coles SL, Looker E, Burt JA (2015) Twenty-year changes in coral near Muscat, Oman estimated from manta board tow observations. Mar Environ Res 103:66–73. https://doi.org/10.1016/j.marenvres.2014.11.006

Coma R, Gili J-M, Zabala M, Riera T (1994) Feeding and prey capture cycles in the aposymbiontic gorgonian Paramuricea clavata. Mar Ecol Prog Ser 115:257–270. https://doi.org/10.1016/S0764-4469(00)00141-4

Coma R, Llorente-Llurba E, Serrano E, Gili JM, Ribes M (2015) Natural heterotrophic feeding by a temperate octocoral with symbiotic zooxanthellae: a contribution to understanding the mechanisms of die-off events. Coral Reefs 34:549–560. http://dx.doi.org/10.1007/s00338-015-1281-3

Coma R, Ribes M (2003) Seasonal energetic constraints in Mediterranean benthic suspension feeders: Effects at different levels of ecological organization. In: Oikos. pp 205–215

Coma R, Ribes M, Gili J, Hughes RN (2001) The ultimate opportunists: consumers of seston. Mar Ecol Prog Ser 219:305–308. https://doi.org/10.3354/meps219305

Coma R, Ribes M, Gili J, Zabala M (2000) Seasonality in coastal benthic ecosystems. Trends Ecol Evol 15:448–453. https://doi.org/10.1016/S0169-5347(00)01970-4

Coma R, Ribes M, Gili JM, Zabala M (2002) Seasonality of *in situ* respiration rate in three temperate benthic suspension feeders. Limnol Oceanogr 47:324–331. https://doi.org/10.4319/lo.2002.47.1.0324

Conlan KE, Rau GH, Kvitek RG (2006) $^{\delta13}$C and $^{\delta15}$N shifts in benthic invertebrates exposed to sewage from McMurdo Station, Antarctica. Mar Pollut Bull 52:1695–1707. https://doi.org/10.1016/j.marpolbul.2006.06.010

Coppari M, Zanella C, Rossi S (2019) The importance of coastal gorgonians in the blue carbon budget. Sci Rep 9:13550. https://doi.org/10.1038/s41598-019-49797-4

Cordes EE, Nybakken JW, VanDykhuizen G (2001) Reproduction and growth of *Anthomastus ritteri* (Octocorallia: Alcyonacea) from Monterey Bay, California, USA. Mar Biol 138:491–501. https://doi.org/10.1007/s002270000470

Corry M, Harasti D, Gaston T, et al (2018) Functional role of the soft coral *Dendronephthya australis* in the benthic food web of temperate estuaries. Mar Ecol Prog Ser 593:61–72. https://doi.org/10.3354/meps12498

Costello MJ, Tsai P, Wong PS, et al (2017) Marine biogeographic realms and species endemicity. Nat Commun 8:1–9. https://doi.org/10.1038/s41467-017-01121-2

Dai C-F, Lin M-C (1993) The effects of flow on feeding of three gorgonians from southern Taiwan. J Exp Mar Bio Ecol 173:57–69. https://doi.org/10.1016/0022-0981(93)90207-5

Dallmeyer DG, Porter JW, Smith GJ (1982) Effects of particulate peat on the behavior and physiology of the Jamaican reef-building coral *Montastrea annularis*. Mar Biol 68:229–233. https://doi.org/10.1007/BF00409589

Daly M, Brugler MR, Cartwright P, et al (2007) The phylum Cnidaria: A review of phylogenetic patterns and diversity 300 years after Linnaeus. Zootaxa 1668:127–182

Done TJ (1992) Phase shifts in coral reef communities and their ecological significance. Hydrobiologia 247:121–132. https://doi.org/10.1007/BF00008211

Donner SD, Skirving WJ, Little CM, et al (2005) Global assessment of coral bleaching and required rates of adaptation under climate change. Glob Chang Biol 11:2251–2265. https://doi.org/10.1111/j.1365-2486.2005.01073.x

Einbinder S, Gruber DF, Salomon E, et al (2016) Novel adaptive photosynthetic characteristics of mesophotic symbiotic microalgae within the reef-building coral, *Stylophora pistillata*. Front Mar Sci 3:1–9. https://doi.org/10.3389/fmars.2016.00195

Elias-Piera F, Rossi S, Gili JM, Orejas C (2013) Trophic ecology of seven Antarctic gorgonian species. Mar Ecol Prog Ser 477:93–106. https://doi.org/10.3354/meps10152

Ezzat L, Fine M, Maguer JF, et al (2017) Carbon and nitrogen acquisition in shallow and deep holobionts of the scleractinian coral *S. pistillata*. Front Mar Sci 4:1–12. https://doi.org/10.3389/fmars.2017.00102

Ezzat L, Merle PL, Furla P, et al (2013) The Response of the Mediterranean Gorgonian *Eunicella singularis* to Thermal Stress Is Independent of Its Nutritional Regime. PLoS One 8:. https://doi.org/10.1371/journal.pone.0064370

Fabricius K, Yahel G, Genin A (1998) *In situ* depletion of phytoplankton by an azooxanthellate soft coral. Limnol Oceanogr 43:354–356. https://doi.org/10.4319/lo.1998.43.2.0354

Fabricius KE, Cséke S, Humphrey C, De'ath G (2013) Does Trophic Status Enhance or Reduce the Thermal Tolerance of Scleractinian Corals? A Review, Experiment and Conceptual Framework. PLoS One 8:. https://doi.org/10.1371/journal.pone.0054399

Fabricius KE, De'ath G (2008) Photosynthetic symbionts and energy supply determine octocoral biodiversity in coral reefs. Ecology 89:3163–3173. https://doi.org/10.1890/08-0005.1

Fabricius KE, Dommisse M (2000) Depletion of suspended particulate matter over coastal reef communities dominated by zooxanthellate soft corals. Mar Ecol Prog Ser 196:157–167. https://doi.org/10.3354/meps196157

Fabricius KE, Klumpp DW (1995) Widespread mixotrophy in reef-inhabiting soft corals: the influence of depth, and colony expansion and contraction on photosynthesis. Mar Ecol Prog Ser 125:195–204. https://doi.org/10.3354/meps125195

Ferrier-Pagès C, Reynaud S, Béraud E, et al (2015) Photophysiology and daily primary production of a temperate symbiotic gorgonian. Photosynth Res 123:95–104. https://doi.org/10.1007/s11120-014-0042-4

Ferrier-Pagès C, Tambutté E, Zamoum T, et al (2009) Physiological response of the symbiotic gorgonian *Eunicella singularis* to a long-term temperature increase. J Exp Biol 212:3007–3015. https://doi.org/10.1242/jeb.031823

Fitt WK (1984) The role of chemosensory behavior of *Symbiodinium microadriaticum*, intermediate hosts, and host behavior in the infection of coelenterates and molluscs with zooxanthellae. Mar Biol 81:9–17. https://doi.org/10.1007/BF00397620

Fleury BG, Coll JC, Tentori E, et al (2000) Effect of nutrient enrichment on the complementary (secondary) metabolite composition of the soft coral *Sarcophyton ebrenbergi* (Cnidaria: Octocorallia: Alcyonaceae) of the Great Barrier Reef. Mar Biol 136:63–68. https://doi.org/10.1007/s002270050009

Fox HE, Pet JS, Dahuri R, Caldwell RL (2003) Recovery in rubble fields: Long-term impacts of blast fishing. Mar Pollut Bull 46:1024–1031. https://doi.org/10.1016/S0025-326X(03)00246-7

Fujii T, Tanaka Y, Maki K, et al (2020) Organic carbon and nitrogen isoscapes of reef corals and algal symbionts: Relative influences of environmental gradients and heterotrophy. Microorganisms 8:1–26. https://doi.org/10.3390/microorganisms8081221

Garra S, Hall A, Kingsford MJ (2020) The effects of predation on the condition of soft corals. Coral Reefs 39:1329–1343. https://doi.org/10.1007/s00338-020-01967-x

Garrabou J, Wainwright SA (1999) Life-history traits of *Alcyonium acaule* and *Parazoanthus axinellae* (Cnidaria, Anthozoa), with emphasis on growth. Mar Ecol Prog Ser 178:1041. https://doi.org/10.1038/2161041a0

Gateño D, Israel A, Barki Y, Rinkevich B (1998) Gastrovascular circulation in an octocoral: Evidence of significant transport of coral and symbiont cells. Biol Bull 194:178–186. https://doi.org/10.2307/1543048

Gili J-M, Coma R, Orejas C, et al (2001) Are Antarctic suspension-feeding communities different from those elsewhere in the world? Polar Biol 24:473–485. https://doi.org/10.1007/s003000100257

Gili JM, Coma R (1998) Benthic suspension feeders: their paramount role in littoral marine food webs. Trends Ecol Evol 13:316–321. https://doi.org/10.1016/S0169-5347(98)01365-2

Gili JM, Rossi S, Pagès F, et al (2006) A new trophic link between the pelagic and benthic systems on the Antarctic shelf. Mar Ecol Prog Ser 322:43–49. https://doi.org/10.3354/meps322043

Girard F, Fu B, Fisher CR (2016) Mutualistic symbiosis with ophiuroids limited the impact of the Deepwater Horizon oil spill on deep-sea octocorals. Mar Ecol Prog Ser 549:89–98. https://doi.org/10.3354/meps11697

Glynn PW (1993) Coral reef bleaching: ecological perspectives. Coral Reefs 12:1–17. https://doi.org/10.1007/BF00303779

Goldberg WM (2018) Coral food, feeding, nutrition, and secretion: a review. In: Marine organisms as model systems in biology and medicine. Springer, Cham, pp 377–421

Gomes PB, Lira AKF, Naud JP, et al (2012) Prey selectivity of the octocoral *Carijoa riisei* at Pernambuco, Brazil. An Acad Bras Cienc 84:157–164. https://doi.org/10.1590/S0001-37652012005000012

Gori A, Bramanti L, López-González P, et al (2012) Characterization of the zooxanthellate and azooxanthellate morphotypes of the Mediterranean gorgonian *Eunicella singularis*. Mar Biol 159:1485–1496. https://doi.org/10.1007/s00227-012-1928-3

Gori A, Linares C, Rossi S, et al (2007) Spatial variability in reproductive cycle of the gorgonians *Paramuricea clavata* and *Eunicella singularis* (Anthozoa, Octocorallia) in the Western Mediterranean Sea. Mar Biol 151:1571–1584. https://doi.org/10.1007/s00227-006-0595-7

Gori A, Linares C, Viladrich N, et al (2013) Effects of food availability on the sexual reproduction and biochemical composition of the Mediterranean gorgonian *Paramuricea clavata*. J Exp Mar Bio Ecol 444:38–45. https://doi.org/10.1016/j.jembe.2013.03.009

Goulet TL (2006) Most corals may not change their symbionts. Mar Ecol Prog Ser 321:1–7. https://doi.org/10.3354/meps321001

Goulet TL, Coffroth MA (2003) Stability of an octocoral-algal symbiosis over time and space. Mar Ecol Prog Ser 250:117–124. https://doi.org/10.3354/meps250117

Goulet TL, Shirur KP, Ramsby BD, Iglesias-Prieto R (2017) The effects of elevated seawater temperatures on Caribbean gorgonian corals and their algal symbionts, Symbiodinium spp. PLoS One 12:1–21. https://doi.org/10.1371/journal.pone.0171032

Goulet TL, Simmons C, Goulet D (2008) Worldwide biogeography of *Symbiodinium* in tropical octocorals. Mar Ecol Prog Ser 355:45–58. https://doi.org/10.3354/meps07214

Grange KR (1991) Mutualism between the antipatharian *Antipathes fiordensis* and the ophiuroid *Astrobrachion constrictum* in New Zealand fjords. Hydrobiologia 216–217:297–303. https://doi.org/10.1007/BF00026478

Grigg RW (1972) Orientation and growth form of sea fans. Limnol Oceanogr 17:185–192

Grinyó J, Viladrich N, Díaz D, et al (2018) Reproduction, energy storage and metabolic requirements in a mesophotic population of the gorgonian *Paramuricea macrospina*. PLoS One 13:1–23. https://doi.org/10.1371/journal.pone.0203308

Grossowicz M, Benayahu Y (2012) Differential morphological features of two *Dendronephthya* soft coral species suggest differences in feeding niches. Mar Biodivers 42:65–72. https://doi.org/10.1007/s12526-011-0093-0

Grossowicz M, Bialik OM, Shemesh E, et al (2020) Ocean warming is the key filter for successful colonization of the migrant octocoral *Melithaea erythraea* (Ehrenberg, 1834) in the Eastern Mediterranean Sea. PeerJ 2020:1–21. https://doi.org/10.7717/peerj.9355

Grottoli AG, Rodrigues LJ, Palardy JE (2006) Heterotrophic plasticity and resilience in bleached corals. Nature 440:1186–1189. https://doi.org/10.1038/nature04565

Guest JR, Baird AH, Maynard JA, et al (2012) Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. PLoS One 7:1–8. https://doi.org/10.1371/journal.pone.0033353

Guinotte JM, Orr J, Cairns S, et al (2006) Will human-induced changes in seawater chemistry alter the distribution of deep-sea scleractinian corals? Front Ecol Environ 4:141–146. https://doi.org/10.1890/1540-9295(2006)004[0141:WHCISC]2.0.CO;2

Haas A, Al-Zibdah M, Wild C (2009) Effect of inorganic and organic nutrient addition on coral-algae assemblages from the Northern Red Sea. J Exp Mar Bio Ecol 380:99–105. https://doi.org/10.1016/j.jembe.2009.09.005

Hatcher BG (1990) Coral Reef Primary Productivity: A Hierarchy of Pattern and Process. 5:149–155. https://doi.org/10.1016/0169-5347(90)90221-X

Heikoop JM, Hickmott DD, Risk MJ, et al (2002) Potential climate signals from the deep-sea gorgonian coral *Primnoa resedaeformis*. Hydrobiologia 471:117–124. https://doi.org/10.1023/A:1016505421115

Hendler G (1984) The association of *Ophiothrix lineata* and *Callyspongia vaginalis*: A brittlestar-sponge cleaning symbiosis? Mar Ecol 5:9–27. https://doi.org/10.1111/j.1439-0485.1984.tb00304.x

Hoegh-Guldberg O, Bruno JF (2010) The Impact of Climate Change on the World’s Marine Ecosystems. Science 328:49. https://doi.org/10.1126/science.1189930

Hoffman TC (2002) Coral reef health and effects of socio-economic factors in Fiji and Cook Islands. Mar Pollut Bull 44:1281–1293. https://doi.org/10.1016/S0025-326X(02)00260-6

Houlbrèque F, Ferrier-Pagès C (2009) Heterotrophy in tropical scleractinian corals. Biol Rev 84:1–17. https://doi.org/10.1111/j.1469-185X.2008.00058.x

Hughes TP, Anderson KD, Connolly SR, et al (2018) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359:80–83. https://doi.org/10.1126/science.aan8048

Imbs AB, Demidkova DA, Dautova TN (2016) Lipids and fatty acids of cold-water soft corals and hydrocorals: A comparison with tropical species and implications for coral nutrition. Mar Biol 163:1–12. https://doi.org/10.1007/s00227-016-2974-z

Inoue S, Kayanne H, Yamamoto S, Kurihara H (2013) Spatial community shift from hard to soft corals in acidified water. Nat Clim Chang 3:683–687. https://doi.org/10.1038/nclimate1855

Jeong HJ, Yoo Y Du, Kang NS, et al (2012) Heterotrophic feeding as a newly identified survival strategy of the dinoflagellate *Symbiodinium*. PNAS 109:12604–12609. https://doi.org/10.1073/pnas.1204302109

Johnson SK, Hallock P (2020) A review of symbiotic gorgonian research in the western Atlantic and Caribbean with recommendations for future work. Coral Reefs 39:239–258. https://doi.org/10.1007/s00338-020-01891-0

Jones RJ, Yellowlees D (1997) Regulation of zooxanthellae in hard corals. Phil Trans R Soc Lond B 352:457–468. https://doi.org/10.1098/rstb.1997.0033

Kaniewska P, Magnusson SH, Anthony KRN, et al (2011) Importance of macro- versus microstructure in modulating light levels inside coral colonies. J Phycol 47:846–860. https://doi.org/10.1111/j.1529-8817.2011.01021.x

Kanwisher JW, Wainwright SA (1967) Oxygen Balance in Some Reef. Biol Bull 133:378–390. https://doi.org/10.2307/1539833

Kemp DW, Cook CB, LaJeunesse TC, Brooks WR (2006) A comparison of the thermal bleaching responses of the zoanthid *Palythoa caribaeorum* from three geographically different regions in south Florida. J Exp Mar Bio Ecol 335:266–276. https://doi.org/10.1016/j.jembe.2006.03.017

Khalesi MK, Beeftink HH, Wijffels RH (2011) Energy budget for the cultured, zooxanthellate octocoral *Sinularia flexibilis*. Mar Biotechnol 13:1092–1098. https://doi.org/10.1007/s10126-011-9373-8

Khalesi MK, Beeftink HH, Wijffels RH (2007) Flow-dependent growth in the zooxanthellate soft coral *Sinularia flexibilis*. J Exp Mar Bio Ecol 351:106–113. https://doi.org/10.1016/j.jembe.2007.06.007

Kim K, Lasker HR (1997) Flow-mediated resource competition in the suspension feeding gorgonian *Plexaura homomalla* (Esper). J Exp Mar Bio Ecol 215:49–64. https://doi.org/10.1016/S0022-0981(97)00015-4

Kinzie RA (1973) The Zonation of West Indian Gorgonians. Bull Mar Sci 23:93–155

Kremien M, Shavit U, Mass T, Genin A (2013) Benefit of pulsation in soft corals. PNAS 110:8978–8983. https://doi.org/10.1073/pnas.1301826110

Kuntz NM, Kline DI, Sandin SA, Rohwer F (2005) Pathologies and mortality rates caused by organic carbon and nutrient stressors in three Caribbean coral species. Mar Ecol Prog Ser 294:173–180. https://doi.org/10.3354/meps294173

LaJeunesse TC (2020) Zooxanthellae. Curr Biol 30:R1110–R1113. https://doi.org/10.1016/j.cub.2020.03.058

LaJeunesse TC (2005) “Species” radiations of symbiotic dinoflagellates in the Atlantic and Indo-Pacific since the Miocene-Pliocene transition. Mol Biol Evol 22:570–581. https://doi.org/10.1093/molbev/msi042

Lasker H (1981) A comparison of the particulate feeding abilities of 3 species of gorgonian soft coral. Mar Ecol Prog Ser 5:61–67. https://doi.org/10.3354/meps005061

Lasker HR, Bramanti L, Tsounis G, Edmunds PJ (2020a) The rise of octocoral forests on Caribbean reefs. Adv Mar Biol 87:361–410. https://doi.org/10.1016/bs.amb.2020.08.009

Lasker HR, Gottfried MD, Coffroth MA (1983) Effects of depth on the feeding capabilities of two octocorals. Mar Biol 73:73–78. https://doi.org/10.1007/BF00396287

Lasker HR, Martínez-Quintana, Bramanti L, Edmunds PJ (2020b) Resilience of Octocoral Forests to Catastrophic Storms. Sci Rep 10:1–8. https://doi.org/10.1038/s41598-020-61238-1

Leal MC, Berger SA, Ferrier-Pagès C, et al (2014a) Temporal changes in the trophic ecology of the asymbiotic gorgonian *Leptogorgia virgulata*. Mar Biol 161:2191–2197. https://doi.org/10.1007/s00227-014-2496-5

Leal MC, Ferrier-Pagès C, Calado R, et al (2014b) Coral feeding on microalgae assessed with molecular trophic markers. Mol Ecol 23:3870–3876. https://doi.org/10.1111/mec.12486

Lenz EA, Bramanti L, Lasker HR, Edmunds PJ (2015) Long-term variation of octocoral populations in St. John, US Virgin Islands. Coral Reefs 34:1099–1109. https://doi.org/10.1007/s00338-015-1315-x

Lesser MP (2011) Coral bleaching: causes and mechanisms. In: Coral reefs: An ecosystem in transition. Springer, Dordrecht, pp 1–552

Lesser MP, Marc S, Michael S, et al (2010) Photoacclimatization by the coral *Montastraea cavernosa* in the mesophotic zone: Light, food, and genetics. Ecology 91:990–1003. https://doi.org/10.1890/09-0313.1

Lesser MP, Stat M, Gates RD (2013) The endosymbiotic dinoflagellates (*Symbiodinium* sp.) of corals are parasites and mutualists. Coral Reefs 32:603–611. https://doi.org/10.1007/s00338-013-1051-z

Leversee GJ (1976) Flow and feeding in fan-shaped colonies of the gorgonian coral, *Leptogorgia*. Biol Bull 151:344–356

Lewis JB (1982) Feeding behaviour and feeding ecology of the Octocorallia (Coelenterata: Anthozoa). J Zool 196:371–384. https://doi.org/10.1111/j.1469-7998.1982.tb03509.x

Lewis JB, Post EE (1982) Respiration and energetics in West Indian Gorgonacea (Anthozoa, octocorallia). Comp Biochem Physiol 71:457–459. https://doi.org/10.1016/0300-9629(82)90434-0

Lin MC, Liao CM, Dai CF (2002) Modeling the effects of satiation on the feeding rate of a colonial suspension feeder, *Acanthogorgia vegae*, in a circulating system under lab conditions. Zool Stud 41:355–365

López-Gonzalez PJ, Bramanti L, Escribano-Álvarez P, et al (2018) Thread-like tentacles in the Mediterranean corals *Paramuricea clavata* and *Corallium rubrum*. Mediterr Mar Sci 19:394–397

Lucas JM, Knapp LW (1997) A physiological evaluation of carbon sources for calcification in the octocoral *Leptogorgia virgulata* (Lamarck). J Exp Biol 200:2653–2662

McCauley M, Banaszak AT, Goulet TL (2018) Species traits dictate seasonal-dependent responses of octocoral–algal symbioses to elevated temperature and ultraviolet radiation. Coral Reefs 37:901–917. https://doi.org/10.1007/s00338-018-1716-8

McFadden CS (1986) Colony fission increases particle capture rates of a soft coral: Advantages of being a small colony. J Exp Mar Bio Ecol 103:1–20. https://doi.org/10.1016/0022-0981(86)90129-2

McFadden CS, France SC, Sánchez JA, Alderslade P (2006) A molecular phylogenetic analysis of the Octocorallia (Cnidaria: Anthozoa) based on mitochondrial protein-coding sequences. Mol Phylogenet Evol 41:513–527. https://doi.org/10.1016/j.ympev.2006.06.010

Mehrotra R, Scott CM, Hoeksema BW (2016) A large gape facilitates predation on salps by *Heteropsammia* corals. Mar Biodivers 46:323–324. https://doi.org/10.1007/s12526-015-0379-8

Mergner H, Svoboda A (1977) Productivity and seasonal changes in selected reef areas in the Gulf of Aqaba (Red Sea). Helgoländer Wissenschaftliche Meeresuntersuchungen 30:383–399. https://doi.org/10.1007/BF02207849

Michalek-Wagner K, Willis BL (2001) Impacts of bleaching on the soft coral *Lobophytum compactum*. II. Biochemical changes in adults and their eggs. Coral Reefs 19:240–246. https://doi.org/10.1007/PL00006959

Migné A, Davoult D (2002) Experimental nutrition in the soft coral *Alcyonium digitatum* (Cnidaria: Octocorallia): Removal rate of phytoplankton and zooplankton. Cah Biol Mar 43:9–16

Moher D, Liberati A, Tetzlaff J, et al (2009) Preferred reporting items for systematic reviews and meta-analyses: The PRISMA statement. PLoS Med 6:. https://doi.org/10.1371/journal.pmed.1000097

Muscatine L (1973) Nutrition of Corals. Biol Geol Coral Reefs 77–115. https://doi.org/10.1016/b978-0-12-395526-5.50012-2

Muscatine L, Falkowski PG, Dubinsky Z, et al (1989) The effect of external nutrient resources on the population dynamics of zooxanthellae in a reef coral. Proc - R Soc London, B 236:311–324. https://doi.org/10.1098/rspb.1989.0025

Nakamura T, Van Woesik R (2001) Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. Mar Ecol Prog Ser 212:301–304. https://doi.org/10.3354/meps212301

Nelson HR, Altieri AH (2019) Oxygen: the universal currency on coral reefs. Coral Reefs 38:177–198. https://doi.org/10.1007/s00338-019-01765-0

Norström A V., Nyström M, Lokrantz J, Folke C (2009) Alternative states on coral reefs: Beyond coral-macroalgal phase shifts. Mar Ecol Prog Ser 376:293–306. https://doi.org/10.3354/meps07815

Orejas C, Gili J, Arntz W (2003) Role of small-plankton communities in the diet of two Antarctic octocorals (*Primnoisis antarctica* and *Primnoella* sp.). Mar Ecol Prog Ser 250:105–116

Orejas C, Gili JM, Arntz WE, et al (2002) Benthic suspension feeders, key players in Antartic marine ecosystems? Contrib to Sci 0:299-311–311. https://doi.org/10.2436/cs.v0i0.256

Orejas C, Gili JM, Lopez-Gonzalez PJ, Arntz WE (2001) Feeding strategies and diet composition of four Antarctic cnidarian species. Polar Biol 24:620–627. https://doi.org/10.1007/s003000100272

Owen DP, Long MH, Fitt WK, Hopkinson BM (2020) Taxon-specific primary production rates on coral reefs in the Florida Keys. Limnol Oceanogr 1–14. https://doi.org/10.1002/lno.11627

Patterson M (1984) Patterns of whole colony prey capture in the octocoral, *Alcyonium sidetium*. Biol Bull 165:791–810

Patterson MR, Sebens KP (1989) Forced convection modulates gas exchange in cnidarians. PNAS 86:8833–8836. https://doi.org/10.1073/pnas.86.22.8833

Picciano M, Ferrier-Pagès C (2007) Ingestion of pico- and nanoplankton by the Mediterranean red coral *Corallium rubrum*. Mar Biol 150:773–782. https://doi.org/10.1007/s00227-006-0415-0

Piccinetti CC, Ricci R, Pennesi C, et al (2016) Herbivory in the soft coral *Sinularia flexibilis* (Alcyoniidae). Sci Rep 6:1–8. https://doi.org/10.1038/srep22679

Porter JW (1976) Autotrophy, Heterotrophy, and Resource Partitioning in Caribbean Reef-Building Corals. Am Nat 110:731–742. https://doi.org/10.1086/283100

Previati M, Scinto A, Cerrano C, Osinga R (2010) Oxygen consumption in Mediterranean octocorals under different temperatures. J Exp Mar Bio Ecol 390:39–48. https://doi.org/10.1016/j.jembe.2010.04.025

Pupier CA, Bednarz VN, Ferrier-Pagès C (2018) Studies with soft corals - recommendations on sample processing and normalization metrics. Front Mar Sci 5:. https://doi.org/10.3389/fmars.2018.00348

Pupier CA, Fine M, Bednarz VN, et al (2019) Productivity and carbon fluxes depend on species and symbiont density in soft coral symbioses. Sci Rep 9:. https://doi.org/10.1038/s41598-019-54209-8

Rakka M, Maier SR, Oevelen D Van, et al (2021) Contrasting metabolic strategies of two co-occurring deep-sea octocorals. Sci Rep 1–12. https://doi.org/10.1038/s41598-021-90134-5

Ramsby BD, Goulet TL (2019) Symbiosis and host morphological variation: *Symbiodiniaceae* photosynthesis in the octocoral *Briareum asbestinum* at ambient and elevated temperatures. Coral Reefs 38:359–371. https://doi.org/10.1007/s00338-019-01782-z

Ramsby BD, Shirur KP, Iglesias-Prieto. R, Goulet TL (2014) *Symbiodinium* photosynthesis in Caribbean octocorals. PLoS One 9:. https://doi.org/10.1371/journal.pone.0106419

Reichert J, Arnold AL, Hoogenboom MO, et al (2019) Impacts of microplastics on growth and health of hermatypic corals are species-specific. Environ Pollut 254:113074. https://doi.org/10.1016/j.envpol.2019.113074

Ribes M, Coma R, Rossi S (2003) Natural feeding of the temperate asymbiotic octocoral-gorgonian *Leptogorgia sarmentosa* (Cnidaria: Octocorallia). Mar Ecol Prog Ser 254:141–150. https://doi.org/10.3354/meps254141

Richmond RH (1993) Coral reefs: Present problems and future concerns resulting from anthropogenic disturbance. Integr Comp Biol 33:524–536. https://doi.org/10.1093/icb/33.6.524

Riegl B, Branch GM (1995) Effects of sediment on the energy budgets of four scleractinian (Bourne 1900) and five alcyonacean (Lamouroux 1816) corals. J Exp Mar Bio Ecol 186:259–275. https://doi.org/10.1016/0022-0981(94)00164-9

Rinkevich B (1996) Do reproduction and regeneration in damaged corals compete for energy allocation? Mar Ecol Prog Ser 143:297–302. https://doi.org/10.3354/meps143297

Rocha RJM, Serôdio J, Leal MC, et al (2013) Effect of light intensity on post-fragmentation photobiological performance of the soft coral *Sinularia flexibilis*. Aquaculture 388–391:24–29. https://doi.org/10.1016/j.aquaculture.2013.01.013

Rodriguez MVB, Segumalian CS, Lalas JAA, Maningas JMC (2020) Octocorals outcompete scleractinian corals in a degraded reef. IOP Conf Ser Earth Environ Sci 420:. https://doi.org/10.1088/1755-1315/420/1/012027

Ross T, Du Preez C, Ianson D (2020) Rapid deep ocean deoxygenation and acidification threaten life on Northeast Pacific seamounts

Rossi S, Gili JM, Coma R, et al (2006) Temporal variation in protein, carbohydrate, and lipid concentrations in *Paramuricea clavata* (Anthozoa, Octocorallia): Evidence for summer-autumn feeding constraints. Mar Biol 149:643–651. https://doi.org/10.1007/s00227-005-0229-5

Rossi S, Isla E, Bosch-Belmar M, et al (2019a) Changes of energy fluxes in marine animal forests of the anthropocene: Factors shaping the future seascape. ICES J Mar Sci 76:2008–2019. https://doi.org/10.1093/icesjms/fsz147

Rossi S, Ribes M, Coma R, Gili JM (2004) Temporal variability in zooplankton prey capture rate of the passive suspension feeder *Leptogorgia sarmentosa* (Cnidaria: Octocorallia), a case study. Mar Biol 144:89–99. https://doi.org/10.1007/s00227-003-1168-7

Rossi S, Rizzo L, Duchêne JC (2019b) Polyp expansion of passive suspension feeders: A red coral case study. PeerJ 2019:1–17. https://doi.org/10.7717/peerj.7076

Rossi S, Schubert N, Brown D, et al (2020) Trophic ecology of Caribbean octocorals: autotrophic and heterotrophic seasonal trends. Coral Reefs 39:433–449. https://doi.org/10.1007/s00338-020-01906-w

Rossi S, Schubert N, Brown D, et al (2018) Linking host morphology and symbiont performance in octocorals. Sci Rep 8:12823. https://doi.org/10.1038/s41598-018-31262-3

Roushdy HM, Hansen VK (1961) Filtration of phytoplankton by the octocoral *Alcyonium digitatum* L. Nature 190:649–650. https://doi.org/10.1038/190649b0

Russo A (1985) Ecological observations on the gorgonian sea fan *Eunicella cavolinii* in the Bay of Naples. Mar Ecol Prog Ser 24:155–159. https://doi.org/10.3354/meps024155

Ruzicka RR, Colella MA, Porter JW, et al (2013) Temporal changes in benthic assemblages on Florida Keys reefs 11 years after the 1997/1998 El Niño. Mar Ecol Prog Ser 489:125–141. https://doi.org/10.3354/meps10427

Sammarco PW, Strychar KB (2013) Responses to High Seawater Temperatures in Zooxanthellate Octocorals. PLoS One 8:. https://doi.org/10.1371/journal.pone.0054989

Sammarco PW, Strychar KB (2009) Effects of climate change/global warming on coral reefs: Adaptation/exaptation in corals, evolution in zooxanthellae, and biogeographic shifts. Environ Bioindic 4:9–45. https://doi.org/10.1080/15555270902905377

Sánchez JA (2004) Evolution and dynamics of branching colonial form in marine modular cnidarians: Gorgonian octocorals. Hydrobiologia 530–531:283–290. https://doi.org/10.1007/s10750-004-2684-2

Santangelo G, Cupido R, Cocito S, et al (2015) Effects of increased mortality on gorgonian corals (Cnidaria, Octocorallia): different demographic features may lead affected populations to unexpected recovery and new equilibrium points. Hydrobiologia 759:171–187. https://doi.org/10.1007/s10750-015-2241-1

Schlichter D (1982) Nutritional strategies of cnidarians: The absorption, translocation and utilization of dissolved nutrients by *Heteroxenia fuscescens*. Am Zool 22:659–669. https://doi.org/10.1093/icb/22.3.659

Schlichter D, Svoboda A, Kremer BP (1983) Functional autotrophy of *Heteroxenia fuscescens* (Anthozoa: Alcyonaria): carbon assimilation and translocation of photosynthates from symbionts to host. Mar Biol 78:29–38. https://doi.org/10.1007/BF00392968

Schmidtko S, Stramma L, Visbeck M (2017) Decline in global oceanic oxygen content during the past five decades. Nature 542:335–339. https://doi.org/10.1038/nature21399

Schubert N, Brown D, Rossi S (2017) Symbiotic Versus Non-symbiotic Octocorals: Physiological and Ecological Implications. In: Marine Animal Forests

Sebens KP (1984) Water flow and coral colony size: Interhabitat comparisons of the octocoral *Alcyonium siderium*. PNAS 81:5473–5477

Sebens KP, Koehl MAR (1984) Predation on zooplankton by the benthic anthozoans *Alcyonium siderium* (Alcyonacea) and *Metridium senile* (Actiniaria) in the New England subtidal. Mar Biol 81:255–271. https://doi.org/10.1007/BF00393220

Servetto N, Rossi S, Fuentes V, et al (2017) Seasonal trophic ecology of the dominant Antarctic coral *Malacobelemnon daytoni* (Octocorallia, Pennatulacea, Kophobelemnidae). Mar Environ Res 130:264–274. https://doi.org/10.1016/j.marenvres.2017.08.003

Sherwood OA, Heikoop JM, Scott DB, et al (2005a) Stable isotopic composition of deep-sea gorgonian corals *Primnoa* spp.: A new archive of surface processes. Mar Ecol Prog Ser 301:135–148. https://doi.org/10.3354/meps301135

Sherwood OA, Jamieson RE, Edinger EN, Wareham VE (2008) Stable C and N isotopic composition of cold-water corals from the Newfoundland and Labrador continental slope: Examination of trophic, depth and spatial effects. Deep Res Part I Oceanogr Res Pap 55:1392–1402. https://doi.org/10.1016/j.dsr.2008.05.013

Sherwood OA, Lapointe BE, Risk MJ, Jamieson RE (2010) Nitrogen Isotopic Records of Terrestrial Pollution Encoded in Floridian and Bahamian Gorgonian Corals. Environ Sci Technol 44:874–880. https://doi.org/10.1021/es9018404

Sherwood OA, Scott DB, Risk MJ, Guilderson TP (2005b) Radiocarbon evidence for annual growth rings in the deep-sea octocoral *Primnoa resedaeformis*. Mar Ecol Prog Ser 301:129–134. https://doi.org/10.3354/meps301129

Shirur KP, Ramsby BD, Iglesias-Prieto R, Goulet TL (2014) Biochemical composition of Caribbean gorgonians: Implications for gorgonian - *Symbiodinium* symbiosis and ecology. J Exp Mar Bio Ecol 461:275–285. https://doi.org/10.1016/j.jembe.2014.08.016

Simpson CJ, Cary JL, Masini RJ (1993) Destruction of corals and other reef animals by coral spawn slicks on Ningaloo Reef, Western Australia. Coral Reefs 12:185–191. https://doi.org/10.1007/BF00334478

Slattery M, McClintock JB, Bowser SS (1997) Deposit feeding: a novel mode of nutrition in the Antarctic colonial soft coral *Gersemia antarctica*. Mar Ecol Prog Ser 149:299–304. https://doi.org/10.3354/meps149299

Slattery M, Pankey MS, Lesser MP (2019) Annual Thermal Stress Increases a Soft Coral's Susceptibility to Bleaching. Sci Rep 9:1–10. https://doi.org/10.1038/s41598-019-44566-9

Sorokin YI (1991) Biomass, metabolic rates and feeding of some common reef zoantharians and octocorals. Mar Freshw Res 42:729–741. https://doi.org/10.1071/MF9910729

Spalding MD, Fox HE, Allen GR, et al (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. Bioscience 57:573–583. https://doi.org/10.1641/B570707

Sponaugle S (1991) Flow patterns and velocities around a suspension-feeding gorgonian polyp: evidence from physical models. J Exp Mar Bio Ecol 148:135–145. https://doi.org/10.1016/0022-0981(91)90152-M

Stambler N, Popper N, Dubinsky Z, Stimson J (1991) Effects of nutrient enrichment and water motion on the coral *Pocillopora damicornis*. Pacific Sci 45:299–307

Stat M, Morris E, Gates RD (2008) Functional diversity in coral-dinoflagellate symbiosis. PNAS 105:9256–9261. https://doi.org/10.1073/pnas.0801328105

Stobart B, Teleki K, Buckley R, et al (2005) Coral recovery at Aldabra Atoll, Seychelles: Five years after the 1998 bleaching event. Philos Trans R Soc A Math Phys Eng Sci 363:251–255. https://doi.org/10.1098/rsta.2004.1490

Stramma L, Schmidtko S, Levin LA, Johnson GC (2010) Ocean oxygen minima expansions and their biological impacts. Deep Res Part I Oceanogr Res Pap 57:587–595. https://doi.org/10.1016/j.dsr.2010.01.005

Taylor ML, Gwinnett C, Robinson LF, Woodall LC (2016) Plastic microfibre ingestion by deep-sea organisms. Sci Rep 6:1–9. https://doi.org/10.1038/srep33997

Todd PA (2008) Morphological plasticity in scleractinian corals. Biol Rev 83:315–337. https://doi.org/10.1111/j.1469-185X.2008.00045.x

Tseng LC, Dahms HU, Hsu NJ, Hwang JS (2011) Effects of sedimentation on the gorgonian *Subergorgia suberosa* (Pallas, 1766). Mar Biol 158:1301–1310. https://doi.org/10.1007/s00227-011-1649-z

Tsounis G, Edmunds PJ (2017) Three decades of coral reef community dynamics in St. John, USVI: A contrast of scleractinians and octocorals. Ecosphere 8:. https://doi.org/10.1002/ecs2.1646

Tsounis G, Edmunds PJ, Bramanti L, et al (2018) Variability of size structure and species composition in Caribbean octocoral communities under contrasting environmental conditions. Mar Biol 165:1–14. https://doi.org/10.1007/s00227-018-3286-2

Tsounis G, Martinez L, Bramanti L, et al (2012) Anthropogenic effects on reproductive effort and allocation of energy reserves in the Mediterranean octocoral *Paramuricea clavata*. Mar Ecol Prog Ser 449:161–172. https://doi.org/10.3354/meps09521

Tsounis G, Rossi S, Laudien J, et al (2006) Diet and seasonal prey capture rates in the Mediterranean red coral (*Corallium rubrum* L.). Mar Biol 149:313–325. https://doi.org/10.1007/s00227-005-0220-1

Tummers B (2006) DataThief III v.1.7. https://datathief.org/

Van Oppen MJH, Mahiny AJ, Done TJ (2005) Geographic distribution of zooxanthella types in three coral species on the Great Barrier Reef sampled after the 2002 bleaching event. Coral Reefs 24:482–487. https://doi.org/10.1007/s00338-005-0487-1

Viladrich N, Bramanti L, Tsounis G, et al (2016) Variation in lipid and free fatty acid content during spawning in two temperate octocorals with different reproductive strategies: surface versus internal brooder. Coral Reefs 35:1033–1045. https://doi.org/10.1007/s00338-016-1440-1

Villamizar E, Díaz MC, Rützler K, De Nóbrega R (2013) Biodiversity, ecological structure, and change in the sponge community of different geomorphological zones of the barrier fore reef at Carrie Bow Cay, Belize. Mar Ecol 1–11. https://doi.org/10.1111/maec.12099

Vollstedt S, Xiang N, Simancas-Giraldo SM, Wild C (2020) Organic eutrophication increases resistance of the pulsating soft coral *Xenia umbellata* to warming. PeerJ 2020:1–16. https://doi.org/10.7717/peerj.9182

Wainwright SA, Dillon JR (1969) On the orientation of sea fans (genus Gorgonia). Biol Bull 136:130–139

Wakeford M, Done TJ, Johnson CR (2008) Decadal trends in a coral community and evidence of changed disturbance regime. Coral Reefs 27:1–13. https://doi.org/10.1007/s00338-007-0284-0

Ward-Paige CA, Risk MJ, Sherwood OA (2005) Reconstruction of nitrogen sources on coral reefs: δ15N and δ13C in gorgonians from Florida Reef Tract. Mar Ecol Prog Ser 296:155–163. https://doi.org/10.3354/meps296155

Weinbauer MG, Velmirov B (1995) Morphological Variations in the Mediterranean Sea Fan Eunicella Cavolini (Coelenterata: Gorgonacea) in Relation to Exposure, Colony Size and Colony Region. Bull Mar Sci 56:283–295

Williams B, Grottoli AG (2010) Stable nitrogen and carbon isotope ($^{\delta15}$N and $^{\delta13}$C) variability in shallow tropical Pacific soft coral and black coral taxa and implications for paleoceanographic reconstructions. Geochim Cosmochim Acta 74:5280–5288. https://doi.org/10.1016/j.gca.2010.06.026

Williams B, Risk M, Stone R, et al (2007) Oceanographic changes in the North Pacific Ocean over the past century recorded in deep-water gorgonian corals. Mar Ecol Prog Ser 335:85–94. https://doi.org/10.3354/meps335085

Williamson EA, Strychar KB, Withers K, Sterba-Boatwright B (2011) Effects of salinity and sedimentation on the Gorgonian Coral, *Leptogorgia virgulata* (Lamarck 1815). J Exp Mar Bio Ecol 409:331–338. https://doi.org/10.1016/j.jembe.2011.09.014

Wood E, Dipper F (2008) What is the future for extensive areas of reef impacted by fish blasting and coral bleaching and now dominated by soft corals? A case study from Malaysia. Proc 11th Int Coral Reef Symp Ft Lauderdale, Florida, 7-11 July 2008 7–11

Woodall LC, Sanchez-Vidal A, Canals M, et al (2014) The deep sea is a major sink for microplastic debris. R Soc Open Sci 1. https://doi.org/10.1098/rsos.140317

Wooldridge SA (2010) Is the coral-algae symbiosis really “mutually beneficial” for the partners? BioEssays 32:615–625. https://doi.org/10.1002/bies.200900182

Zuur AF, Ieno EN, Smith GM (2007) Analysing Ecological Data. Springer,

Supplementary material

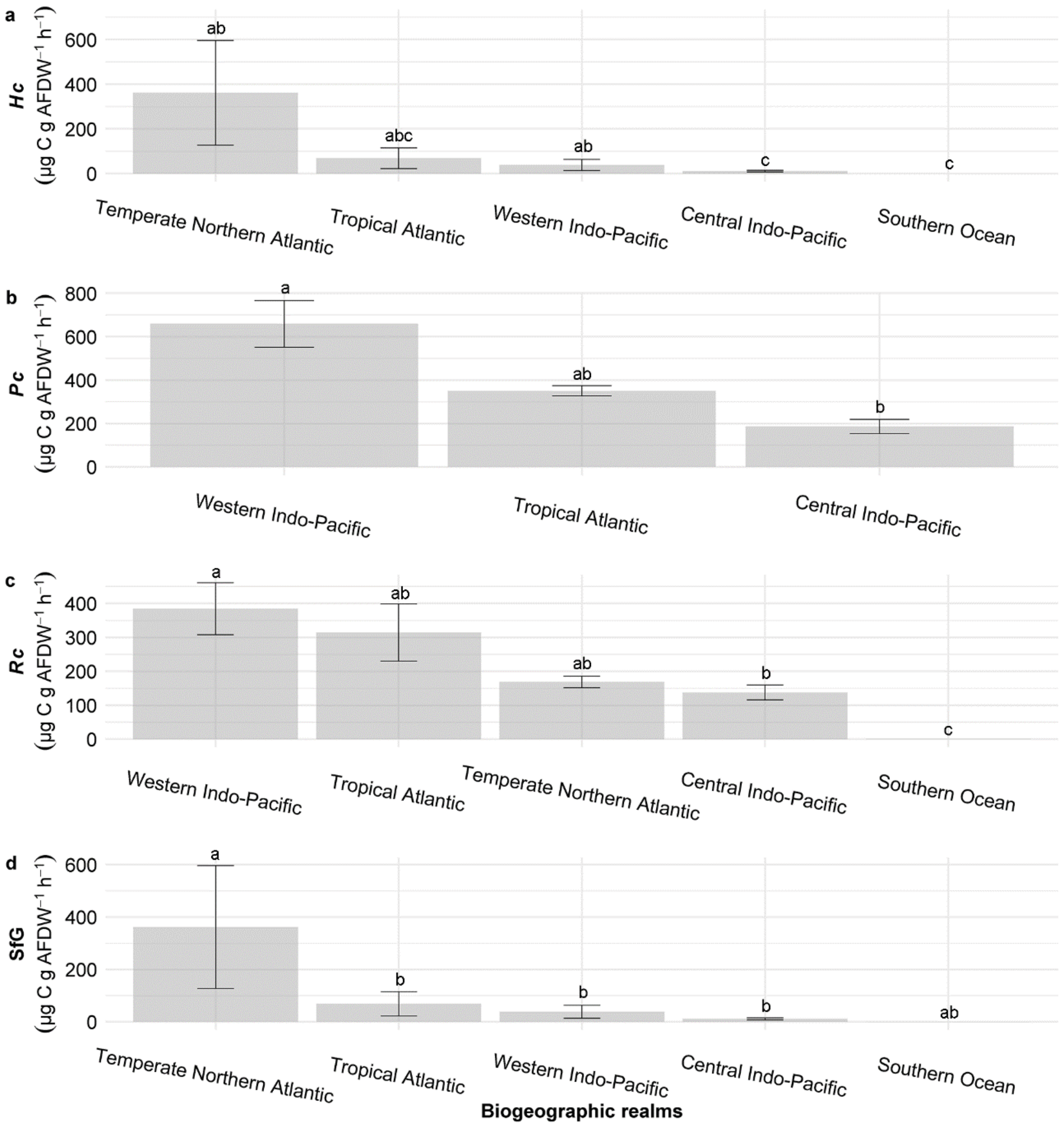

Fig S1 Heterotrophic carbon input – HC (**a**), photosynthetic carbon input – PC (**b**), respiratory carbon demand – RC (**c**), and scope for growth and reproduction – SfG (**d**) (µgC gAFDW-1 hour-1) of octocorals across the biogeographic realms. Letters represent significance (p value < 0.05) between groups according to the post hoc GLHT test

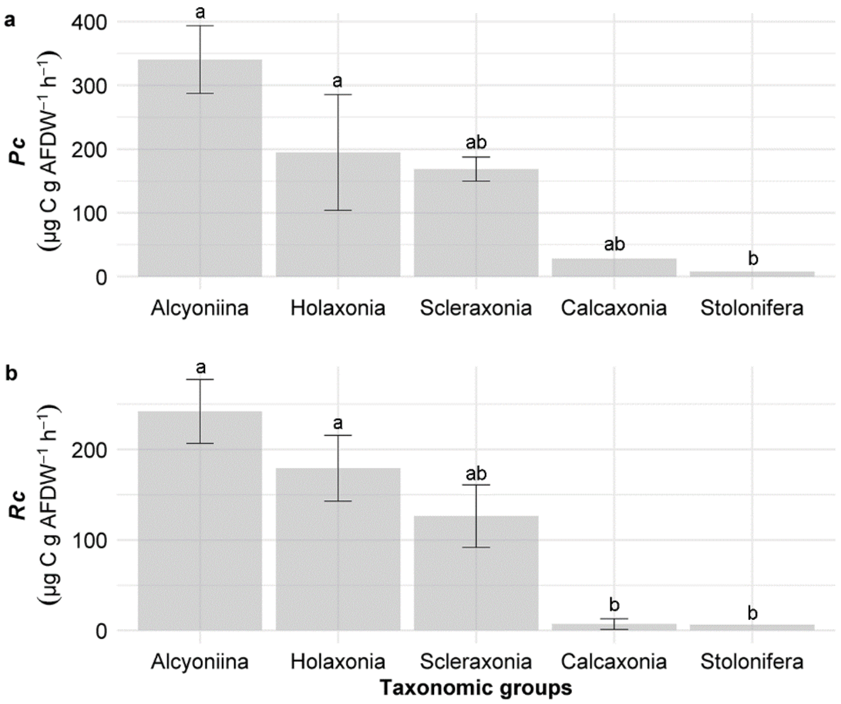

Fig S2 Photosynthetic carbon input – P_C (**a**) and respiratory carbon demand – R_C (**b**) (µgC gAFDW^{-1} hour^{-1}) across taxonomic groups. Letters represent significance (*p* value < 0.05) between groups according to the *post hoc* GLHT test

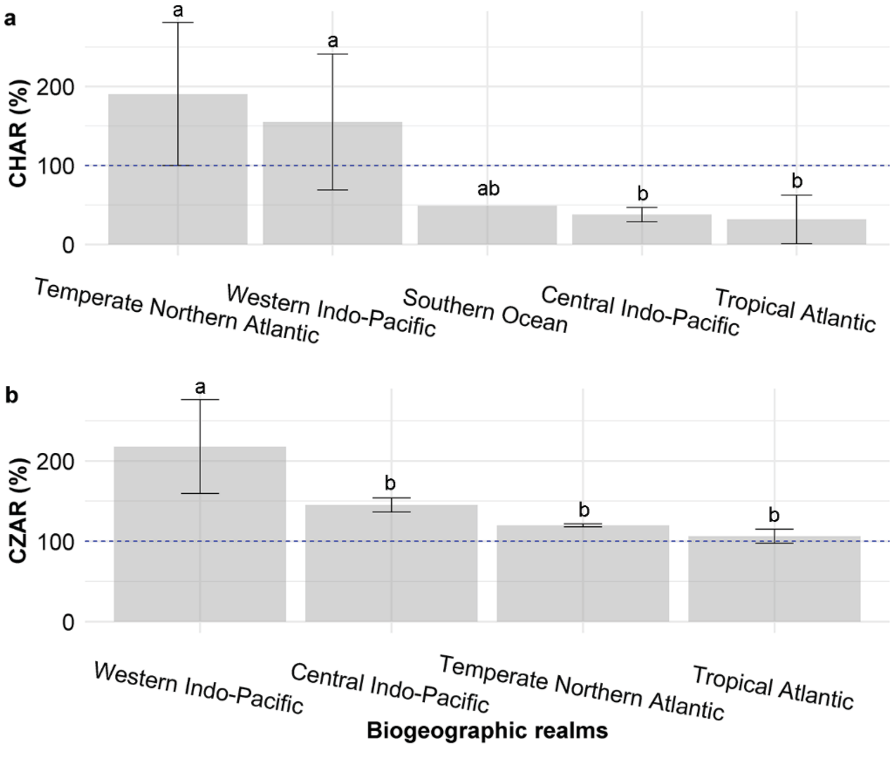

Fig S3 The contribution of heterotrophically acquired carbon to octocoral respiration – CHAR (**a**) and the contribution of autotrophically acquired carbon to octocoral respiration – CZAR (**b**) across the biogeographic realms. Letters represent significance (p value < 0.05) between groups according to the *post hoc* GLHT test. The blue dashed line indicates the threshold at which H_C and Pc meet Rc

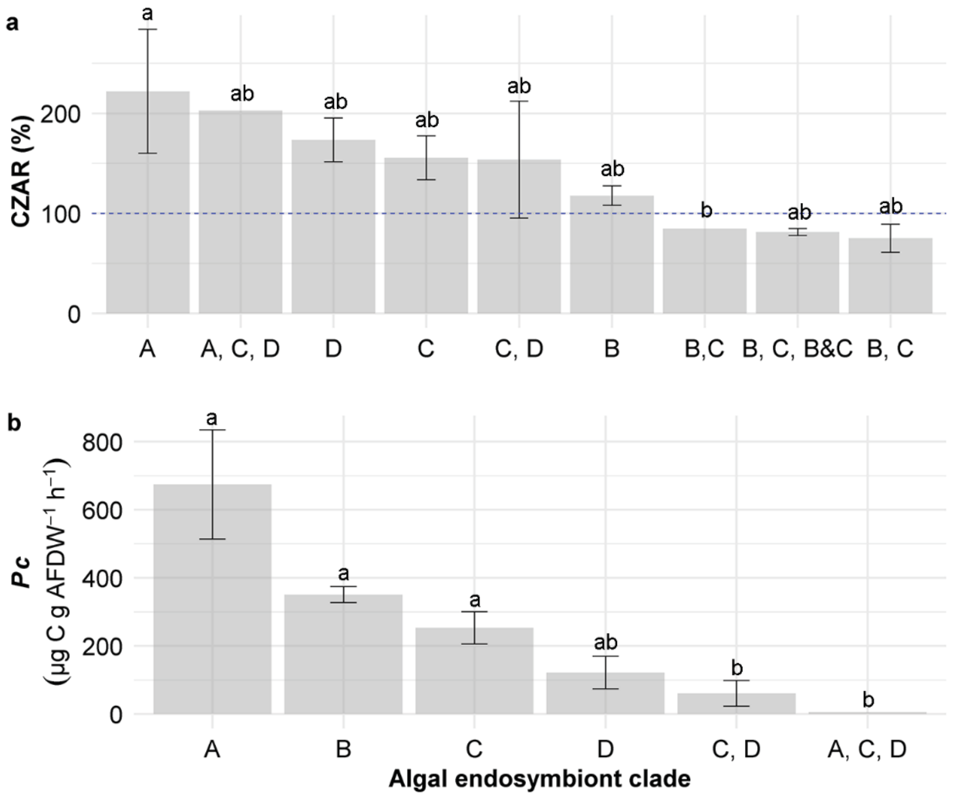

Fig S4 The contribution of autotrophically acquired carbon to octocoral respiration – CZAR (**a**) and the photosynthetic carbon input – P_C (**b**) according to the algal endosymbiont clade

Conclusão geral

Em conclusão, esta dissertação teve o objetivo geral de avaliar a ecologia alimentar de octocorais, examinando as respostas no desempenho alimentar pela colonização de um ofiuroide invasor e correlacionado com as atuais tendências mundiais na sua expansão. No primeiro capítulo, procuramos avaliar os impactos do ofiuroide não-nativo *Ophiothela mirabilis* na performance alimentar do octocoral *Leptogorgia punicea* através de experimentos manipulativos de campo. No segundo capítulo, correlacionamos a ecologia alimentar dos octocorais às tendências de aumento da sua distribuição observadas em todo mundo através de uma revisão sistemática da literatura e reavaliação dos dados.

As altas densidades relatadas do ofiuroide não-nativo *O. mirabilis* em hospedeiros octocorais ao longo do Atlântico ocidental levantaram preocupações sobre os efeitos potencialmente negativos (Mantelatto et al. 2016; Derviche et al. 2021). Avaliamos se a simbiose entre ofiuroides e *L. punicea* hospedeiros pode ser considerada parasitismo estrutural por meio de experimentos de campo usando câmaras de incubação *in situ*. No entanto, não foram observados efeitos significativos no desempenho alimentar de *L. punicea* causado pelo ofiuroide, dessa maneira, indicando uma relação simbiótica comensalística. Os alimentadores suspensívoros bênticos desempenham um papel significativo nos processos de acoplamento bento-pelágico de costões rochosos e de recifes de coral (Gili and Coma 1998). Portanto, efeitos negativos em espécies-chave ou engenheiros ecológicos podem afetar a estrutura e funcionamento desses sistemas. Uma vez que a aptidão de *L. punicea* permanece similar impendentemente da colonização ou não do ofiuroide, é possível inferir que o fluxo de carbono conduzido por este alimentador de suspensão passiva também não é afetado, indicando impactos mínimos (Blackburn et al. 2011). Mesmo assim, são necessários mais estudos experimentais de laboratório e de campo que avaliem os efeitos nos taxa hospedeiros com características morfológicas e funcionais distintas para melhor compreender as respostas da biodiversidade receptora e do ecossistema do Atlântico ocidental às densidades crescentes de *O. mirabilis.*

Ao contrário dos corais escleractíneos, os octocorais estão aumentando sua distribuição e abundância em vários costões rochosos e recifes de coral em todo o mundo (Done 1992; Norström et al. 2009; Ruzicka et al. 2013; Inoue et al. 2013; Lenz et al. 2015; Owen et al. 2020), o que pode ser explicado por diferenças no funcionamento da sua ecologia alimentar. Nós realizamos uma revisão sistemática e abrangente da ecologia alimentar de octocorais, compilando e reavaliando dados de orçamentos de carbono, o que proporcionou uma compreensão mais profunda do equilíbrio entre as entradas autotróficas e heterotróficas para atender às suas demandas metabólicas. A menor dependência da autotrofia e a capacidade de diminuir os gastos de energia para compensar a autotrofia em eventos de estresse são características da ecologia alimentar dos octocorais que difere dos corais escleractíneos. A alimentação suspensívora de octocorais tem implicações importantes para o acoplamento bento-pelágico, uma vez que suas extensas formações podem atuar como um importante sumidouro de carbono. Os octocorais talvez possuam vantagens no modo de alimentação competitivamente mais altas do que os corais escleractíneos, o que, combinado com outros fatores comportamentais e fisiológicos (por exemplo, reprodução, tolerância térmica), pode explicar as mudanças de fase observadas em todo o mundo.

Por fim, a ecologia alimentar de octocorais tem um papel significativo no acoplamento bento-pelágico de costões rochosos e recifes de coral (Coppari et al. 2019). Uma vez que o desempenho alimentar de octocorais pode ser influenciado por relações simbióticas, é essencial avaliar se novas simbioses resultantes de invasões biológicas podem ser consideradas desarmônicas. Além disso, as tendências de mudança de fase observadas em costões rochosos e recifes de coral mundialmente, podem estar relacionadas com diferenças no modo de alimentação de octocorais e corais escleractíneos. Portanto, os experimentos *in situ* e a revisão da literatura permitiram identificar o relevante papel da ecologia alimentar na resiliência dos octocorais, frente à invasões biológicas e nas mudanças de fase.

Referências

Baum, G., Januar, H.I., Ferse, S.C.A., Kunzmann, A., 2015. Local and regional impacts of pollution on coral reefs along the thousand islands north of the megacity Jakarta, Indonesia. PLoS One 10, 1–26. https://doi.org/10.1371/journal.pone.0138271

Benayahu, Y., Bridge, T.C.L., Colin, P.L., Liberman, R., McFadden, C.S., Pizarro, O., Schleyer, M.H., Shoham, E., Reijnen, B.T., Weis, M., Tanaka, J., 2019. Octocorals of the Indo-Pacific, in: Mesophotic Coral Ecosystems. Springer. Springer, Cham, pp. 709–728. https://doi.org/10.1007/978-3-319-92735-0_38

Blackburn, T.M., Essl, F., Evans, T., Hulme, P.E., Jeschke, J.M., Kühn, I., Kumschick, S., Marková, Z., Mrugała, A., Nentwig, W., Pergl, J., Pyšek, P., Rabitsch, W., Ricciardi, A., Richardson, D.M., Sendek, A., Vilà, M., Wilson, J.R.U., Winter, M., Genovesi, P., Bacher, S., 2014. A unified classification of alien species based on the magnitude of their environmental impacts. PLoS Biol. 12, e1001850. https://doi.org/10.1371/journal.pbio.1001850

Blackburn, T.M., Pyšek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarošík, V., Wilson, J.R.U., Richardson, D.M., 2011. A proposed unified framework for biological invasions. Trends Ecol. Evol. 26, 333–339. https://doi.org/10.1016/j.tree.2011.03.023

Brandl, S.J., Rasher, D.B., Côté, I.M., Casey, J.M., Darling, E.S., Lefcheck, J.S., Duffy, J.E., 2019. Coral reef ecosystem functioning: eight core processes and the role of biodiversity. Front. Ecol. Environ. 17, 445–454. https://doi.org/10.1002/fee.2088

Cerpovicz, A.F., Lasker, H.R., 2021. Canopy effects of octocoral communities on sedimentation: modern baffles on the shallow-water reefs of St. John, USVI. Coral Reefs. 40,295–303. https://doi.org/10.1007/s00338-021-02053-6

Cesar, H.S.J., van Beukering, P.J.H., 2004. Economic valuation of the coral reefs of Hawai'i. Pacific Sci. 58, 231–242. https://doi.org/10.1353/psc.2004.0014

Coma, R., Ribes, M., Gili, J., Hughes, R.N., 2001. The ultimate opportunists: consumers of seston. Mar Ecol Prog Ser 219, 305–308. https://doi.org/10.3354/meps219305

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302–1310. https://doi.org/10.2307/4081809

Coppari, M., Gori, A., Viladrich, N., Saponari, L., Canepa, A., Grinyó, J., Olariaga, A., Rossi, S., 2016. The role of Mediterranean sponges in benthic-pelagic coupling processes: *Aplysina aerophoba* and *Axinella polypoides* case studies. J. Exp. Mar. Bio. Ecol. 477, 57–68. https://doi.org/10.1016/j.jembe.2016.01.004

Coppari, M., Zanella, C., Rossi, S., 2019. The importance of coastal gorgonians in the blue carbon budget. Sci. Rep. 9, 13550. https://doi.org/10.1038/s41598-019-49797-4

Cornwall, C.E., Comeau, S., Kornder, N.A., Perry, C.T., van Hooidonk, R., DeCarlo, T.M., Pratchett, M.S., Anderson, K.D., Browne, N., Carpenter, R., Diaz-Pulido, G., D'Olivo, J.P., Doo, S.S., Figueiredo, J., Fortunato, S.A.V., Kennedy, E., Lantz, C.A., McCulloch, M.T., González-Rivero, M., Schoepf, V., Smithers, S.G., Lowe, R.J., 2021. Global declines in coral reef calcium carbonate production under ocean acidification and warming. Proc. Natl. Acad. Sci. U. S. A. 118. https://doi.org/10.1073/pnas.2015265118

Deaker, D.J., Agüera, A., Lin, H.A., Lawson, C., Budden, C., Dworjanyn, S.A., Mos, B., Byrne, M., 2020. The hidden army: Corallivorous crown-of-thorns seastars can spend years as herbivorous juveniles. Biol. Lett. 16. https://doi.org/10.1098/rsbl.2019.0849

Derviche, P., Saucsen, A., Spier, D., Lana, P., 2021. Distribution patterns and habitat suitability of the non-native brittle star *Ophiothela mirabilis* Verrill, 1867 along the Western Atlantic. J. Sea Res. 168, 101994. https://doi.org/10.1016/j.seares.2020.101994

Done, T.J., 1992. Phase shifts in coral reef communities and their ecological significance. Hydrobiologia 247, 121–132. https://doi.org/10.1007/BF00008211

Fabricius, K.E., Klumpp, D.W., 1995. Widespread mixotrophy in reef-inhabiting soft corals: the influence of depth, and colony expansion and contraction on photosynthesis. Mar Ecol Prog Ser 125, 195–204. https://doi.org/10.3354/meps125195

Fabricius, K.E., Genin, A., Benayahu, Y., 1995. Flow-dependent herbivory and growth in zooxanthellae-free soft corals. Limnol Oceanogr 40, 1290–1301. https://doi.org/10.4319/lo.1995.40.7.1290

Fung, T., Seymour, R.M., Johnson, C.R., 2011. Alternative stable states and phase shifts in coral reefs under anthropogenic stress. Ecology 92, 967–982. https://doi.org/10.1890/10-0378.1

Gili, J.M., Coma, R., 1998. Benthic suspension feeders: their paramount role in littoral marine food webs. Trends Ecol. Evol. 13, 316–321. https://doi.org/10.1016/S0169-5347(98)01365-2

Girard, F., Fu, B., Fisher, C.R., 2016. Mutualistic symbiosis with ophiuroids limited the impact of the Deepwater Horizon oil spill on deep-sea octocorals. Mar. Ecol. Prog. Ser. 549, 89–98. https://doi.org/10.3354/meps11697

Glynn, P.W., Coffman, B., Primov, K., et al, 2019. Benthic ctenophore (Order Platyctenida) reproduction, recruitment, and seasonality in south Florida. Invertebr Biol 138, e12256. https://doi.org/10.1111/ivb.12256

Glynn, P.W., Gillette, P.R., Dettloff, K., et al, 2021. Experimental evidence of minimal effects on octocoral hosts caused by the introduced ophiuroid *Ophiothela mirabilis*. Coral Reefs. https://doi.org/10.1007/s00338-021-02067-0

Goldberg, W.M., 2018. Coral food, feeding, nutrition, and secretion: a review. In: Marine organisms as model systems in biology and medicine. Springer, Cham, pp 377–421

Grange, K.R., 1991. Mutualism between the antipatharian *Antipathes fiordensis* and the ophiuroid *Astrobrachion constrictum* in New Zealand fjords. Hydrobiologia 216–217, 297–303. https://doi.org/10.1007/BF00026478

Hendler, G., 1984. The association of *Ophiothrix lineata* and *Callyspongia vaginalis*: A brittlestar-sponge cleaning symbiosis? Mar. Ecol. 5, 9–27. https://doi.org/10.1111/j.1439-0485.1984.tb00304.x

Hendler, G., Littman, B.S., 1986. The ploys of sex: relationships among the mode of reproduction, body size and habitats of coral-reef brittlestars. Coral Reefs 5, 31–42. https://doi.org/10.1007/BF00302169

Heron, S.F., Maynard, J.A., Van Hooidonk, R., Eakin, C.M., 2016. Warming Trends and Bleaching Stress of the World’s Coral Reefs 1985-2012. Sci. Rep. 6, 1–14. https://doi.org/10.1038/srep38402

Hoegh-Guldberg, O., Bruno, J.F., 2010. The Impact of Climate Change on the World’s Marine Ecosystems. Science 328, 49. https://doi.org/10.1126/science.1189930

Inoue, S., Kayanne, H., Yamamoto, S., Kurihara, H., 2013. Spatial community shift from hard to soft corals in acidified water. Nat. Clim. Chang. 3, 683–687. https://doi.org/10.1038/nclimate1855

Johnson, S.K., Hallock, P., 2020. A review of symbiotic gorgonian research in the western Atlantic and Caribbean with recommendations for future work. Coral Reefs 39, 239–258. https://doi.org/10.1007/s00338-020-01891-0

LaJeunesse, T.C., 2020. Zooxanthellae. Curr Biol 30:R1110–R1113. https://doi.org/10.1016/j.cub.2020.03.058

Lasker, H.R., Martínez-Quintana, Bramanti, L., Edmunds, P.J., 2020. Resilience of Octocoral Forests to Catastrophic Storms. Sci. Rep. 10, 1–8. https://doi.org/10.1038/s41598-020-61238-1

Leal, M.C., Berger, S.A., Ferrier-Pagès, C., Calado, R., Brandes, J., Frischer, M.E., Nejstgaard, J.C., 2014. Temporal changes in the trophic ecology of the asymbiotic gorgonian *Leptogorgia virgulata*. Mar. Biol. 161, 2191–2197. https://doi.org/10.1007/s00227-014-2496-5

Lenz, E.A., Bramanti, L., Lasker, H.R., Edmunds, P.J., 2015. Long-term variation of octocoral populations in St. John, US Virgin Islands. Coral Reefs 34, 1099–1109. https://doi.org/10.1007/s00338-015-1315-x

Lesser, M.P., 2011. Coral bleaching: causes and mechanisms, in: Coral Reefs: An Ecosystem in Transition. Springer, Dordrecht, pp. 1–552. https://doi.org/doi.org/10.1007/978-94-007-0114-4_23

Lombard, F., Boss, E., Waite, A.M., Uitz, J., Stemmann, L., Sosik, H.M., Schulz, J., Romagnan, J.B., Picheral, M., Pearlman, J., Ohman, M.D., Niehoff, B., Möller, K.O., Miloslavich, P., Lara-Lopez, A., Kudela, R.M., Lopes, R.M., Karp-Boss, L., Kiko, R., Jaffe, J.S., Iversen, M.H., Irisson, J.O., Hauss, H., Guidi, L., Gorsky, G., Giering, S.L.C., Gaube, P., Gallager, S., Dubelaar, G., Cowen, R.K., Carlotti, F., Briseño-Avena, C., Berline, L., Benoit-Bird, K.J., Bax, N.J., Batten, S.D., Ayata, S.D., Appeltans, W., 2019. Globally consistent quantitative observations of planktonic ecosystems. Front. Mar. Sci. 6. https://doi.org/10.3389/fmars.2019.00196

Mantelatto, M.C., Vidon, L.F., Silveira, R.B., Menegola, C., Rocha, R.M. da, Creed, J.C., 2016. Host species of the non-indigenous brittle star *Ophiothela mirabilis* (Echinodermata: Ophiuroidea): an invasive generalist in Brazil? Mar. Biodivers. Rec. 9, 1–7. https://doi.org/10.1186/s41200-016-0013-x

Mekhova, E.S., Martynov, A. V., Britayev, T.A., 2018. Host selection and host switching in *Gymnolophus obscura* – a symbiotic ophiuroid associated with feather stars (Crinoidea: Comatulida). Symbiosis 76, 313–320. https://doi.org/10.1007/s13199-018-0566-z

Mosher, C. V, Watling, L., 2009. Partners for life: A brittle star and its octocoral host. Mar. Ecol. Prog. Ser. 397, 81–88. https://doi.org/10.3354/meps08113

Norström, A. V., Nyström, M., Lokrantz, J., Folke, C., 2009. Alternative states on coral reefs: Beyond coral-macroalgal phase shifts. Mar. Ecol. Prog. Ser. 376, 293–306. https://doi.org/10.3354/meps07815

Ohtsuka, S., Kondo, Y., Sakai, Y., Shimazu, T., Shimomura, M., Komai, T., Yanagi, K., Fujita, T., Nishikawa, J., Miyake, H., Maran, B.A.V., Go, A., Nagaguchi, K., Yamaguchi, S., Dechsakulwatana, C., Srinui, K., Putchakarn, S., Mulyadi, Mujiono, N., Sutomo, Yusoff, F.M., 2010. *In-situ* observations of symbionts on medusae occurring in Japan, Thailand, Indonesia and Malaysia. Bull. Hiroshima Univ. Museum 2, 9–18.

Owen, D.P., Long, M.H., Fitt, W.K., Hopkinson, B.M., 2020. Taxon-specific primary production rates on coral reefs in the Florida Keys. Limnol. Oceanogr. 1–14. https://doi.org/10.1002/lno.11627

Pupier, C.A., Fine, M., Bednarz, V.N., et al, 2019. Productivity and carbon fluxes depend on species and symbiont density in soft coral symbioses. Sci Rep 9:. https://doi.org/10.1038/s41598-019-54209-8

Ribes, M., Coma, R., Gili, J.M., Svoboda, A., Julia, A., Parera, J., 2000. A “semi-closed” recirculating system for the *in situ* study of feeding and respiration of benthic suspension feeders. Sci. Mar. 64, 265–275. https://doi.org/10.3989/scimar.2000.64s1265

Rich, L.P., Dennis, M.M., Freeman, M.A., 2020. New record of the non-native *Ophiothela mirabilis* (Verrill 1867) in St. Kitts, West Indies. Adv Oceanogr Mar Biol 2, 2–6. https://doi.org/10.33552/AOMB.2020.02.000526

Richmond, R.H., 1993. Coral reefs: Present problems and future concerns resulting from anthropogenic disturbance. Integr. Comp. Biol. 33, 524–536. https://doi.org/10.1093/icb/33.6.524

Rodriguez, M.V.B., Segumalian, C.S., Lalas, J.A.A., Maningas, J.M.C., 2020. Octocorals outcompete scleractinian corals in a degraded reef. IOP Conf. Ser. Earth Environ. Sci. 420. https://doi.org/10.1088/1755-1315/420/1/012027

Roth, F., Wild, C., Carvalho, S., Rädecker, N., Voolstra, C.R., Kürten, B., Anlauf, H., El-Khaled, Y.C., Carolan, R., Jones, B.H., 2019. An *in situ* approach for measuring biogeochemical fluxes in structurally complex benthic communities. Methods Ecol. Evol. 10, 712–725. https://doi.org/10.1111/2041-210X.13151

Ruzicka, R.R., Colella, M.A., Porter, J.W., Morrison, J.M., Kidney, J.A., Brinkhuis, V., Lunz, K.S., MacAulay, K.A., Bartlett, L.A., Meyers, M.K., Colee, J., 2013. Temporal changes in benthic assemblages on Florida Keys reefs 11 years after the 1997/1998 El Niño. Mar. Ecol. Prog. Ser. 489, 125–141. https://doi.org/10.3354/meps10427

Schlichter, D., Svoboda, A., Kremer, B.P., 1983. Functional autotrophy of *Heteroxenia fuscescens* (Anthozoa: Alcyonaria): carbon assimilation and translocation of photosynthates from symbionts to host. Mar Biol 78, 29–38. https://doi.org/10.1007/BF00392968

Schröder, A., Persson, L., De Roos, A.M., 2005. Direct experimental evidence for alternative stable states: A review. Oikos 110, 3–19. https://doi.org/10.1111/j.0030-1299.2005.13962.x

Shick, J., Lesser, M., Jokiel, P., 1996. Effects of ultraviolet radiation on corals and other coral reef organisms. Glob. Chang. Biol. 2, 527–545.

Tsounis, G., Edmunds, P.J., Bramanti, L., et al, 2018. Variability of size structure and species composition in Caribbean octocoral communities under contrasting environmental conditions. Mar Biol 165, 1–14. https://doi.org/10.1007/s00227-018-3286-2

Tsounis, G., Rossi, S., Aranguren, M., Gili, J.M., Arntz, W., 2006. Effects of spatial variability and colony size on the reproductive output and gonadal development cycle of the Mediterranean red coral (*Corallium rubrum* L.). Mar. Biol. 148, 513–527. https://doi.org/10.1007/s00227-005-0100-8

Vollstedt, S., Xiang, N., Simancas-Giraldo, S.M., Wild, C., 2020. Organic eutrophication increases resistance of the pulsating soft coral *Xenia umbellata* to warming. PeerJ 2020, 1–16. https://doi.org/10.7717/peerj.9182

Wainwright, S.A., 1967. Diurnal activity of hermatypic gorgonians. Nature 216, 1041

Zhao, H., Yuan, M., Strokal, M., Wu, H.C., Liu, X., Murk, A.T., Kroeze, C., Osinga, R., 2021. Impacts of nitrogen pollution on corals in the context of global climate change and potential strategies to conserve coral reefs. Sci. Total Environ. 774, 145017. https://doi.org/10.1016/j.scitotenv.2021.145017