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INTERAÇÕES TRÓFICAS EM AMBIENTES RECIFAIS AO LONGO DE DIFERENTES ESCALAS ESPACIAIS

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

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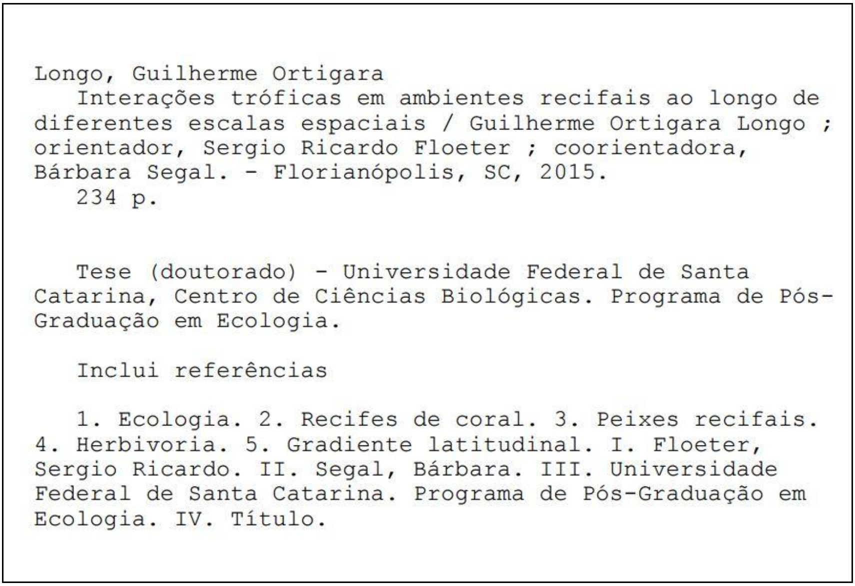

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"Interações tróficas em ambientes recifais ao longo de diferentes escalas espaciais"

Por

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Ao mar e aos ambientes recifais, pela inspiração
e persistência

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“Não sabendo que era impossível, foi lá e fez”
Jean Cocteau

RESUMO

Interações tróficas são fundamentais para a estrutura e funcionamento de ecossistemas, alterando padrões de densidade e biomassa de espécies de diferentes níveis tróficos. Atividades humanas podem afetar negativamente a estrutura e intensidade dessas interações, causando mudanças drásticas nos ecossistemas. Os ambientes recifais, por exemplo, têm sofrido uma variedade de impactos antrópicos (*e.g.*, sobrepesca, poluição), levando à perda de diversidade e processos ecossistêmicos críticos, sobretudo aqueles mediados por interações tróficas. Por exemplo, quando peixes herbívoros e ouriços foram experimentalmente removidos (cenário de sobrepesca) de recifes de coral, macroalgas rapidamente dominaram o recife. Nesses ambientes, a pressão alimentar dos peixes recifais sobre a comunidade bentônica é um bom modelo de interação trófica já que tem uma importância fundamental na estruturação das comunidades bentônicas. A intensidade e composição de interações tróficas podem ser influenciadas por múltiplos fatores ao longo de diferentes escalas espaciais, com consequências importantes para o funcionamento dos ecossistemas. Por exemplo: na escala do centímetro, a qualidade nutricional de uma presa ou suas defesas químicas moldam a identidade de seus predadores e intensidade de predação; na escala do habitat (centenas de metros), diferentes níveis de tolerância à condições abióticas extremas podem resultar em refúgios contra predação; em largas escalas espaciais (centenas de quilômetros), a temperatura pode interferir na demanada metabólica do predador, moldando suas interações tróficas; em escala latitudinal, esses fatores ecológicos se combinam a fatores biogeográficos, como diferentes composições taxonômicas. Esta tese apresenta diferentes abordagens sobre interações tróficas desde a escala do centímetro até a escala latitudinal, em quatro capítulos: (1) "*Can seaweed-coral competition make seaweeds more palatable?*", que aborda questões de competição direta entre corais e macroalgas e sua relação com herbivoria; (2) "*Between-habitat variation in benthic communities, reef fish assemblage and feeding pressure at the only atoll in South Atlantic: Rocas atoll, NE Brazil*", que avalia padrões das comunidades e processos ecológicos relacionados à sua estruturação em habitats com diferentes condições abióticas; (3) "*Herbivory drives large-scale spatial variation in reef fish trophic interactions*", que explora a intensidade e composição da pressão alimentar dos peixes recifais sobre as comunidades bentônicas, identificando espécies-chave para esses ecossistemas; e (4) "*Latitudinal gradients in reef fish trophic interactions on the benthos*", que investiga a variação latitudinal (34°N–27°S) da intensidade e composição das interações tróficas dos peixes sobre o bentos no Oceano Atlântico Ocidental, e sua relação com fatores ambientais (*e.g.*, temperatura) e contexto biogeográfico (*e.g.*, regiões biogeográficas). Observou-se que: (1) na escala do centímetro, a competição com corais pode tornar a alga mais susceptível à herbivoria; (2) na escala do habitat, a sinergia entre fatores abióticos e interações tróficas é determinante na estruturação de comunidades recifais (peixes e bentos); (3) em larga escala espacial, a contribuição desproporcional de alguns grupos, indicam que o funcionamento dos ambientes recifais é variável de acordo com condições locais específicas (*e.g.*, temperatura); e (4) em escala latitudinal, observou-se que embora recifes compartilhem os mesmos grupos funcionais, a identidade das espécies nesses grupos varia de acordo com o contexto biogeográfico. Esses múltiplos fatores ao longo de diferentes escalas espaciais demonstram a complexidade das interações tróficas e indicam abordagens possíveis de aplicação em conservação de processos críticos mediados por essas interações.

Palavras-chave: Pressão alimentar. Herbivoria. Recife de coral. Ouriços. Alelopatia. Gradiente latitudinal.

ABSTRACT

Trophic interactions are critical to the structure and functioning of ecosystems, altering density and biomass patterns of species across different trophic levels. Human activities have been negatively impacting these interactions, causing drastic changes in ecosystems. Reef habitats, for instance, have suffered a variety of human-related impacts (*e.g,* overfishing, pollution) leading to loss of biodiversity and critical ecosystem processes, particularly those mediated by trophic interactions. For example, when herbivorous fish and sea urchins were experimentally excluded from coral reefs (overfishing scenario) seaweeds rapidly overgrew corals. In these habitats, reef fish feeding pressure on the benthos is a good metric of trophic interaction because it is critically important to the structure of benthic communities. The intensity and composition of trophic interactions can be influenced by multiple factors across different spatial scales and have important consequences to ecosystem functioning. For example: at the scale of centimeters, prey nutritional quality or chemical defenses can shape the identity of predators and predation intensity; at the habitat scale (hundreds of meters), different tolerance levels to harsh abiotic conditions can result in predation refugees; at large spatial scales (hundreds of kilometers), temperature can interfere in the predator's metabolic demand and thus influencing its trophic interactions; at latitudinal scales (thousands of kilometers), these ecological factors meet biogeography, for example with different taxonomic composition. This thesis presents different approaches on trophic interactions in reef systems from the centimeter to the latitudinal scales, along four chapters: (1) "*Can seaweed-coral competition make seaweeds more palatable?*", encompassing direct coral-seaweed competition and its effect on herbivory by sea urchins; (2) "*Between-habitat variation in benthic communities, reef fish assemblage and feeding pressure at the only atoll in South Atlantic: Rocas atoll, NE Brazil*", on patterns in reef fish and benthic assemblages and ecological processes associated to its structure in habitats with different abiotic conditions; (3) "*Herbivory drives large-scale spatial variation in reef fish trophic interactions*", exploring the intensity and composition of reef fish feeding pressure on the benthos and identifying key groups to the studied ecosystems; and (4) “*Latitudinal gradients in reef fish trophic interactions on the benthos*”, exploring the latitudinal variation (34°N–27°S) in the intensity and composition of reef fish feeding pressure on the benthos in the Western Atlantic Ocean, and its relation to environmental factos (*e.g.*, temperature) and biogeographic context (*e.g.*, biogeographic regions). The main outcomes are: (1) at the scale of centimeters, competition with corals can enhance seaweed’s susceptibility to herbivory by sea urchins; (2) at the habitat scale, the synergy between abiotic conditions and trophic interactions is critical to structure reef communities (fish and benthos); (3) at large spatial scales, the disproportional contribution of some groups indicate that the functioning of the reefs are variable and dependent on specific local conditions (*e.g.*, temperature). And (4) at the latitudinal scale, it was observed that although reefs in different regions share the same functional groups, species within these groups vary according to the biogeographic context. These multiple factors across different spatial scales demonstrate the complexity of trophic interactions and indicate potential approaches to be applied in the conservation of critical processes they mediate.

Keywords: Feeding pressure. Herbivory. Coral reef. Sea urchin. Alellopathy. Latitudinal gradient.

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INTRODUÇÃO GERAL

Interações tróficas são fundamentais para a estrutura e funcionamento de ecossistemas, alterando padrões de densidade e biomassa de espécies de diferentes níveis tróficos (Paine 1980; Duffy 2002). Atividades humanas afetam negativamente a intensidade e composição dessas interações, causando mudanças drásticas nos ecossistemas como a perda de diversidade, mudanças na complexidade estrutural e condições abióticas como temperatura e umidade (Estes et al. 2011). Um dos exemplos mais clássicos da importância das interações tróficas vem de experimentos em costões rochosos, onde a exclusão da estrela-do-mar *Pisaster ochraceus* provocou uma diminuição na riqueza de espécies compondo a comunidade (Paine 1992). Este fenômeno foi atribuído à perda das interações tróficas dessa espécie, que através da predação de diversos organismos, favorecia maior co-ocorrência e riqueza de espécies na comunidade. Exemplos semelhantes emergem de outros ecossistemas marinhos, mas também de sistemas terrestres e dulcícolas onde a remoção de predadores de topo, geralmente em decorrência de ações humanas, ocasionou mudanças drásticas nesses ambientes (Estes et al. 2011).

Em ambientes marinhos, a herbivoria têm sido amplamente reconhecida entre as principais interações tróficas críticas (Poore et al. 2012) para a estrutura e o funcionamento de diferentes sistemas (*e.g.*, recifes rochosos – Sala & Bouderesque 1997; recifes de coral – Mumby 2006; florestas de laminárias – Carter, Van Blaricom & Allen 2007). Uma meta-análise explorando a importância relativa da herbivoria (*i.e.*, efeito descendente ou "*top-down*") e o aporte de nutrientes (*i.e.*, efeito ascendente ou "*bottom-up*") na estruturação das comunidades bentônicas marinhas indicou que a herbivoria pode exercer um impacto maior sobre macroalgas tropicais e angiospermas que o aporte de nutrientes (Burkepile & Hay 2006). Quando peixes herbívoros foram excluídos de recifes de coral no Caribe e no Pacífico, macroalgas rapidamente dominaram o ambiente, revelando um forte efeito descendente ("*top-down*") exercido pelos herbívoros (Lewis 1986; McClanahan et al. 2003; Bellwood et al. 2006; Hughes et al. 2007). De maneira análoga, eventos de mortalidade em massa e consequente declínio populacional do ouriço *Diadema antillarum* no Atlântico Ocidental (particularmente no Caribe entre 1983-1984) foi relacionado a um posterior aumento drástico nas populações de macroalgas folhosas e uma redução na cobertura de corais; enquanto que no Atlântico Oriental uma superpopulação desta espécie levou à transformação de recifes em verdadeiros desertos (“*barrens*”; Tuya et al. 2005). Dessa forma, em ambientes recifais, peixes herbívoros e ouriços são considerados críticos para a manutenção do balanço entre corais e macroalgas.

Os ambientes recifais em todo o globo têm sofrido uma variedade de impactos antrópicos, incluindo degradação de habitat, sobrepesca, poluição costeira, introdução de espécies exóticas invasoras e aquecimento global, levando à perda de diversidade e processos ecossistêmicos (Hughes 1994; Bellwood et al. 2004; Jackson et al. 2014). A sobrepesca de predadores de topo (*e.g.*, tubarões) e peixes herbívoros (*e.g.*, budiões e cirurgiões), bem como o declínio populacional de ouriços (*e.g.*, *D. antillarum*) resultou em mudanças drásticas na estruturação dos recifes prejudicando organismos bioconstrutores como corais e algas calcárias, favorecendo o aumento da cobertura de algas epilíticas e macroalgas frondosas (Bruno et al. 2009; Estes et al. 2011; Jackson et al. 2014). O declínio global na cobertura de corais e aumento na cobertura de macroalga favorece a competição coral-macroalga em áreas onde as algas não são mais controladas por herbívoros (Hughes 1994; Mumby & Steneck 2008; Bruno et al. 2009).

Na escala do centímetro, macroalgas podem competir diretamente com corais através de abrasão, sombreamento, alelopatia, sobrecrescimento, ou ainda através de efeitos indiretos como atuando como vetores de patógenos, predadores ou liberando compostos que desestabilizam a microbiota associada aos corais (McCook et al. 2001; Nugues et al. 2004; Smith et al. 2006; Rasher et al. 2011; Nelson et al. 2003; Wolf & Nugues 2013; Rasher & Hay 2014). Enquanto a habilidade dos herbívoros controlarem as populações de macroalgas depende principalmente de uma combinação de: (1) características das algas (*e.g.*, defesas e valor nutricional); e (2) diversidade, *i.e.*, diferentes tolerâncias à defesas anti-herbivoria, preferências alimentares e estratégias nutricionais (Rasher et al. 2013). Esta natureza dinâmica das interações coral-alga-herbívoros, bem como custos e benefícios envolvidos têm recebido pouca atenção (Diaz-Pulido et al. 2009; Venera-Ponton et al. 2011; Bonaldo & Hay 2014; Rasher & Hay 2014). Essas informações, no entanto, podem ser fundamentais para entender a dominância dos recifes de corais por macroalgas e basear ações de manejo. Por exemplo, trabalhos recentes demonstraram que algas que utilizam compostos alelopáticos para competir com corais tem suas defesas químicas anti-herbivoria comprometidas, ficando mais susceptíveis à herbivoria por peixes (Rasher & Hay 2014; Pacífico) e por ouriços (Longo & Hay 2015; Caribe). Se esta relação for comum, então outras macroalgas com potencial alelopático podem também se tornar mais palatáveis ao competir com corais, ressaltando a importância de compreender as nuances das interações corais-macroalgas-herbívoros nas bordas das colônias de corais onde a competição (especialmente química) ocorre com maior intensidade (Rasher et al. 2011; Andras et al. 2012; Dixson & Hay 2012). Aspectos importantes dessas interações podem estar ocorrendo mais frequentemente na escala dos milímetros ou centímetros nas bordas dos corais, uma escala espacial ainda insuficientemente investigada.

Na escala de habitat (*i.e.*, dezenas ou centenas de metros), sabe-se que diferenças nos fatores abióticos como exposição a ondas, correntes de marés, sedimentação e nutrientes podem afetar diretamente a composição das comunidades bentônicas (Hughes & Connel 1999; Williams et al. 2003). De maneira similar, as assembleias de peixes também respondem a diferenças na hidrodinâmica de acordo com a habilidade de natação de cada espécie (Bellwood & Wainwright 2001; Fulton & Bellwood 2005), o que acaba influenciando sua atividade alimentar (Krajewski et al. 2011). Na grande barreira de corais, por exemplo, houve uma maior remoção de macroalgas por peixes herbívoros em ambientes rasos expostos (maior hidrodinâmica) em comparação à ambientes menos expostos, independente da profundidade Hoey & Bellwood 2010). Portanto, a contribuição relativa entre processos ecológicos (*e.g.*, interações tróficas) e fatores abióticos (*e.g.*, hidrodinamismo) para a estruturação das comunidades recifais podem ter efeitos contexto-dependentes, variando dentro e entre habitats (Menge & Sutherland 1987). Compreender a contribuição relativa desses componentes é fundamental para que estratégias de manejo possam incluir processos ecológicos críticos e ambientes com condições abióticas diversas (Bellwood et al. 2004; McClanahan & Karnauskas 2011).

Quantificar diretamente interações tróficas (*e.g.*, taxas de interação), como herbivoria e predação, em vez de realizar inferências baseadas em riqueza e abundância de espécies é desafiador (Pennings & Silliman 2005; Freestone et al. 2011). Como resultado, grande parte da informação sobre interações tróficas em ambientes marinhos e sobretudo recifais provém de estudos focados na remoção de macroalgas ou inferências baseadas em riqueza e abundância de herbívoros, em geral desconsiderando outras interações tróficas com o bentos nesses ambientes (*e.g.*, predação de invertebrados móveis e sésseis; Ferreira et al. 2004; Floeter et al. 2005; Bennett & Bellwood 2011; Cheal et al. 2013). Entretanto, os efeitos *per capita* entre as espécies em vez de diferenças de riqueza e abundância podem estar gerando mudanças nas forças de interação que precisam ser compreendidas (Pennings & Silliman 2005). Além disso, outras interações tróficas importantes, além da herbivoria, são frequentemente negligenciadas. Portanto, a pressão alimentar dos peixes recifais sobre a comunidade bentônica (*sensu* Longo et al. 2014) é um bom modelo para comparações em larga escala, já que essas interações têm uma importância fundamental na estruturação das comunidades bentônicas, levando em conta interações como herbivoria e a predação de crustáceos meso-podadores (Lewis 1986; Duffy & Hay 2000; Ceccarelli, Jones & McCook 2001; Kramer et al. 2013), além de poder ser observada e quantificada em ambientes recifais ao longo de grandes amplitudes geográficas.

Comparações de interações tróficas ao longo de escalas geográficas (centenas ou milhares de quilômetros) podem prover uma melhor compreensão de sua importância nos ecossistemas, beneficiando-se de gradientes naturais, por exemplo, riqueza de espécies ou temperatura (Pennings & Silliman 2005). Ainda assim, a maior parte dos estudos de interações tróficas em ampla escala espacial, tanto em ambientes terrestres quanto marinhos, são focados em herbivoria e apresentam resultados pouco conclusivos (Moles et al. 2011; Poore et al. 2012; para exceção ver Freestone et al. 2011). Além da intensidade das interações, mudanças na identidade das espécies interagindo podem afetar a produtividade e estabilidade de teias alimentares (Worm & Duffy 2003). Por exemplo, insetos de diferentes guildas produziram diferentes níveis de herbivoria e danos aos produtores ao longo de um gradiente latitudinal (Andrew & Hughes 2005). Essas mudanças geralmente ocorrem ao longo de amplas escalas geográficas, ressaltando a necessidade de estudos que quantifiquem interações tróficas através de métodos padronizados em múltiplos locais ao longo de um gradiente latitudinal (Pennings & Silliman 2005).

Uma predição ecológica clássica defende que a intensidade de interações bióticas diminui com o aumento da latitude (revisado por Schemske et al. 2009). Por exemplo, um estudo recente ao longo de um gradiente de 32^{o} de latitude em bancos de angiospermas marinhas demonstrou que a predação sobre comunidades de organismos sésseis marinhos e seus efeitos sobre a riqueza de espécies eram mais intensos em regiões tropicais que em regiões temperadas (Freestone et al. 2011). No entanto, existe ainda um intenso debate sobre esta predição, uma vez que existem resultados contrastantes para diferentes interações (*e.g.*, herbivoria, parasitismo, predação) e que a maior parte das abordagens serem meta-análises ou com escopo latitudinal limitado (Schemske et al. 2009; Moles et al. 2011; Poore et al. 2012; Salazar & Marquis 2012).

Estudos de interações tróficas em diferentes escalas espaciais, desde a escala do centímetro até a escala latitudinal, podem permitir a identificação de espécies e grupos funcionais críticos para os ecossistemas. Consumidores que impactam o ecossistema desproporcionalmente à sua abundância, por exemplo, podem ter um papel central na estruturação e funcionamento dos sistemas (Power et al. 1996). Uma vez que a redução das interações tróficas dominantes pode levar a declínios na biodiversidade, identificar essas espécies centrais e os processos ecológicos mediados por elas pode ser importante para orientar esforços de manejo e conservação (Paine 1992; Duffy 2002; Green & Bellwood 2009).

Esta tese apresenta diferentes abordagens sobre interações tróficas em ambientes recifais, desde a escala do centímetro até a escala latitudinal, em quatro capítulos distintos (Fig. 1). No primeiro capítulo, intitulado "*Can seaweed-coral competition make seaweeds more palatable?*" são abordadas questões de competição direta entre corais e macroalgas através de interações de contato, e de que forma este contato pode interferir no processo de herbivoria. O segundo capítulo, intitulado "*Between-habitat variation in benthic communities, reef fish assemblage and feeding pressure at the only atoll in South Atlantic: Rocas atoll, NE Brazil*", explorou diferenças naturais de condições abióticas entre habitats, principalmente em relação ao hidrodinamismo, avaliando padrões das comunidades e processos ecológicos relacionados à sua estruturação. No terceiro capítulo, intitulado "*Herbivory drives large-scale spatial variation in reef fish trophic interactions*", explorou-se em três locais da costa brasileira compreendendo um intervalo de 10^{o} de latitude (Abrolhos-BA, Arraial do Cabo-RJ e Arvoredo-SC) a intensidade e composição da pressão alimentar dos peixes recifais sobre as comunidades bentônicas, sua relação com a abundância e biomassa de peixes, identificando espécies centrais para esses ecossistemas. O quarto e último capítulo resulta do maior esforço de coleta de dados padronizados de interações tróficas conhecido, compreendendo 16 localidades ao longo de 60° de latitude entre o estado da Carolina do Norte nos Estados Unidos (latitude 34^{o}N) até Santa Catarina, Brasil (latitude 27^{o}S). Intitulado "*Latitudinal gradients in reef fish trophic interactions on the benthos*", este trabalho aborda questões ecológicas centrais como se a intensidade de interações tróficas diminui com o aumento da latitude em ambos os sentidos do globo; como a composição dessas interações muda ao longo do gradiente em termos de grupos funcionais e espécies, investigando as relações com fatores ecológicos e biogeográficos.

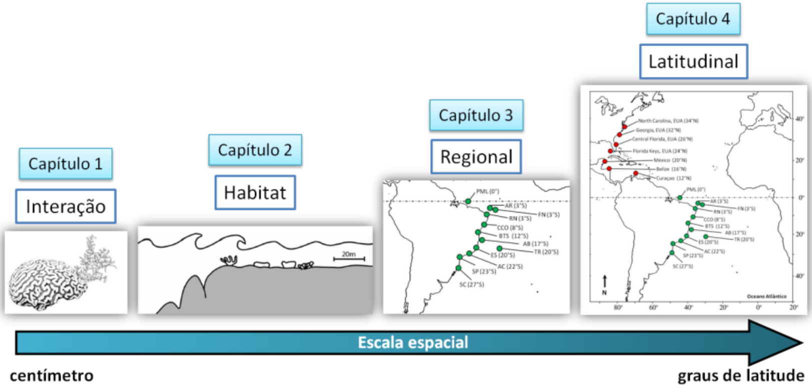

Figura 1. Estrutura da tese que, através de estudos que abordam interações tróficas em ambientes recifais, transita entre a escala do centímetro e a escala latitudinal.

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CAPÍTULO 1

Does seaweed-coral competition make seaweeds more palatable?

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Does seaweed-coral competition make seaweeds more palatable?

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Abstract

Seaweed-coral interactions are increasingly common on modern coral reefs, but the dynamics, processes, and mechanisms affecting these interactions are inadequately understood. We investigated the frequency and effect of seaweed-coral contacts for common seaweeds and corals in Belize. Effects on corals were evaluated by measuring the frequency and extent of bleaching when contacted by various seaweeds, and effects on a common seaweed were evaluated by assessing whether contact with coral made the seaweed more palatable to the sea urchin *Diadema antillarum*. Coral-seaweed contacts were particularly frequent between *Agaricia* corals and the seaweed *Halimeda opuntia*, with this interaction being associated with coral bleaching in 95% of contacts. Pooling across all coral species, *H. opuntia* was the seaweed most commonly contacting corals and most frequently associated with localized bleaching at the point of contact. Articulated coralline algae, *Halimeda tuna* and *Lobophora variegata* also frequently contacted corals and were commonly associated with bleaching. The common corals *Agaricia* and *Porites* bleached with similar frequency when contacted by *H. opuntia* (95 and 90%, respectively), but *Agaricia* experienced more damage than *Porites* when contacted by articulated coralline algae or *H. tuna*. When spatially paired individuals of *H. opuntia* that had been in contact with *Agaricia* and not in contact with any coral were collected from the reefs offered to *Diadema antillarum*, urchins consumed about 150% more of thalli that had been competing with *Agaricia*. Contact and non-contact thalli did not differ in nutritional traits (ash-free-dry-mass, C or N concentrations), suggesting that *Halimeda* chemical defenses may have been compromised by coral-algal contact. If competition with corals commonly enhances seaweed palatability, then the dynamics and nuances of small-scale seaweed-coral-herbivore interactions at coral edges is deserving of greater attention in that such interactions could scale-up to have important consequences for coral resilience and the persistence of reef structure and function.

Introduction

The global decline in coral cover and increase in macroalgal cover is augmenting the frequency of coral-seaweed competition in areas where seaweeds are no longer controlled by herbivores (Hughes 1994; Mumby & Steneck 2008; Bruno et al. 2009; Bonaldo & Hay 2014). Seaweeds may compete with corals via overgrowth, shading, abrasion, allelopathy, and via indirect effects such as vectoring coral pathogens and predators or releasing compounds that destabilize the coral's beneficial microbiome (McCook et al. 2001; Nugues et al. 2004; Smith et al. 2006; Rasher et al. 2011; Barott & Rohwer 2012; Nelson et al. 2013; Wolf & Nugues 2013; Rasher & Hay 2014).

The outcomes of coral-seaweed contacts are dependent on the pair of interactors, both because corals differ in their ability to compete with seaweeds and seaweeds differ in the strength and mechanisms of their impact on corals (Jompa & McCook 2003; Nugues & Bak 2006; Rasher et al. 2011; Bonaldo & Hay 2014). As an example, some chemically rich seaweeds are allelopathic to corals with seaweeds differing in allelopathic potency and corals differing in their resistance to these effects (Rasher et al. 2011; Bonaldo & Hay 2014). However, these interactions are not static, seaweeds may also induce greater allelopathic potency following contact with a competing coral (Rasher & Hay 2014) and some corals chemically signal mutualistic fishes to remove allelopathic seaweeds contacting the coral (Dixson & Hay 2012).

The dynamic nature of seaweed-coral interactions and the costs and benefits involved in these interactions are not well investigated (Diaz-Pulido et al. 2009; Venera-Ponton et al. 2011; Bonaldo & Hay 2014; Rasher & Hay 2014) but could be critical for understanding coral to macroalgal phase shifts and for informed management of coral reefs. For seaweeds using allelopathic chemicals to damage corals, enhancing allelopathic potency when in contact with corals could compromise the seaweed's anti-herbivore defenses and leave the seaweed more susceptible to herbivores (Rasher & Hay 2014). However, if the same bioactive metabolites serve both as anti-herbivore defenses and as allelopathic compounds, then seaweeds inducing allelopathy could be even more herbivore resistant and even less likely to be removed by natural biotic processes.

A recent investigation on a Pacific coral reef demonstrated that the allelopathic red seaweed *Galaxaura filamentosa* induces more potent allelopathy following contact with the coral *Porites cylindrica*. However, this induced allelopathy co-occurred with a decline in the seaweed's anti-herbivore chemical defenses, demonstrating that: i) this seaweed produces different compounds for allelopathy versus anti-herbivore defense; ii) the deployment of these compounds is dynamic and context dependent; and iii) there may be a trade-off between chemically-mediated competitive ability and defense against consumers (Rasher & Hay 2014). If such a trade-off is common, then chemically-rich seaweeds competing with corals may be more palatable than those not competing. Hence, critical aspects of seaweed-herbivore-coral interactions that are recognized as important for reef structure and function may be occurring most frequently at spatial scales of millimeters or centimeters at coral borders, a spatial scale that has not been sufficiently investigated.

If interactions at small spatial scales near coral borders are of overlooked importance, they might be especially relevant on Caribbean coral reefs where coral loss has been especially great (Gardner et al. 2003; Bruno et al. 2009) and where seaweed-coral interactions appear to have shifted more strongly in favor of seaweeds (Roff & Mumby 2012). Numerous reefs in the Caribbean are currently dominated by chemically-rich seaweeds such as species of *Dictyota*, *Halimeda* and *Lobophora* (Hughes 1994, Shulman & Robertson 1996, McClanahan et al. 1999, Edmunds 2002). With this shift to chemically-rich seaweeds, contacts between seaweeds and corals became more common, increasing the importance of understanding the nuances of seaweed-herbivore-coral interactions at coral edges where seaweeds contact corals and where competition (especially chemically-mediated competition) may be most intense (Rasher et al. 2011, Andras et al. 2012, Dixson & Hay 2012).

Our goals in this study were to: (i) determine the most common seaweeds and corals physically interacting via contact on a reef in Belize, (ii) determine how frequently seaweed-coral contacts were associated with coral bleaching; (iii) compare the effects of different seaweeds on various corals; and (iv) determine whether coral-seaweed contacts affected the palatability to herbivores of a common seaweed, and whether this might occur due to changes in seaweed nutritional value or via other mechanisms.

Materials and methods

Study area

This study was conducted at Curlew Bank, Belize (16^{o}46$'$N, 88^{o}04$'$W), a part of the Mesoamerican Barrier Reef System that runs between Mexico and Honduras (Carter & Sedberry 1997). We investigated interactions in both a shallow area (3-6m; consisting of patchy coral formations, mainly colonies of *Agaricia tenuifolia* and *Porites astreoides,* separated by flat areas of sand, coral rubble and octocorals) and a deeper area (10-12m; consisting of patchy coral formations, mainly *P. astreoides*, *Orbicella* spp. and *Agaricia* spp., separated by sand, coral rubble, and a dense cover of gorgonians). Prominent seaweeds in the shallow area were *Halimeda* spp., articulated coralline algae, and filamentous algal turfs while in the deep area *Lobophora variegata*, *Sargassum* sp. and *Halimeda* spp. were most common.

Surveys of seaweed-coral contacts

The frequency of seaweed-coral contacts was assessed with 20 m length video transects (N = 12 on the shallow reef; N = 18 on the deeper reef). Transects were spaced 2-4 m from each other (with no overlap of surveyed area) and every 2 meters colonies of the corals *Agaricia*, *Pseudodiploria*, *Favia*, *Meandrina*, *Montastraea*-*Orbicella* (*M. cavernosa* and species of the former *M. annularis* complex), *Porites* and *Siderastrea* were carefully investigated if they occurred within 1 meter from each side of the transect tape (as in Barott et al. 2012). These colonies were video recorded from the top and from around the edge to assess the seaweed-coral contacts and determine if contacts were associated with coral bleaching at the site of contact. When contacts occurred, seaweeds were pulled back from the coral to look for bleaching in areas of contact. Bleaching was noted because it is visually obvious and was a local response immediately adjacent to the area of algal contact; it can be assessed quickly in the field and is well correlated with the coral’s photosynthetic efficiency (Rasher & Hay 2010, Rasher et al. 2011). Seaweeds were identified to the lowest taxonomic level possible from the videos. The extent of seaweed-coral contacts was evaluated using a top view picture of each colony with a scale of known size, obtained from the videos. These images were analyzed with the software Image J (Abramoff et al. 2004) to determine the perimeter and area of contacts relative to the total perimeter and area of the colony (*i.e.* the proportion of coral perimeter and proportion of coral area in contact with seaweed).

Palatability trials

To evaluate if coral contact affected seaweed palatability, we collected specimens of the green alga *Halimeda opuntia* growing in contact with the coral *Agaricia tenuifolia* and a separate nearby *H. opuntia* (within 1-2 m) not in contact with any coral or other macro-organism. These species were chosen because they were both abundant and were the most common seaweed-coral pair contacting each other on the reefs. Individuals of the sea urchin *Diadema antillarum* with ≥ 10 cm test diameters (i.e. not including the spines) were collected from a depth of about 1.5m in the lagoon behind the Smithsonian’s Carrie Bow Cay Marine Station (16^{o}48$^{'}$N, 88^{o} 04$^{'}$W). Sea urchins and seaweeds were collected from different locations because *D. antillarum* were uncommon on the fore-reef. We did however observe a few *D. antillarum* co-occurring with *H. opuntia* and *A. tenuifolia* on the reef sites we investigated. Additionally, prior to the large-scale die-off of *D. antillarum* in the early 1980s, *D. antillarum* were common on many reef slopes throughout the Caribbean, with densities varying from less than one to as many as a hundred individuals per square meter; their feeding influenced algal abundance, distribution and productivity, coral recruitment, and bioerosion, and they commonly co-ocurred with *Agaricia* and *Halimeda* species (Hay 1984; Lewis 1986; Lessios 1988).

In the presence of predators, they aggregated around corals as a refuge from attack (Carpenter 1984) and thus potentially concentrated feeding near coral edges.

Both seaweeds and sea urchins were brought into the lab and held overnight in separate tanks with constant sea water flow and exposed to natural day-night cycles from the adjacent windows. The following day, clumps of *H. opuntia* that had been in contact with *Agaricia* and not in contact with any corals were divided into similar sized portions (~5cm height), simultaneously spun in a salad spinner to remove excess water, and wet-weighted. Care was taken to choose clean individuals or to carefully remove epiphytes and fauna associated with the seaweeds before using them in feeding trials.

For feeding trials, one pre-weighed thallus of *H. opuntia* that had been in contact with *Agaricia* was paired with a pre-weighed thallus that had not been in contact, these were each cable tied to a mesh grid, presented to an individual urchin in a 8 liter container of flow-through seawater (N = 25). Equivalent portions of these same individual seaweeds were placed in a similar, adjacent container (without an urchin) to control for changes in mass unrelated to urchin consumption. Dividing the same seaweed clump in two pieces ensured that parts of the same seaweed were used in the paired trials (with and without urchins) minimizing individual variance in traits that might affect mass change (*e.g.* growth or respiration rates). Replicates were checked every two hours and ended within 48h or as soon as we noticed 50% consumption of either thallus in a replicate. When a replicate ended, seaweeds, and their paired controls, were spun and weighted following the same procedures used to initiate the experiment. Mass consumed was calculated using the formula [Ti x (Cf/Ci)] – Tf, where T_i and T_f were the initial and final masses (respectively) of the seaweed offered to sea urchins and C_i and C_f the initial and final masses (respectively) of the paired control without urchins (Rasher & Hay 2014).

Seaweed nutritional value

Samples of *H. opuntia* both in contact and not in contact with the coral *A. tenuifolia* were frozen after having any epiphytes or associated fauna carefully removed (N = 10 of each type). In the lab, samples were dried to a constant mass at 60°C for 48h, ground to a fine powder, divided in two portions, and one portion acidified with 10% HCL to remove carbonate. The non-carbonate carbon and nitrogen concentrations were obtained from acidified and unacidified samples, respectively, using an NC2500 elemental analyzer (Carlo Erba Strumentazione, Milan, Italy) interfaced to a Micromass Optima (Micromass LLC, Manchester, UK) continuous-flow isotope ratio mass spectrometer (CF-IRMS). Ash-free-dry-mass of non-acidified samples were obtained using aliquots from treatment and control samples that were dried, weighted, ashed at 450°C for 4h, and re-weighted to obtain percent ash-free-dry-mass.

Data analysis

When data met the assumption of homogeneity of variances (assessed with Levene's test), or could be made to do so via transformation, we employed parametric analyses. When transformed data still violated this assumption, we used non-parametric analyses on non-transformed data. Differences in the frequency of contacts (response variable) between coral genera (grouping variable) were assessed separately for shallow and deep areas with the non-parametric Kruskal-Wallis test. Differences in the frequency of contacts associated with bleaching (response variable) between coral genera (grouping variable) were tested with a one-way ANOVA on square-root transformed data for the shallow areas of the reef, while data for the deep area did not require transformation. Similar procedures were used to investigate differences in the frequency of contacts and contacts associated with bleaching (response variables) by seaweed (grouping variable). A Kruskal-Wallis test was used for the frequency of contacts (response variable) in both shallow and deep areas (grouping variable), and for the frequency of contacts associated with bleaching in the deep area, while a one-way ANOVA on square-root transformed data was used for this response variable in the shallow area.

The extent of seaweed-coral contacts (area and perimeter; response variables) between coral genera (grouping variable) and depth (grouping variable) was investigated using a two-way ANOVA on square-root transformed data, run separately for area in contact and perimeter in contact. A binomial logistic regression model was used to compare the proportion of contacts associated with bleaching (response variable; yes or no) for the most common corals (*Agaricia* and *Porites*), accounting for the interaction between corals (fixed factors) and seaweeds (random factors). Only seaweeds with more than two observations per coral species were included in this test.

Differences in the consumption of *H. opuntia* (response variable) that had been in contact and not in contact with *A. tenuifolia* (grouping variables) were assessed with a paired t-test. Differences in seaweed nutritional value (ash-free-dry-mass, carbon and nitrogen concentrations; response variables) between thalli that had been in contact or not in contact with coral (grouping variables) were assessed using t-tests.

Results

Frequency, extent and outcomes of seaweed-coral contacts

On the shallow reef, 95% of *Agaricia* colonies were in contact with some species of macroalgae, and 80% of these contacts were associated with localized coral bleaching (Fig. 1). For *Porites*, *Montastraea-Orbicella*, and *Siderastrea*, 21-44% were in contact with seaweeds and 25-50% of these contacts resulted in localized bleaching. Contact frequency was significantly higher for *Agaricia* than for any other coral (Kruskal-Wallis, $p < 0.001$; Fig. 1a). On the deeper reef, seaweeds were in contact with 61-65% of *Agaricia*, *Porites,* and *Montastraea-Orbicella* colonies (Fig. 1b). Contact frequency ranged from 31-39% for *Siderastrea* and *Meandrina* and from 10-17% for *Favia* and *Pseudodiploria*. Contact frequencies were significantly higher for *Agaricia*, *Porites,* and *Montastraea-Orbicella* than for *Meandrina, Favia,* or *Pseudodiploria,* with *Siderastrea* being intermediate between these groups (Kruskal-Wallis, $p < 0.001$; Fig. 1b). On both the deep and shallow reef, 42-83% of *Agaricia* or *Porites* colonies in contact with seaweeds were bleached at points of contact (Fig. 1c and d).

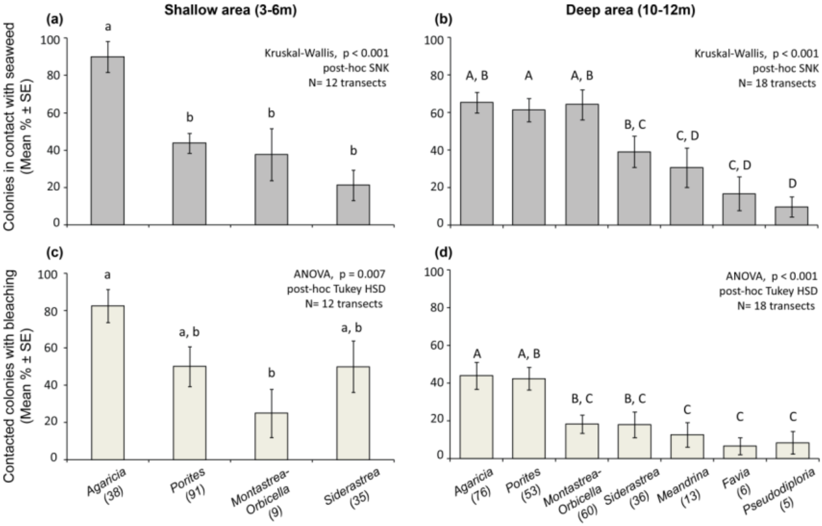

Figure 1 Frequency of contacts with seaweeds by coral genera (a and b) and frequency of contacts associated with bleaching by coral genera (c and d) in transects for the shallow and deep areas (right and left graphs, respectively). Lowercase letters above the bars indicate significant differences within the shallow area and uppercase within the deep area. Numbers below genus names indicate the total number of colonies assessed.

When evaluating the extent of seaweed contact with corals (area and perimeter in contact), rather than just frequency of contact, proportion of coral colony area in contact with seaweed varied with coral genera, but not with depth, and there was no interactions between coral genus and depth (Fig. 2a; two-way ANOVA, Genera: F = 5.077, p = 0.002; Depth: F = 0.030; p = 0.861; Interaction: F = 0.548; p = 0.649). For perimeter of the coral in contact with seaweed, shallow corals had more contact than deeper corals but this did not vary with coral genus and there was no genus by depth interaction (Fig. 2b; Depth: F = 4.444, p = 0.036; Genera: F = 0.662, p = 0.576; Interaction: F = 0.225, p = 0.879). Thus, in terms of the frequency of contact and bleaching (Fig. 1), the area in contact, or the perimeter in contact with seaweeds (Fig. 2), *Agaricia* and *Porites* were among the most common corals and the most impacted by seaweeds, with *Agaricia* being more frequently impacted than *Porites* (Fig. 1a).

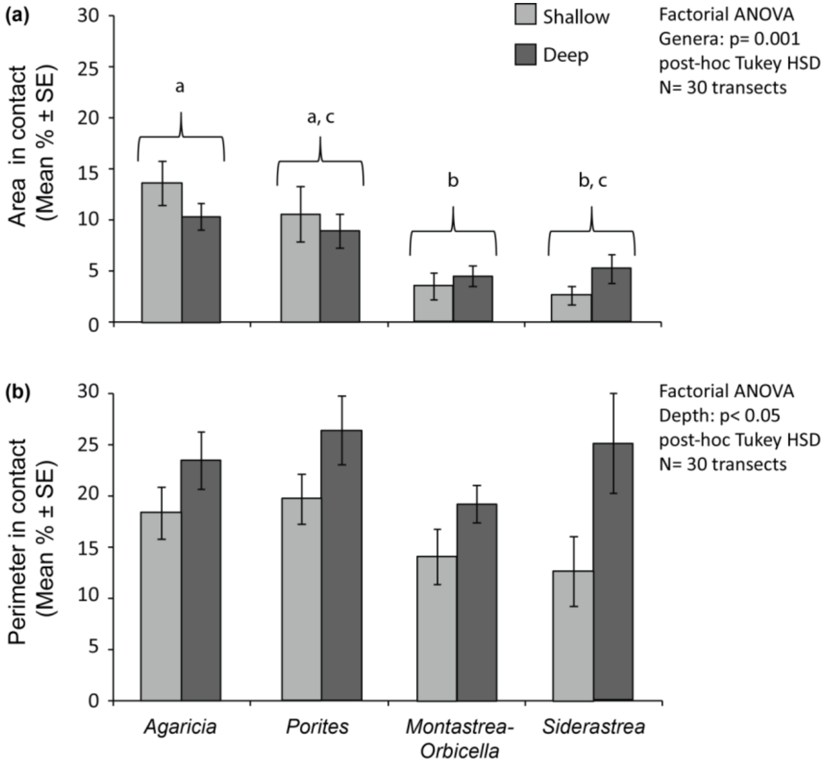

Figure 2 Proportion of area and perimeter in contact with seaweeds per coral genera and depth. Lowercase letters indicate post-hoc comparisons within the significant factor genera.

We identified 14 seaweed species or types commonly in contact with coral colonies (of any species). Five of these seaweeds occurred in the shallow area and 13 in the deeper area (we did not observe Gelidiacea in contact in deeper areas; Fig. 3). In the shallow area, 60% of corals were contacted by *Halimeda opuntia* and 96% of the contacted corals were bleached at the point of contact. Both frequency of contact with and bleaching of corals were greater for *H. opuntia* than for any other seaweed (Fig. 3a and c; Kruskal-Wallis, p < 0.001). In deeper areas, contacts were more evenly distributed among seaweeds (Fig. 3b). About 35% of corals were in contact with *Halimeda tuna*. About 20% were in contact with *Lobophora*, *Halimeda goreaui*, *H. opuntia*, and articulated coralline algae, while filamentous algae and *Sargassum* were in contact with 5-10% of corals. Another six seaweed species contacted corals, but only infrequently (Fig. 3b). Bleaching at the site of contact was common (50-80%) for corals contacting *Lobophora*, articulated corallines and *H. opuntia*. Bleaching occurred in about 20-30% of contacts with filamentous algae and *H. tuna*, and was infrequent for all other algae (less than 10%).

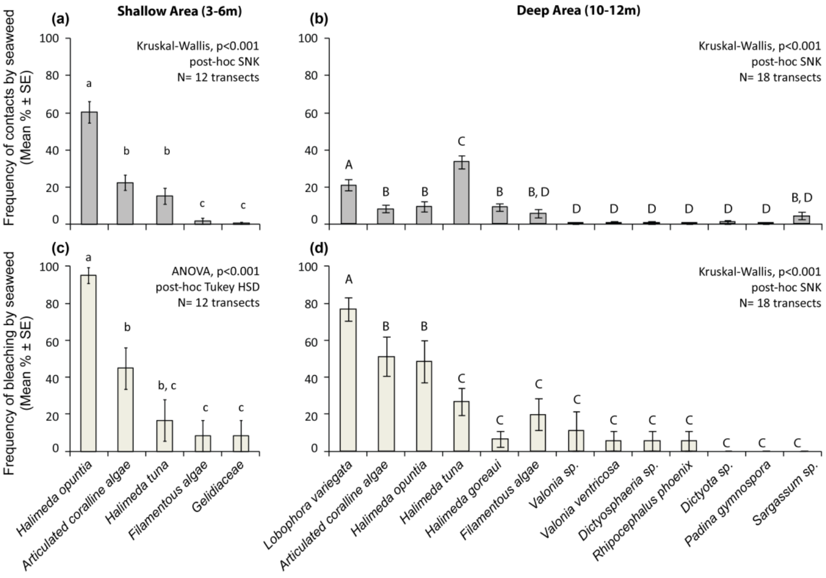

Figure 3 Frequency of contacts by seaweed (a and b) and frequency of contacts associated with bleaching by seaweed (c and d) in the shallow and deep areas (right and left graphs, respectively). Lowercase letters above the bars indicate significant differences within the shallow area and uppercase within the deep areas.

Restricting the comparisons to *Agaricia* and *Porites* - the two most common and most contacted corals in terms of area contacted (see Fig. 1 and Fig. 3), *H. opuntia* was the most frequent seaweed to contact both genera on the shallow reef (68% and 25%, respectively; Fig. 4a and b). On the deeper reef, seaweed contact with corals was more evenly distributed across seaweed species for *Agaricia*, while *H. tuna* and *Lobophora variegata* contacts with *Porites* were the most frequent interactions (42 and 43%, respectively; Fig. 4c and d). Contacts of both corals with each of the three species of *Halimeda* were frequent, ranging from 11-43% across all coral genera-*Halimeda* species pairings (Fig. 4c and d).

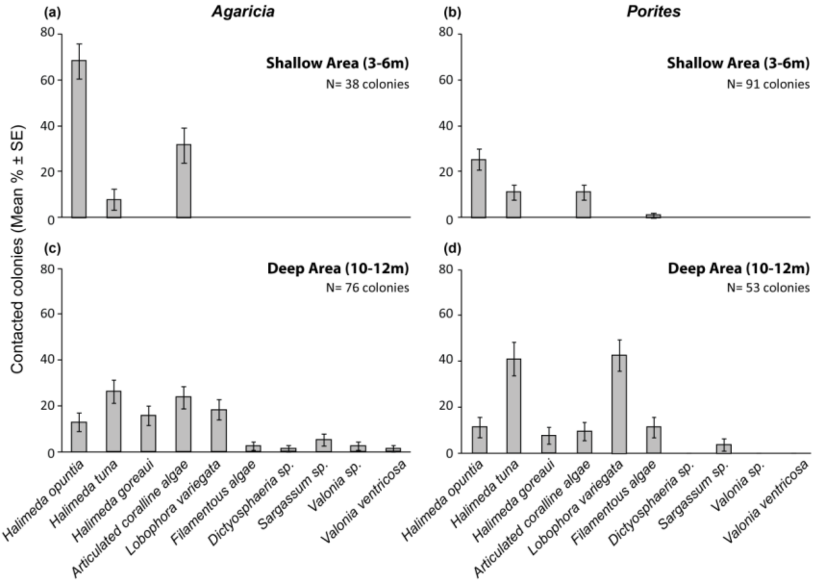

Figure 4 Proportion of contacted colonies for the two most common coral genera, *Agaricia* and *Porites,* by seaweed in the shallow and deep area (top and bottom graphs, respectively).

Contact outcomes differed as a function of coral and seaweed species pairings (Logistic Regression, Interaction $p < 0.001$, Seaweed $p < 0.001$; Coral $p = 0.01$; Table 1). This signal was generated by the differential effects of articulated coralline algae and *H. tuna*, both of which bleached *Agaricia* more frequently than *Porites* colonies (83 and 47%; 57 and 38%; respectively). Contacts with *H. opuntia* and *Lobophora variegata* were consistently associated with bleaching (90-94% and 78-79%, respectively) for both coral genera. Pooling across all seaweeds, contacts with *Agaricia* were more frequently associated with bleaching than were contacts with *Porites*.

Table 1 Proportion of contacts associated with bleaching per seaweed for the two most common coral genera, *Agaricia* and *Porites*, and depths combined. Numbers in italic indicate the total number of contacts with that seaweed. Differential effects detected in the logistic regression are displayed in bold. Only seaweeds with more than two observations per coral species were included in this test.

Seaweeds in contact with corals	*Agaricia* bleached	*Porites* bleached
Articulated coralline algae	**83%** *(48)*	**47%** *(15)*
Dictyosphaeria cavernosa	100% *(3)*	-
Filamentous algae	50% *(2)*	50% *(6)*
Halimeda goreaui	59% *(22)*	25% *(4)*
Halimeda opuntia	94% *(47)*	90% *(29)*
Halimeda tuna	**57%** *(42)*	**38%** *(32)*
Lobophora variegata	79% *(28)*	78% *(23)*
Sargassum sp.	0% *(8)*	0% *(2)*
Valonia sp.	100% *(2)*	-
Ventricaria sp.	0% *(1)*	-
All seaweeds combined	**73%** *(203)*	**60%** *(111)*

Palatability trials and seaweed nutritional value

Diadema antillarum urchins consumed 150% more *Halimeda opuntia* that had been in contact with the coral *Agaricia tenuifolia* than *H. opuntia* that had not been in contact with this coral (Paired t-test, p = 0.035; Fig. 5). This response was not associated with greater nutritional value of seaweed thalli that had been in contact with corals (Fig. 6). Organic content, carbon concentration, and nitrogen concentration did not vary significantly between *H. opuntia* thalli that had and had not been growing in contact with *Agaricia* (t-test, Organic matter p = 0.986; Carbon p = 0.223; Nitrogen p = 0.521; Fig. 6).

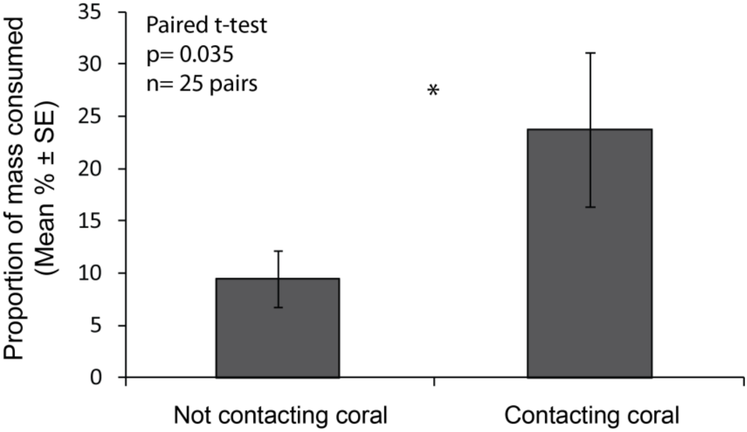

Figure 5 Mass of *Halimeda opuntia* that had and had not been in contact with the coral *Agaricia tenuifolia* consumed by sea urchins *Diadema antillarum* when both were simultaneously offered in laboratory feeding trials. (*) indicate significant differences between the bars.

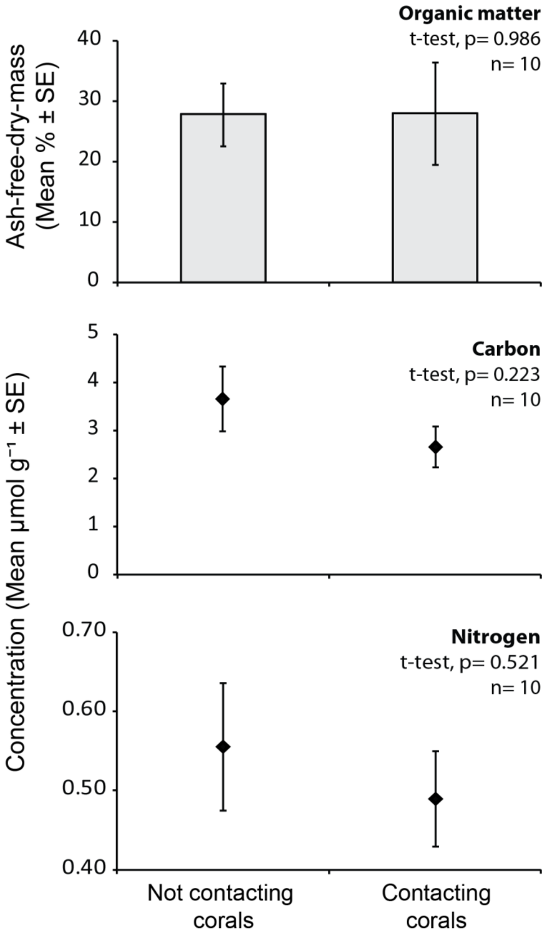

Figure 6 Nutritional traits of *Halimeda opuntia* thalli collected 1-2m from *Agaricia tenuifolia* versus thalli growing in contact with the coral.

Discussion

Most coral colonies were in contact with seaweeds and a large portion of these contacts were associated with coral bleaching. Coral-seaweed contacts were particularly frequent between *Halimeda opuntia* and corals in the genus *Agaricia*, with this interaction being associated with bleaching in 95% of the cases. Although the mechanisms producing bleaching in this study were not investigated, *H. opuntia* is allelopathic to other corals in the Caribbean (Rasher and Hay 2010). This chemically-rich seaweed is also chemically defended against Caribbean reef herbivores (Paul and Fenical 1983, Hay et al. 1988). If different chemicals serve as anti-herbivore defenses versus allelopathic compounds and are induced in response to these different challenges this could impose a trade-off where competing with corals could affect the seaweed's susceptibility to herbivory, as recently demonstrated for an allelopathic and herbivore deterrent red alga in the tropical Pacific (Rasher & Hay 2014). In contrast, if the same compounds serve as both herbivore deterrents and as allelopathic agents, then induction in response to either challenge could make seaweeds more resistant to both. The patterns we found here, suggest that competition with corals may in some manner compromise this alga's resistance to herbivory.

Following the decline of acroporid corals throughout the Caribbean, *Agaricia* spp., *Porites* spp. and *Orbicella* spp. (former *Montastraea*) became the dominant corals on Caribbean reefs, which were becoming increasingly dominated by seaweeds in the the genera *Sargassum*, *Dictyota*, *Lobophora*, and *Halimeda* (Hughes 1994;Williams & Polunin 2001; Alvarez-Filip et al. 2009; Jackson et al. 2014). As a result, the most ecologically important coral-seaweed interactions are likely to be concentrated among these genera (McCook et al. 2001). In the present study, *Agaricia*, *Porites* and *Montastraea-Orbicella* were the corals most frequently in contact with seaweeds (40-90% of individuals in contact), but *Agaricia* and *Porites* were consistently among the most contacted and the most frequently bleached at areas of contact.

The coral genus *Agaricia* experienced a severe decline between the 1970's and the 2000's in the Caribbean (Shulman & Robertson 1996; Nugues & Bak 2006). This decline is often associated with the die-off of the sea urchin *Diadema antillarum* (de Ruyter van Steveninck & Bak 1986). The loss of *Diadema* might have had more important implications for *Agaricia* than are immediately apparent if it selectively attacked seaweeds in contact with corals and thus slowed the impacts of seaweed-coral competition. *Agaricia* corals may be especially dependent on such interactions because they appear to be poor competitors against seaweeds. When the seaweed *Lobophora variegata* was experimentally put in contact with different corals in Curaçao, *Agaricia agaricites* was the only coral not able to reduce algal growth, proving to be a poor competitor (Nugues & Bak 2006).

Corals can respond differently when competing with different seaweeds, which can determine the outcomes of the interaction (McCook et al. 2001). Some corals use microfilaments to damage *H. opuntia*, but colonies of *Montastrea* and *Orbicella* were most effective in comparison to other corals including *Agaricia* and *Porites* (Nugues et al. 2004). In the present study, contacts between *Agaricia* and articulated coralline algae were more frequently associated with coral bleaching than when this seaweed group contacted *Porites*. These differences could be associated with characteristics of the seaweed (*e.g.* functional groups) but also with traits or life form of the corals (McCook et al. 2001; Jompa & McCook 2003). Corals with encrusting and plate-like life forms were previously suggested to be more susceptible to competition from seaweeds (Hughes 1989; McCook et al. 2001), which agrees with the greater susceptibility of *Agaricia* than *Porites* to the seaweeds we found contacting these corals in our field surveys. For example, corals with a plate-like form, such as some *Agaricia* species, may generate areas beneath their projecting borders where seaweeds can escape herbivores. In contrast, seaweeds at the border of massive corals, such as *Porites*, appear more exposed to herbivores.

The differences in life forms between *Agaricia* and *Porites* were not associated with differences in their resistance to *H. opuntia*. When either of these corals contacted *H. opuntia*, more than 90% of the colonies were bleached in areas of contact. The mechanisms leading to this high association with coral bleaching were not investigated, but *H. opuntia* is allelopathic to *Porites porites* in the Caribbean (Rasher and Hay 2010). In addition to being allelopathic to corals, *Halimeda* can harm corals by hosting corallivores that consume coral tissues (Wolf & Nugues 2013) and by vectoring coral diseases (Nugues et al. 2007). It is also a low preference food for herbivores due to chemical and structural defenses (Hay et al. 1988, 1994; Paul & Hay 1996; Paul & van Alstyne 1988) and to nocturnal growth that allows its most herbivore-susceptible new growth to avoid herbivory until this growth begins to calcify and alter chemical defenses as the sun rises (Hay et al. 1988). *Halimeda*'s productivity may also be enhanced by higher nutrient levels that inhibit some corals (Lapointe et al. 1987; Littler & Littler 2007). The combination of these traits may allow *Halimeda* to be a frequent and extensive competitor of corals on numerous Caribbean reefs.

In the present study, sea urchins consumed ~150% more *H. opuntia* that had been in contact with the coral *Agaricia tenuifolia* than nearby *H. opuntia* that was not contacting coral, even though no differences in their nutritional values could be detected. This suggests that previous contact with the coral may have compromised the seaweed's anti-herbivore defenses and enhanced susceptibility to herbivory. Given the frequency of these contacts, the vulnerability of *Agaricia* to seaweed damage, and the importance of herbivores in the mediation of coral-seaweed competition (Lewis 1986; Mumby and Steneck 2008; Hughes et al. 2010; Rasher et al. 2013) this could have important implications for ecosystem function. It is well known that resilience of reef function is dependent on herbivores removing seaweeds and preventing reef degradation (Bellwood et al. 2004; Mumby and Steneck 2008; Hughes et al. 2010), but how this feeding activity varies on a small scale is relatively uninvestigated. Corals profit from preventing direct contact with seaweeds (Rasher et al. 2011; Andras et al. 2012), and recent studies of specific interactions have demonstrated that some corals can chemically signal mutualistic fishes to remove competing seaweeds once they contact corals (Dixson and Hay 2012). Additionally, the seaweed *Galaxaura filamentosa* has been demonstrated to induce greater allelopathy when in contact with the coral *Porites cylindrica*, but this induced allelopathy co-occurs with a compromise in anti-herbivore chemical defenses, making the seaweed more palatable to herbivores when in contact with coral (Rasher and Hay 2014). This potential tradeoff could explain the pattern of palatability we observed for *H. opuntia*. If such interactions are common, then coral-seaweed interactions may make competing seaweeds more palatable and slow the rate at which seaweeds damage corals, but on an overlooked scale of millimeters or centimeters instead of at scales of reefs. At present there are only 3 instances of this being investigated. The green alga *H. opuntia* (this study) and the red alga *Galaxaura filamentosa* are both allelopathic to corals and became more palatable when in contact with a competing coral (Rasher and Hay 2014). In contrast, the brown alga *Sargassum polycystum* is not allelopathic, does not induce allelopathy when contacting coral, but also does not become more palatable following competition with coral (Rasher and Hay 2014). This sample size is still too small to draw general conclusions, but the interaction is worthy of additional investigation.

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CAPÍTULO 2

Between-habitat variation of benthic cover, reef fish assemblage and feeding pressure at the only atoll in South Atlantic: Rocas Atoll, NE Brazil

(em revisão no periódico *PloS One*)
formatação de acordo com os moldes da revista

Between-habitat variation of benthic cover, reef fish assemblage and feeding pressure at the only atoll in South Atlantic: Rocas Atoll, NE Brazil

Short-title: Ecosystem function at Rocas Atoll, NE – Brazil

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Author Contributions

Conceived and designed the experiments: GOL RAM BS SRF. Performed the experiments: GOL RAM MBS SRF. Analyzed the data: GOL RAM AWA. Contributed reagents/materials/analysis tools: GOL RAM CDLM TCM AWA DVC JCdO LTN LF MNS MMT MBS FR LPG PAH BS CELF SRF. Wrote the paper: GOL RAM CDLM TCM AWA MMT PAH BS CELF SRF.

Abstract

The South Atlantic harbors unique and relatively understudied reef systems, including the only atoll in South Atlantic: Rocas Atoll. Located 230 km off the NE Brazilian coast, Rocas is formed by coralline red algae and vermetid mollusks, and is potentially one of the most “pristine” areas in the Southwestern Atlantic. We provide the first comprehensive and integrative description of the fish and benthic communities inhabiting different shallow reef habitats of Rocas. We studied open pools, which communicate with the open ocean even during low tides, being more exposed to wave action; and closed pools, which remain isolated during low tide and are comparatively less exposed. Reef fish assemblages, benthic cover, algal turfs and fish feeding pressure on the benthos remarkably varied between open and closed pools. Planktivores were the most abundant functional group. In terms of biomass, macrocarnivores (lemon shark) were the most representative group in open pools and herbivorous fishes (surgeonfish) in closed pools. Benthic cover was dominated by algal turfs, composed of articulated calcareous algae in open pools and non-calcified algae in closed pools. Feeding pressure was dominated by acanthurids and was 10-fold lower in open pools than in closed pools. Besides different hydrodynamic conditions, such pattern could also be related to the presence of sharks in open pools, leading herbivorous species to feed in closed pools. This might indirectly affect the structure of reef fish assemblages and benthic communities. The macroalgae *Digenea simplex*, which is relatively rare in closed pools and abundant in the reef flat, was highly preferred in herbivory assays, indicating that herbivory by fishes might be shaping this distribution pattern. The dynamics in open pools seems mostly driven by physical factors and the tolerance of organisms to harsh conditions, while in closed pools direct and indirect effects of species interactions also play an important role.

Introduction

Reef ecosystems around the globe have suffered from a variety of anthropogenic activities including habitat degradation, overfishing, coastal pollution, introduction of invasive species and global warming, leading to the loss of biodiversity and critical ecosystem processes [1-3]. The combination of species interactions and abiotic conditions shape the complexity of reef systems, which highlights the need to understand the relative contribution of these components to ecosystem structure and functioning [4-5]. Physical factors, such as wave energy and tidal currents, have been recognized as one of the main forces regulating reef dynamics [6-7]. For instance, the diversity and cover of hard corals can be negatively related to wave energy, as it can result in physical damage to less robust branching corals. On the other hand, turf algae cover can prevail in high-hydrodynamic habitats because of its tolerance to disturbances and ability to colonize newly available substrate [8-9].

In dynamic systems, such as atolls, tidal regimes are particularly important in determining current strength, nutrient availability and particulate matter, hence influencing benthic communities [7, 10]. Likewise, reef fish communities respond to wave-induced water motion according to species' swimming abilities [11-12]. More exposed areas can favor planktivores and piscivores, while site-attached species with limited swimming capability tend to live closely associated with the reef, such as territorial pomacentrids [13]. These physical factors can also influence fish feeding behavior [14]. At the Great Barrier Reef, for instance, reef fish herbivory varied among habitats with different exposure conditions, with higher rates of macroalgae removal in more exposed sites [15].

The effect of herbivory on reef structure and dynamics is largely recognized as a critical ecological process in coral reefs [2, 16-19]. A meta-analysis exploring the relative importance of herbivory (top-down force) and nutrient supply (bottom-up force) in structuring benthic communities found that herbivory can exert a stronger effect on tropical macroalgae and seagrass than nutrient supply [20]. When herbivorous fishes were excluded from reef areas both in the Caribbean and the Great Barrier reef, macroalgae rapidly outgrew other benthic organisms, revealing a critical top-down control [18-19, 21-22]. However, the ability of herbivores to control macroalgae also depends on a combination between algal traits (*e.g.* defenses, nutritional value) and herbivore diversity, reflected, for instance, in their tolerance to anti-herbivore defenses and feeding preferences [23]. Thus, the relative contribution of ecological processes and physical factors in structuring reef communities may have context-dependent effects, varying within and between-habitats [4]. Understanding these factors is critical for informed conservation strategies, for example by protecting critical ecological processes and habitats with different abiotic conditions [2, 10].

The South Atlantic Ocean harbors unique reef systems with different characteristics and dynamics when compared to the Indo-Pacific and Caribbean, as a result of different historical and biogeographical factors (*e.g.* isolation, biogeographic barriers, reef type, geomorphological features [24-26]). Among these reef systems, there is only one atoll formation in the South Atlantic Ocean: Rocas Atoll, 230 km off the northeastern coast of Brazil at the state of Rio Grande do Norte [27]. Unlike most atolls in the world, Rocas is not predominantly constructed by corals, but by coralline algae, vermetid gastropods and encrusting foraminiferans [28]. Rocas is also smaller than most atolls, comprising an area of 5.5 km^2 [29], in comparison to others such as Palmyra Atoll in the Pacific with ca. 52 km^2 [9] and Glover's Reef in the Caribbean with ca. 260 km^2 [10]. Despite these differences, Rocas has equivalent habitats such as: a shallow lagoon, small sandy islands, algal crest and different reef zones [28]. Additionally, it was the first Brazilian marine protected area, established in 1978, and one of the first no-entry marine reserves in the world [30], being potentially the most effective marine protected area in Brazil. Rocas is also a very dynamic ecosystem prone to the arrival and establishment of new species both through natural or human-mediated processes, with potential consequences to the ecosystem function that are still unknown in terms of magnitude and duration [31].

Despite the uniqueness of Rocas Atoll and some staggered efforts to describe its reef fish assemblages, benthic communities and herbivory patterns [*e.g.*, 29, 32, 33], an integrated approach is still missing. Here we provide the first comprehensive and integrative description of patterns of reef fish assemblages, benthic communities and fish trophic interactions on the benthos in this reef system. Particularly, we describe and compare habitats with different hydrodynamic conditions regarding: (1) the structure of reef fish assemblages; (2) benthic community; (3) composition, nutritional value and associated cryptofauna of algal turfs; (4) fish feeding pressure on the benthos and herbivory. We expected that: (1) fish species with higher mobility (*e.g.*, sharks and jacks) would be more common in habitats with high hydrodynamics; (2) algal turfs would be more abundant in habitats with high hydrodynamics, however with a lower abundance of associated cryptofauna and lower nutritional value; and (3) a higher feeding pressure would be expected in habitats with lower hydrodynamics, mostly by herbivorous fishes.

Materials and Methods

Study Area

Rocas Atoll is located in the South Atlantic Ocean laying approximately 230 km off the NE coast of Brazil (03^{o}50’S, 33^{o}49’W). Rocas is the only atoll formation in the South Atlantic part of a seamount chain in the E-W direction known as the Fracture Zone of Fernando de Noronha [27]. The atoll is subject to an intense wave action in comparison to coastal systems, with predominant winds from S and SE, leading to an intense wave action in this side of the atoll; the leeward side can also be occasionally affected by large wave surges [28]. Sea surface temperature in the atoll rim varies between 27^{o}–29^{o}C, while in shallow habitats inside the atoll it may vary between 24^{o}–36^{o}C [29]. The tides range from 0–3.8 m in a semi-diurnal and mesotidal regime [28], resulting in a half-daily cycle of almost complete submersion during high tide (only the sandy islands remain emerged) and almost complete emersion during low tide. The available reef area in its internal portion during the low tide, when tidal currents have ceased, can be distinguished in three main habitats: the shallow permanent lagoon, open and closed pools. Open pools communicate with the exterior of the atoll even during low tides and are more exposed to wave action than closed pools, which remain completely isolated from the exterior area of the atoll during low tide (Fig. 1). This tidal dynamics results in strong currents when the atoll is either filling or draining and during high tides, reason why diving inside the atoll is concentrated during low tide [28]. Established as a marine reserve in 1978, only in 1991 constant and effective enforcement was implemented through the establishment of a permanent monitoring station at the atoll. Rocas figures as an important study area and natural laboratory because: (1) it is a unique atoll formation and the only one in the South Atlantic; (2) it offers a great variety of habitats with different conditions and under the influence of tidal dynamics; (3) it is probably the most effective marine reserve and most similar to a pristine reef in the Tropical Southwestern Atlantic (SISBIOTA–Mar *unpublished data* – www.sisbiota.ufsc.br).

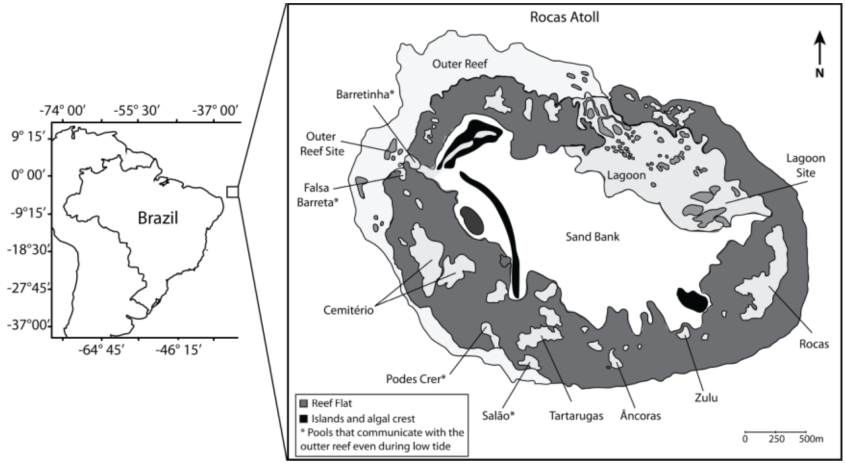

Figure 1 Studied areas in Rocas Atoll, NE Brazil. (*) Indicates open pools, which keep the connected with the outside part of the atoll even during low tide.

Data collection

Fieldwork was conducted during the austral summer (January to February 2012), always in low tide conditions (except for the outer reef sampling) and between 09:00–16:00 h. Four different habitats were studied, with depth varying from 2 to 10 m: open pools, closed pools, the lagoon and one outer reef site (see Table S1 in Supporting Information). Water temperature during fieldwork varied between 27^{o}–29^{o}C. In May 2013, individuals of the most abundant herbivorous fish species (*Acanthurus chirurgus* and *A. coeruleus*) were collected in the same tidal conditions for dietary analysis.

Reef fish assemblages

The structure of fish assemblages was assessed through underwater visual censuses during low tide in 10 sites inside the atoll (five closed pools, four open pools and the lagoon) and in one site at the outer reef during high tide. Visual censuses consisted of belt transects in which a diver identified, counted and estimated the total length (cm) of fish species inside an area of 40 m² (20 x 2 m; [13]). The same diver returned searching for small, cryptic and hidden species. Each fish was assigned to a functional group following the literature (see Table S3 for the categories [34-36]). Fish biomass was estimated using length–weight relationships available in the literature (*e.g.* [37]). A total of 153 visual censuses were performed along the four studied habitats and the number of transects in each habitat varied from 5 to 25, depending on the pool area (Table S1).

Reef fish feeding pressure on the benthos

Reef fish feeding pressure on the benthos was evaluated through remote video recordings of 2 m^2 reef areas, demarcated with a 2 m transect tape, that was removed within the first minute of the video [35-36]. A total of 85 reef areas were sampled, 40 in open and 45 in closed pools (see Table S1). Each area was recorded for 15 min and the central 10 min of each video were analyzed. Each fish recorded feeding on the benthos was identified, assigned into a functional group, had its total length estimated based on the transect tape initially deployed, and its bites on reef substratum were counted during the observational period [36]. Feeding pressure was determined by the product of the number of bites taken and body mass (kg) of each fish, to account for body size variation in the potential bite impact [15, 36]. Individual body mass was obtained using the same procedure described for estimating fish biomass in transects. Reef fishes were assigned to the same functional groups used for fish assemblages, from which only six were recorded feeding on the benthos: scrapers, fine browsers, territorial herbivores, sessile invertebrate feeders, mobile invertebrate feeders and omnivores. Thus, fish feeding pressure on the benthos was evaluated from the perspective of several functional groups within different trophic categories, and accounted for body size variation, per unit of time and area [(Bites x kg) / (2 m^2 x 10 min)] [36].

Benthic cover

Inside each of the recorded areas, benthic cover was estimated using a set of five 25 x 25 cm photoquadrats. Each photograph was analyzed with the software Coral Point Count with Excel extensions [38], where fifty points were randomly positioned over each image and the organism below each point was identified into morpho-functional groups, by species or genus level [39-41]. Sponges, ascidians and cyanobacteria were kept as broad groups due to limitations in identifying these groups in the photoquadrats [42] and algae were identified to the lowest taxonomic level as possible. Algal assemblages were classified as turfs when they formed thick mats, with a low lying layer of tightly packed algae less than 2 cm high (*sensu* 43-45) and divided in calcareous or non-calcified turfs according to the dominant algae [46].

Algal turfs

In two closed (Tartarugas and Rocas) and two open pools (Falsa Barreta and Podes Crer), 10 x 10 cm quadrats were haphazardly positioned inside the recorded areas and algal turfs (*sensu* [47]) within these quadrats were scraped and collected until the bare reef was apparent. A total of 20 quadrats were collected, equally distributed among two closed and two open pools (*i.e.* 5 samples per pool; see Table S1). The samples were frozen right after collection, defrosted in the lab and washed with ammonium formiate to remove salts and sand from macroalgal thalli prior to identification. Identified species were dried separately at 38°C (± 2°C) for 24 hours to determine the dry weight as a measure of biomass. Subsequently, all dried species within a sample were combined, powdered in liquid nitrogen and aliquots were separated for nutritional analyzes. The cryptofauna specimens were also separated and further identified to the lowest taxonomic level possible. This sampling method might be underestimating the cryptofauna's abundance, therefore the interpretation of such data in comparison to other studies with more specific methods should be made cautiously and on a relative basis.

Herbivory Assays

Multiple-choice herbivory assays were conducted to quantify algal removal and selectivity by herbivores [23, 48-49]. Seven macroalgae species (*Caulerpa verticillata*, *Canistrocarpus cervicornis*, *Dictyopteris jolyana*, *Dictyopteris plagiogramma*, *Digenea simplex*, *Padina gymnospora* and *Sargassum* sp.) were collected from open pools and from the reef flat and transplanted to a closed pool (Tartarugas). These algae were chosen because of their relatively high abundance in open pools and on the reef flat, contrasting to their low abundance in closed pools, with herbivory being suggested as the main driver of such pattern (see [33]). Algae were collected in the same day of the experiment, placed in a mesh bag and rotated ten times to remove the excess of water before being weighted. Algae were then attached to a 1 m length rope in randomized species ordering, distant at least 10 cm from each other. All the ropes were transported in buckets to the experiment site and one of them was placed in a cage of 2 cm mesh size to control for biomass loss due to hydrodynamics and handling procedures. Ropes and controls were placed over the sand bottom adjacent to the reef. An underwater video camera was positioned in front of each rope, approximately 1 to 2 m from the assay, to record the feeding activity of herbivorous fishes over the transplanted algae and surrounding substrate. Because of the tidal conditions, the assays were conducted for two hours and algae were re-weighted right after this period using the same procedure prior to the trials. The videos were analyzed for the entire period or until a reduction of 70-80% of one of the algae [23], which occurred in most videos within 37 minutes on average (9 from 11). The proportion of consumed algae was calculated through the formula: $[Wr_i \times (Wc_F)/Wc_i] / Wr_F$, where Wr_i and Wr_F are, respectively, the initial and final algae biomasses in the trial rope, and Wc_i and Wc_F are the initial and final algae biomasses in the control rope, respectively [23]. A total of 13 trials were conducted within 3 days, from which 11 were coupled with video recording.

Algal nutritional quality

Total protein, soluble sugars and starch contents from algal turf samples and species used in the herbivory assays were taken from dried and milled aliquots. Lipid content was determined only for species used in the herbivory assays, through the gravimetric procedure developed by [50] and modified from [51]. The extraction of total proteins was performed according to [52]. An aliquot of 50 mg was extracted with 2 ml of sodium hydroxide solution (NaOH) 0.1 mol/L and centrifuged twice at 3000 rpm for 5 min. The supernatants of both extractions were pooled and total soluble protein contents were determined according to [53], using the reagent Coomassie brilliant blue G-250 and BSA as standard. The extraction of total soluble sugars was performed according to [54]. An aliquot of 50 mg was extracted with 2 ml of methanol:chloroform:water (MCW; 12:5:3) and centrifuged at 3000 rpm for 5 min. The supernatant was recovered and the pellet was re-extracted using 2 ml MCW. One part of chloroform and 1.5 part of water were added to each four parts of supernatant, followed by centrifuging at 3000 rpm for 5 min, from which two phases were obtained. The upper aqueous phase was collected and dosage was estimated using anthrone 0.2% [55]. Starch extraction was performed according to [56]. Pellets used in total soluble sugar extraction were ground with perchloric acid (HClO4) 30% (v/v) and centrifuged at 3000 rpm for 5 min. The supernatant was collected and the precipitate was extracted again as specified above. The extract was also centrifuged and the supernatants of both extractions were pooled and analyzed according to [55], using the reagent anthrone 0.2% (w/v). Sugar and starch concentration were calculated using D-glucose as standard.

Diet of herbivorous fish

Individuals of *Acanthurus chirurgus* (n=14) and *Acanthurus coeruleus* (n=12) were collected with hand spears in the closed pools of Rocas, Âncoras and Tartarugas in May 2013. Fish were collected in the afternoon to assure they had full guts, since this is the expected period of higher feeding activity for most nominally herbivorous fishes [57]. After collection, all individuals were measured to the nearest millimeter (total length) and had their stomach removed and preserved in formalin. In the laboratory, the whole stomach contents of each individual was spread in a Petry dish over a graph paper with 50 random points. Items above each of these points were identified using a stereoscopic microscope to the lowest taxonomic category when possible [58].

Data Analysis

Multivariate approach

Differences in the structure of reef fish assemblages (response variable) between the four habitat types (grouping variables) were assessed using an analysis of similarity (ANOSIM [59]) and a multidimensional scaling (MDS [59]; square-root transformed data; Bray-Curtis similarity). The same tests were used to evaluate differences in benthic cover (response variables; arcsin transformed; Euclidean distance) between closed and open pools (grouping variables). A cluster analysis was also performed on benthic cover data ([59]; UPGMA) and overlaid on the MDS to highlight groups with a resemblance of 0.8. The relation between the benthic groups and the grouping of samples between closed and open pools was assessed through a principal components analysis. Differences in both the composition of algal turfs (dry weight) and associated cryptofauna (density) between closed and open pools (grouping variables) were evaluated using ANOSIM (square-root transformed data; Bray-curtis similarity).

Univariate approach

Differences between open and closed pools (grouping variables) were tested using independent t-tests on square-root transformed data. This test was used to compare the habitats in terms of: (1) mean biomass of *Acanthurus chirurgus* and *A. coeruleus*; (2) percent cover of the main benthic groups; (3) mean total dry weight of algal turfs, total density of cryptofauna and mean density of each cryptofauna group; (4) nutritional quality of algal turfs (total protein, soluble sugars and starch); and (5) mean total feeding pressure. Differences in the concentration of different nutritional components (sugar, starch, protein and lipid) of algae used in the herbivory assay (grouping variables) were independently assessed using a one-way analysis of variance (ANOVA) on square-root transformed data to meet parametric assumptions. The relation between the mean total dry weight of algal turf (independent variable) and the mean total density of cryptofauna (dependent variable) was investigated using a linear regression. In the herbivory assays, differences in the mean proportion of consumed biomass (response variable) among algae species (grouping variables) were evaluated through a Friedman's test followed by Friedman *a posteriori* multiple comparison tests using square-root transformed data. The same approach was used to compare the mean number of bites (response variable) between algae species (grouping variable) for the two herbivore species. A paired t-test on square-root transformed data was used to assess differences in the proportion of bites taken by each fish species (response variables) on each algae species (grouping variables). Differences in the relative abundance (response variable) of dietary items (grouping variables) of herbivorous fishes were evaluated through a Friedman's test followed by Friedman *a posteriori* multiple comparison tests.

Permutational approach

The selectivity patterns were investigated using the Strauss' Linear Selection Index (L):$L = r_i - p_i$, where r_i is the number of bites taken from algae *I*, as a percentage of the total number of bites from all algae in each assay, and p_i is the mass of alga *I* in relation to the total algal mass presented at the beginning of each assay [48,60]. Thus, different values of selectivity indices were obtained for each algae and each of the two herbivorous species and averaged over all the assays. A 95% confidence interval (CI) was generated for each averaged index through 1,000 iterations of the observed values. CI intervals higher than

0 indicate selection, lower than 0 indicate avoidance and intervals that include 0 indicate that the selection of the algae did not differ significantly from random [48]. Data from herbivory assays did not vary significantly across days and were grouped in all these analysis (Table S2).

Results

Reef fish assemblages

A total of 53 fish species distributed in 28 families and 10 functional groups were recorded across four studied habitats (Table S3; closed pools, open pools, the lagoon and the outer reef). The structure of fish assemblages differed between open and closed pools ($\text{ANOSIM}_{\text{Open-Closed}}$; R = 0.50, p = 0.001), and the outer reef site ($\text{ANOSIM}_{\text{Open-Outer reef}}$; R = 0.78, p = 0.001; $\text{ANOSIM}_{\text{Closed-Outer reef}}$; R = 0.70, p = 0.001; Fig. 2). The lagoon assemblage differed from the open pools ($\text{ANOSIM}_{\text{Lagoon-Open}}$; R = 0.68, p = 0.001) and the outer reef ($\text{ANOSIM}_{\text{Lagoon-Outer reef}}$; R = 0.79, p = 0.001), but not from closed pools ($\text{ANOSIM}_{\text{Lagoon-Closed}}$; R = 0.10, p = 0.07), and thus is treated as a closed pool in further analysis of reef fish assemblage structure.

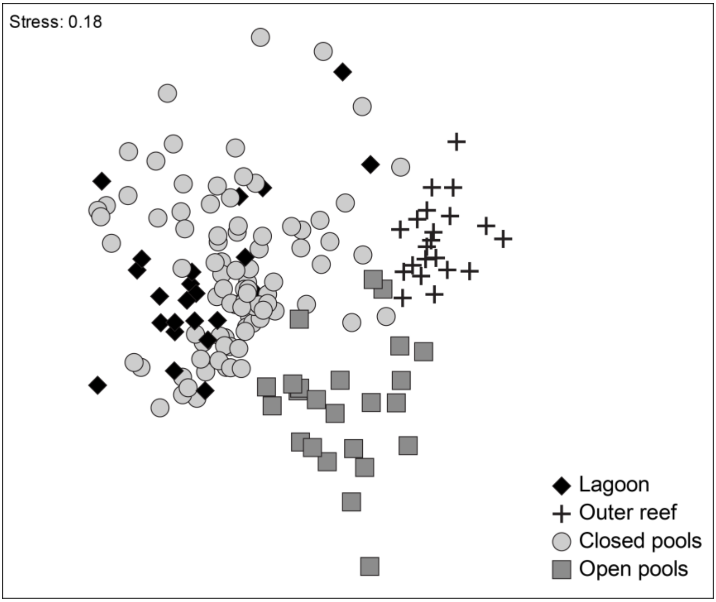

Figure 2 Multidimensional Scaling (MDS) of the composition of reef fish assemblages among different habitats based on a Bray-Curtis similarity matrix.

Diurnal planktivores, omnivores, territorial herbivores and scrapers were the most abundant fish functional groups, while scrapers, macrocarnivores and mobile invertebrate feeders comprised most of the fish biomass (Figure S1). Macrocarnivores were represented especially by apex predators, such as the dog snapper, *Lutjanus jocu,* the lemon shark, *Negaprion brevirostris*, and the nurse shark, *Ginglymostoma cirratum*. *Thalassoma noronhanum* was the most abundant species in both closed and open pools, but *Stegastes rocasensis* was also abundant in both habitats (Fig. 3). *Coryphopterus* sp. and *Acanthurus chirurgus* were particularly abundant in closed pools, while *Albula vulpes* occurred only in one of the open pools (Barretinha), in large schools associated to sandy patches (Fig. 3), comprising a high biomass. Since these schools were ephemeral and spatially localized, they were excluded from the ordination analysis. Apart from this species, biomass in open pools was composed mainly by the shark *N. brevirostris*, followed by *Melichthys niger, A. chirurgus* and *A. coeruleus*. Schools of *A. chirurgus* comprised the greatest biomass in closed pools (Figure 3), with *L. jocu,* and *A. coeruleus* also contributing considerably. The biomass of the two most abundant herbivorous fishes in the Atoll, *A. chirurgus* and *A. coeruleus*, were respectively five and three times higher in closed pools in comparison to open pools (t-test for *A. chirurgus*: $t = 7.02$, $p<0.001$; t-test for *A. coeruleus*: $t = 2.16$, $p<0.05$; Fig. S2).

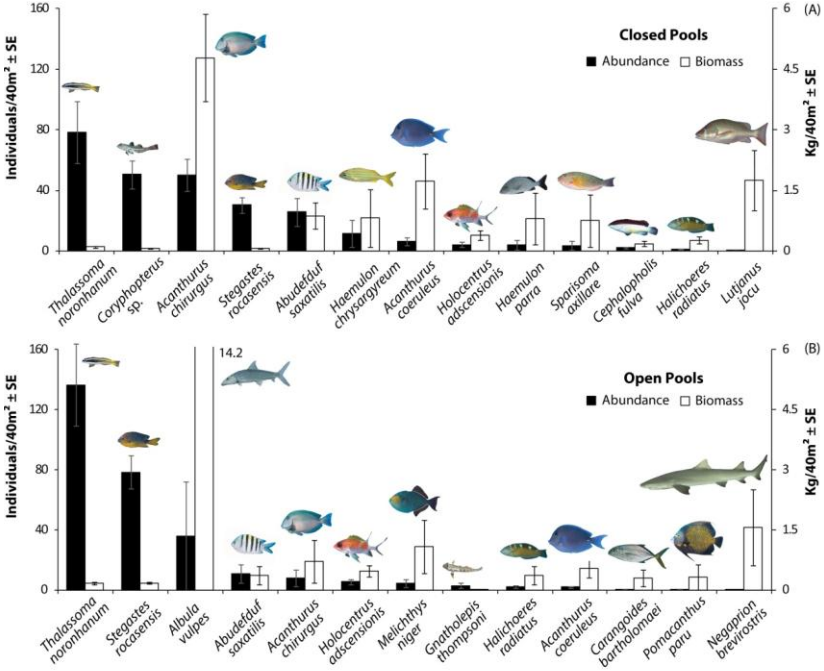

Figure 3 Abundance and biomass of reef fishes in open and closed pools at Rocas Atoll. Displayed species were chosen based on a ranking combining their abundance and biomass. Error bars represent standard errors.

Benthic cover

The benthic community was characterized by 37 functional and taxonomic groups and presented different physiognomy between open and closed pools (Table S4; $\text{ANOSIM}_{\text{Open-Closed}}$; $R = 0.53$, $p<0.001$; Fig. 4). Differences in algal turfs (dominated by non-calcified or articulated calcareous algae in open and closed pools, respectively) and the cover of sediment determined the grouping of samples between closed and open pools, and the variability within these categories. While samples from open pools were grouped by calcareous algal turfs, irrespective of pool identity, samples from closed pools were separated in those characterized by non-calcified algal turfs (pertaining to Âncoras and Tartarugas) and Rocas pool that presented a large amount of sediments covering the reef and often algal turfs (Fig. 4). The most abundant group in closed pools was the non-calcified algal turfs (51%), followed by sediment (31%) and crustose coralline algae (6%). In open pools, turf dominated by articulated calcareous algae was the most abundant group (33%), followed by the alga *Caulerpa verticillata* (15%) and non-calcified turf (14%). The percent cover of all main benthic groups (i.e. those that pooled comprised between 80 and 100% of the cover) differed between closed and open pools, with closed pools presenting three times more sediment than open pools (Fig. 5; Table S5). Hard corals were mainly represented by *Siderastrea stellata*, with a significantly higher cover in open pools (8%) in comparison to closed pools (3%; Fig. 5). The corals *Favia gravida*, *Mussismilia hispida* and *Porites astreoides* were also recorded in samples, but represented less than 1% of benthic cover.

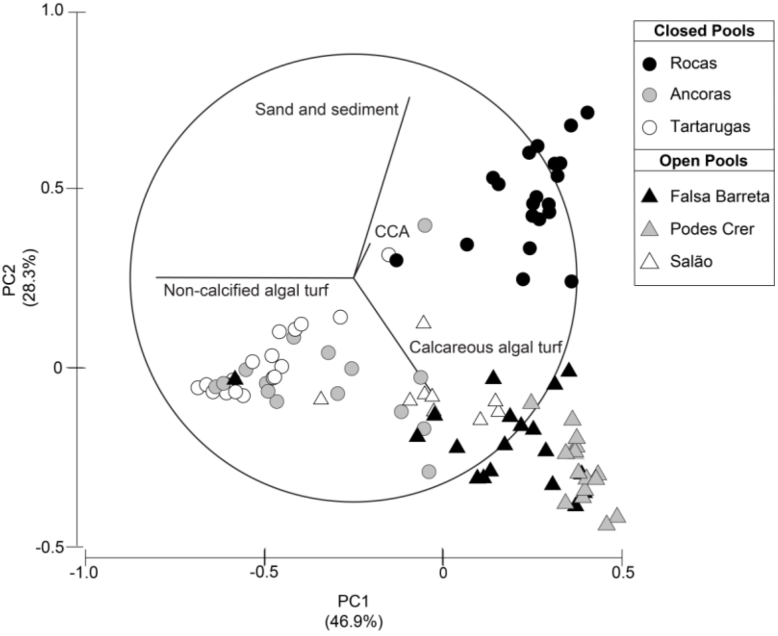

Figure 4 Principal component analysis (PCA) on the composition of benthic cover of closed and open pools. CCA – Crustose coralline algae.

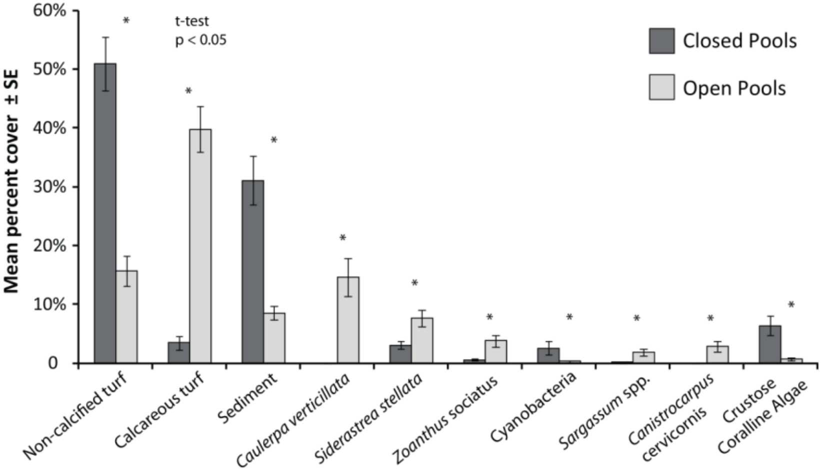

Figure 5 Mean percent cover of the main benthic groups (i.e. those that pooled comprise between 80 and 100% of total cover). (*) Indicates significant differences between closed and open pools (t-test, p<0.05; Table S5). Error bars represent standard errors.

Algal turfs, associated cryptofauna and nutritional traits

Algal turf assemblages were composed by 47 infrageneric macroalgae taxa, with 9 species and 6 genera that are new records to Rocas Atoll (Table S6). Total algal biomass was three times higher in open pools than in closed pools (t-test; t = 2.66, p = 0.016). Algal turf composition also varied between closed and open pools ($\text{ANOSIM}_{\text{Closed-Open}}$; R = 0.48, p<0.002) based on their biomass (Fig. 6A). Rhodophyta was the most representative group in terms of species richness and biomass (*e.g. Amphiroa* sp., *Jania* sp., *Digenea simplex, Gelidium crinale*). While algal turfs in closed pools were predominantly composed by small-cropped thallus of the red algae *D. simplex* and other non-calcified algae, articulated calcareous algae (*e.g. Jania* sp. and *Amphiroa* sp.) were the major component in open pools (Fig. 6A). Similarly, mean density of cryptofauna on algal turfs from open pools was roughly five times higher than on algal turfs from closed pools (t-test; t = 2.49, p<0.05; Fig. 6B). Invertebrates from five different phyla were recorded and identified to different taxonomic levels (Table S7), depending on the available material (specimen or fragment). Although the composition of cryptofauna varied between closed and open pools ($\text{ANOSIM}_{\text{Open-Closed}}$;

R = 0.40, p = 0.01), only the density of amphipods varied between these habitats (t-test; t = 3.26, $p<0.05$; Fig. 6B), as it was about 30 times higher in open pools. The total density of cryptofauna was positively related to total algal biomass in samples ($R^2 = 0.65$; $p<0.001$; Fig. 6C). Algal turfs from closed pools presented higher concentration of soluble sugars and starch content in comparison to open pools, but they did not vary in protein concentration (t-tests; Sugars, t = -2.89, p = 0.014; Starch, t = -7.476, p <0.001; Proteins, t = 0.628, p = 0.538; Fig. S3).

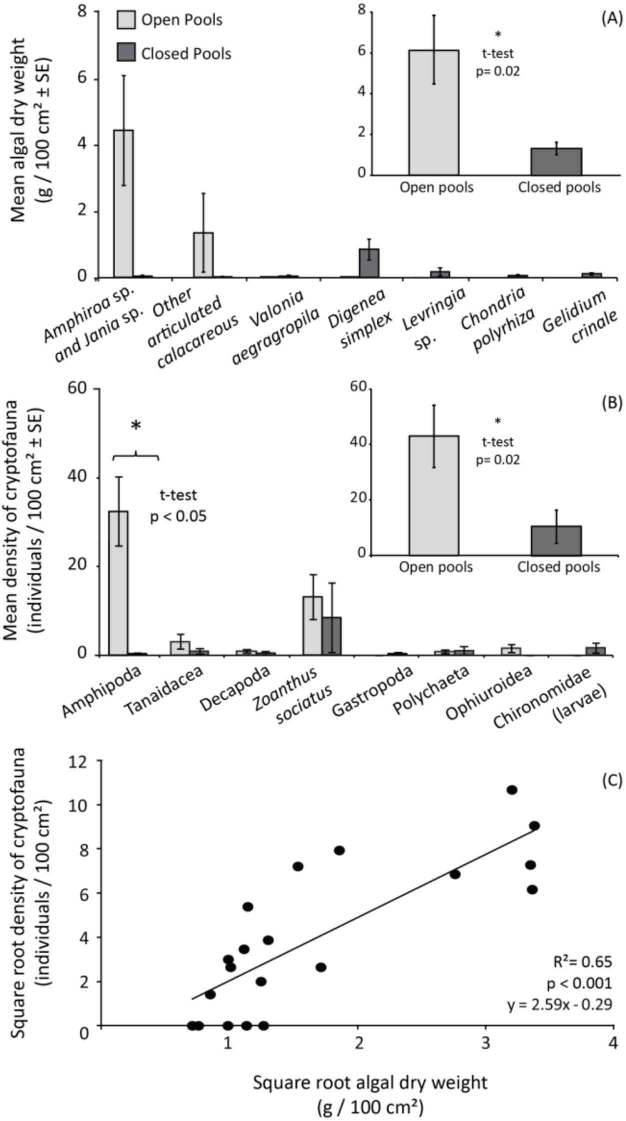

Figure 6 Algal turf species composition and density of associated cryptofauna in open and closed pools. (A) Mean biomass of the main turf-forming macroalgae; (B) mean density of cryptofauna associated to algal turfs; (C) correlation between cryptofauna density and algal turf biomass. The displayed macroalgae species account for 90% of total biomass in the studied habitats. Error bars represent the standard errors.

Feeding pressure and herbivory assays

Six functional groups, represented by 14 fish species, exerted feeding pressure in closed and open pools, particularly herbivores (scrapers, fine browsers and territorial herbivores; Fig. 7). Scrapers performed most of the feeding pressure and represented the highest number of species feeding on the benthos (five). Most of the feeding activity occurred in closed pools, where the total feeding pressure was roughly 20 times higher than in open pools (t-test; t = 2.19, p = 0.03), with the scraper *Acanthurus chirurgus* performing more than 90% (Fig. S3). The fine browser *Acanthurus coeruleus* was recorded feeding on the benthos exclusively in closed pools. The territorial herbivore *Stegastes rocasensis* performed similar feeding pressure in closed and open pools, while mobile and sessile invertebrate feeders, and omnivores exerted low feeding pressure in both habitats.

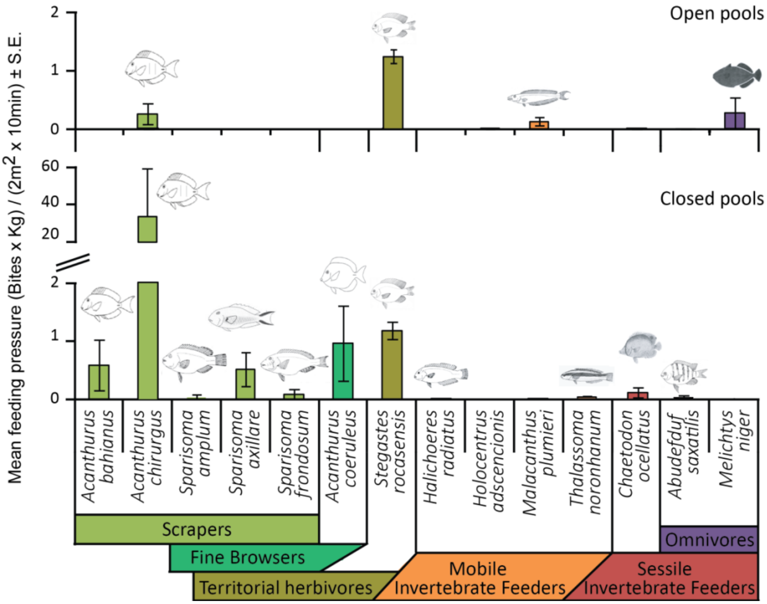

Figure 7 Reef fish feeding pressure on the benthos in closed and open pools. Colored bars indicate species functional groups. Error bars represent standard error of the mean.

Herbivory assays revealed a higher consumption of the red algae *Digenea simplex* over the other six algae (Friedman Test, x^2 = 37.49, p<0.001; Fig 8 A). Only two fish species were recorded removing macroalgae from the experiment: the scraper *A. chirurgus* and the fine browser *A. coeruleus*. However, most of the algal removal was performed by *A. chirurgus*, comprising 95% of the total number of bites recorded in the assays. This species took more bites of *D. simplex* than from any other algae, followed by *Sargassum* sp. and *Dictyopteris plagiogramma* (Friedman Test, x^2 = 45.03, p<0.001; Fig 8 B). *A. coeruleus* also took a greater number of bites over *D. simplex*, but not significantly different from the number of bites over *Caulerpa verticillata* and *Canistrocarpus cervicornis* (Friedman Test, x^2 = 16.04, p = 0.02; Fig 8 C). When comparing the proportion of bites taken by each herbivorous species on each algae, *A. chirurgus* contributed to a greater proportion of bites on *D. simplex* (Paired t-test, t = 3.19; p<0.05) and *Sargassum* sp. (Paired t-test, t = 2.58; p<0.05) in comparison to *A. coeruleus* Fig 8 D). The selectivity index indicates that *A. chirurgus* significantly selected the macroalgae *D. simplex* and avoided the other six algae (Fig. 8 E). Conversely, *A. coeruleus* did not select or avoid *D. simplex*, *C. verticillata* and *C. cervicornis* but significantly avoided the other four algae (Fig. 8 D).

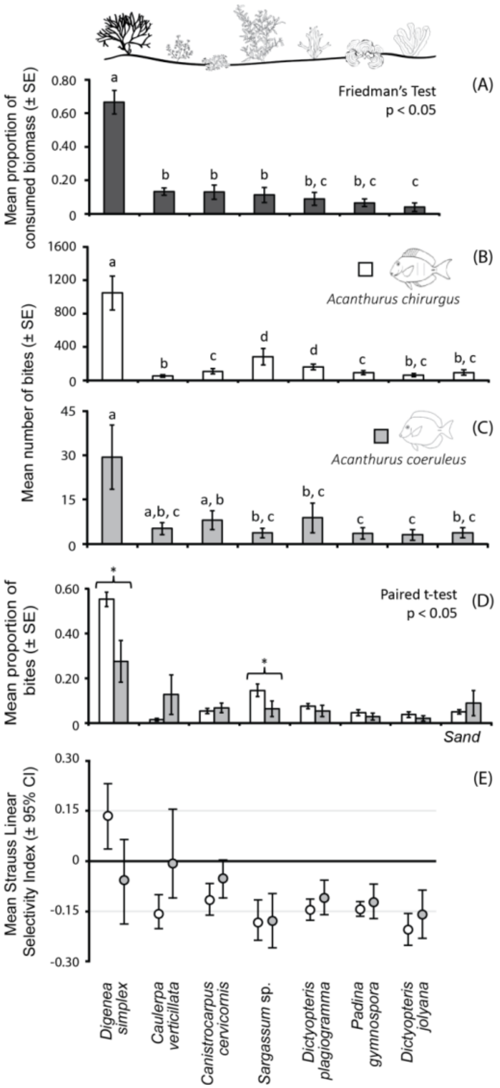

Figure 8 Macroalgal removal and selectivity at the closed pool Tartarugas. (A) Mean proportion of consumed algae biomass; (B) and (C) Mean number of bites on each macroalgae by the herbivorous fishes *Acanthurus chirurgus* and *A. coeruleus*, respectively; (D) Mean proportion of bites taken by the two herbivorous species on each algae; (E) Strauss linear selectivity index for the two herbivores on each algae. (*) indicates significant differences at a 5% significance level. In (A), (B), (C) and (D) error bars represent standard error of the mean, and in (E) it represents the 95% confidence interval.

The algae used in the assays did not differ in the concentration of soluble sugars but did in starch, protein and lipid concentration (ANOVA, Soluble Sugar: $F = 2.327$, $p = 0.067$; Starch: $F = 827.900$, $p< 0.001$; Protein: $F = 8.641$; $p< 0.001$; Lipids: $F = 87.87$; $p< 0.001$; Fig. 9). *Digenea simplex* and *Dictyopteris jolyana* presented the highest starch concentration, with the later also presenting the highest protein content. along with *Sargassum* sp.. The alga *Caulerpa verticillata* presented the highest lipid concentration, around three times higher than *D. simplex*, the most consumed algae in the experiment.

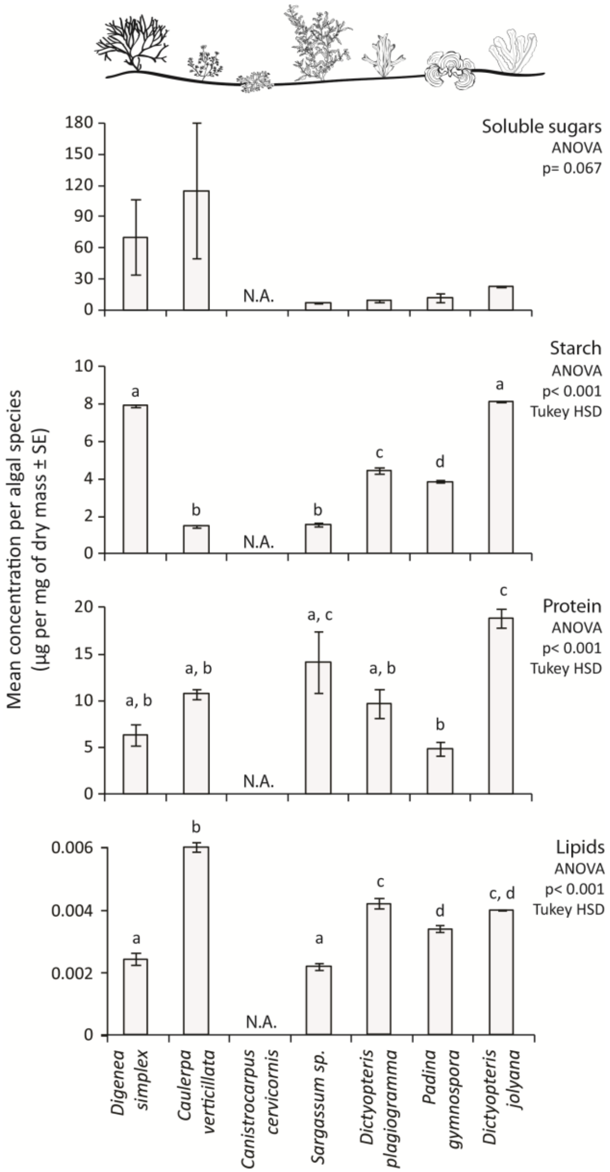

Figure 9 Concentration of soluble sugars, starch, protein and lipid in the algae offered to herbivorous fishes. Letters indicate significant differences according to an analysis of variance followed by a Tukey HSD test. N.A. – not available. Error bars represent standard errors of the mean.

Diet of herbivorous fishes

The stomach contents of *Acanthurus chirurgus* were dominated by sediment (44%) and detritus (30%), followed by red articulated calcareous algae, mainly *Jania* spp. (12%), and red corticated, especially *Digenea simplex* (8%), with the other components comprising 6% of the diet (Friedman Test, $x^2 = 111.04$, $p<0.001$; Fig. 10). On the other hand, the contents of *A. coeruleus* were dominated by red corticated algae, especially *D. simplex* and *Gelidium* spp. (78%), followed by green filamentous algae (7%) and Cyanophyceae (6%), while detritus (1%) and sediment (3%) presented low abundance (Friedman Test, $x^2=74.63$, $p<0.001$; Fig. 12). Excluding detritus and sediment, there was a higher proportion of articulated calcareous algae in the contents of *A. chirurgus* (48%) followed by red corticated algae (27%), while other items were between 6-12%. Conversely, for *A. coeruleus* the dominance of red corticated algae increased to 81% (Table S8).

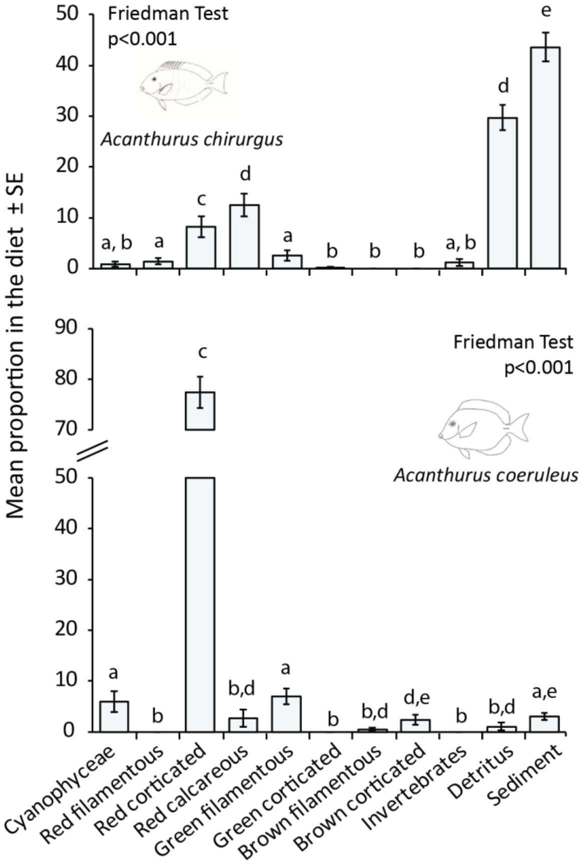

Figure 10 Diet of the two main roving herbivores at Rocas Atoll: *Acanthurus chirurgus* and *A. coeruleus*. Letters above bars indicate post-hoc comparisons of the Friedman test. Error bars represent standard error of the mean.

Discussion

As an oceanic system, Rocas Atoll is subject to intense wave action and strong tidal currents, which are created as water fills and empties the atoll interior, resulting in an extremely dynamic reef system. In this study, there were remarkable differences in patterns of community structure and feeding pressure on the benthos between closed and open pools surveyed in Rocas Atoll. This was evident considering comparative analysis of the reef fish assemblage, benthic cover, the composition, nutritional traits and associated cryptofauna of algal turfs, and fish feeding pressure on the benthos. These differences were probably driven by the distinct hydrodynamic conditions and assoiated amount of sediment in open and closed pools. Fish feeding pressure, for instance, was more intense in closed pools which are less exposed in comparison to open pools. Algal turfs were the dominant benthic group in both habitats, however with remarkable differences in their composition. Thus, differences in fish feeding pressure could also be related to the higher nutritional quality (*e.g.* higher sugar and starch contents) of algal turfs in closed pools. These habitats can function as feeding refuges for reef fishes during low tide (*e.g.* roving herbivores), where they would be more prone to feed because of the protection from intense wave action and currents of the open pools or the outside part of the atoll. Also, closed pools are potentially good refuges against predation, since sharks seem to avoid getting trapped in these environments during low tides and were more common in open pools and outside the atoll. Therefore, fish feeding activities, particularly macroalgal removal, might be determining benthic cover in closed pools by limiting the abundance and restricting the distribution of certain species to less grazed habitats (*e.g.*, the reef flat and/or open pools). This was particularly evident for *Digenea simplex*, a red corticated macroalga with low lipid and high soluble sugars concentration. This species was highly consumed in the herbivory assays and figured as an important feeding item in *Acanthurus* spp. stomach contents, but presented low overall abundance or mostly small cropped individuals in both types of pools. Thus, while the benthic patterns observed in open pools seem to be mostly influenced by physical factors, in closed pools the synergy between physical factors and biotic interactions (*e.g.* reef fish feeding pressure and herbivory) are likely determining its structure and functioning.

Reef fish assemblages

Reef fish species composition between Rocas Atoll and its closest oceanic island, the rocky archipelago of Fernando de Noronha, is remarkably similar from the functional and taxonomic perspectives [25]. These islands are part of the same volcanic mountain ridge, roughly 140 km apart, a common biogeographic history, endemic fish species, and similar physical and oceanographic conditions [28, 61]. Conversely, Rocas Atoll and Fernando de Noronha differ in their geomorphology, topography, substrate and sediment composition [28, 62-64]. Still, the dominant species in the present study, both in terms of abundance (the planktivores/mobile invertebrate feeder *Thalassoma noronhanum* and the territorial herbivore *Stegastes rocasensis*) and biomass (the scraper *Acanthurus chirurgus*), correspond to the same reported for reef fish assemblages from Fernando de Noronha [65]. On the other hand, some important aspects of the structure of reef fish assemblages differ between these islands, for instance, the species composition of the macrocarnivore functional group. While in Fernando de Noronha the small-sized mesopredator *Cephalopholis fulva* is the dominant species [65], at Rocas Atoll larger top predators such as *Lutjanus jocu*, *Ginglymostoma cirratum* and *Negaprion brevirostris* are the main macrocarnivores (Fig. 4). Even though all these species are important fishing targets, the dominant species recorded at Rocas Atoll are under major threats elsewhere especially due to their large body sizes in comparison to the grouper *C. fulva* which is still categorized by the IUCN as “Least Concern” [26, 66-67]. Fishing at Rocas Atoll is banned from inside the atoll to depths up to 1,000 m, although some occasional poaching further from the atoll rim still occur due to logistical difficulties to enforce the area. Conversely, most of the coastal waters of Fernando de Noronha are protected by a marine park but only up to the isobaths of 50 m. Additionally, fishing efforts targeting top predators (*e.g.* sharks) has historically occurred and still occurs close to Fernando de Noronha, thus populations of macrocarnivores of Fernando de Noronha are potentially more impacted by fishing when compared to populations of Rocas Atoll [65, 68]. Reef fish assemblages at Rocas Atoll varied between habitats with higher and lower hydrodynamic conditions (outer reef and open pools, lagoon and closed pools, respectively). Wave exposure interacting with fish swimming abilities can determine the structure and feeding behavior of reef fish assemblages [12, 14]. The black triggerfish *Melichthys niger*, for instance, known to inhabit areas with higher wave exposure, was only recorded in open pools [65, 69]. Conversely, the biomass of the main acanthurid species *A. chirurgus* and *A. coeruleus* was respectively five and three times higher in closed than in open pools. Similarly, at Laamu Atoll, in the Indian Ocean, assemblages of roving herbivores remarkably varied between habitats inside and outside the atoll rim as a response to wave action [70]. Because at Rocas Atoll *A. chirurgus* was responsible for 90% of the feeding pressure on the benthos, it is likely that the high hydrodynamic condition of the open pools could limit the feeding behavior of *A. chirurgus* and therefore influence the permanency of this species in closed pools. Additionally, reef fish assemblages could also be responding to differences in the benthic cover that could result in different food or shelter availability (*e.g.* [13, 65]).

Benthic cover and algal turfs

In the present study, algal turfs composed between 40 to 55% of benthic cover in tidal pools inside the atoll. The different algal turf composition between open and closed pools determined the differences in overall benthic cover between these habitats. Articulated calcareous algae largely dominated algal turfs of open pools, whereas turf from closed pools presented a greater contribution of non-calcified algae. The water circulation and the shape of these pools can affect nutrient availability and sediment dynamics [71-72]. Closed pools retain more sediment than open pools, which can cause smothering and shading, reducing the potential primary production [73]. The availability of sediments represents additional abrasion, compromising specially organisms with fleshy composition [20, 74-76]. Conversely, there was a higher abundance of crustose coralline algae in closed pools, which could be related to the relatively higher abundance and feeding pressure of herbivores controlling macroalgae in these areas [40, 76], or to the tolerance of crustose corallines to burial periods [47]. Similarly, the overall low coral cover at Rocas Atoll might be related to the sediment dynamics [77] that, throughout the year, can temporarily burrow coral colonies (Silva *pers. obs.*). With increasing disturbance (*e.g.* hydrodynamic conditions, herbivory) algal community structure tends to shift to resistant functional forms, such as turfs and crustose corallines [40,78].

Algal turfs, forming the epilithical algal matrix, are directly linked to two of the most important trophic pathways for fishes on coral reefs through the consumption of algae, detritus and predation of invertebrates [47, 79-80]. Likewise, at Rocas Atoll, algal turfs potentially represent the main trophic pathway between benthic primary production and reef fish consumers irrespective of habitat type. The biomass of algal turfs from open pools was three times higher than in closed pools, with a positive relationship between turf biomass and density of associated cryptofauna. Although this relationship might be caused by a higher biomass providing more habitat, it might also be due to the greater structural complexity conferred by articulated coralline algae in comparison to species forming algal turfs in closed pools (*i.e.*, the same biomass of these types of algae will have different structural complexity). We can also hypothesize that, by selectively feeding on filamentous algae and epiphytes, mesograzers among the cryptofauna promote the dominance of articulated calcareous algae and contribute to the maintenance of a more complex physiognomy in open pools.

The density and composition of cryptofauna associated to algal turfs have been explored between habitats, at different spatial scales, and relative to the volume of particulate matter [81-82]. The ecological roles of cryptofauna organisms are still poorly understood, but they can be the main protein sources to a variety of mobile invertebrate feeders and even some herbivorous fish [80-83]. Alongside with cryptofauna, organic detritus associated with turf algae further increases the nutritional quality of this substrate [47,79]. Although detritus load within turfs were not assessed in the present study, it is likely that it followed the pattern identified for sediments (greater amounts in closed pools) because the hydrodynamic of open pools could wash out detritus from the algal matrix more easily. A number of nominally herbivorous fishes are heavily dependent on protein to meet their energetic demands and a large portion of their diets and nutrition is complemented by detritus and invertebrates found within turf algae [84-85]. The identity of seaweeds forming the algal turfs can also play an important role in determining feeding pressure. Some fish might avoid articulated coralline algae because calcified structures can act as physical defenses (see [86-88]). Turf-forming species are specialized for areas subjected to moderate and high grazing pressure and physical stresses (*e.g.* hydrodynamic), to prevent their competitive exclusion by more productive but less resistant seaweeds [16]. Hence, identifying the algal species that compose algal turfs is critical to understand the trophic pathways involving these assemblages.

Reef fish feeding pressure on the benthos

Feeding pressure on the benthos was 20 fold greater in closed pools, where algal turfs presented a higher content of soluble sugars and starch than turfs in open pools. Carbohydrates in general are related to energy acquisition in fishes, but the digeston of complex carbohydrates often demands endosymbiontic bacteria that break them down to simpler assimilable components [89]. Most reef fish species present a very limited fermenting capability making soluble sugars and starch the only carbohydrate types possibly used [84]. Both soluble sugar and starch contents can be highly variable, but soluble sugars contents in particular, tend to increase with environmental stress [90]. Thus, the higher soluble sugar content on algal turfs from closed pools could be reinforcing the higher feeding pressure by grazing fishes, creating a stressing environment to the algal turf and a positive feedback between grazing activity and turf sugar content.

Most of the feeding pressure on the benthos was performed by scrapers (especially *Acanthurus chirurgus*), with mobile invertebrate feeders performing a small to negligible feeding pressure. Although this could be contributing to the lack of relation between feeding pressure and density of cryptofauna, invertebrate feeders usually feed by the end of the day or during the night so their feeding pressure might be underestimated through the applied sampling method [35, 91]. Scrapers were also the most representative functional group in terms of feeding pressure in other tropical reef systems in the Brazilian coast [36]. The territorial herbivore *Stegastes rocasensis* performed a similar feeding pressure in both pool typesof Rocas Atoll and was abundant across the different habitats. Adults of this species were described to use shallow turf-rich areas, while juveniles would inhabit deeper habitats [92]. Damselfishes of the genus *Stegastes* are territorial, small-sized fishes with restricted home ranges [93]. Their intimate association with the substrate allows them to occupy small caves and crevices potentially unaffected or lightly affected by hydrodynamic fluxes.

The dominance of feeding pressure by one species (*A. chirurgus*) and functional group (scrapers), could result in low functional redundancy because there are few species within this functional group and because feeding pressure is not evenly distributed between them [36]. The important contribution of *A. chirurgus* to feeding pressure follows its large abundance and biomass. Closed pools, which contained a particularly high sediment load, concentrated large shoals of this species regularly seen feeding on sand. Although sediment is known to reduce herbivory pressure on the benthos [94-95], *A. chirurgus* is a herbivorous-detritivorous species and sediment is commonly found in its digestive tracts, possibly ingested alongside detritus trapped in algal turfs [58, present work]. The diet of *Acanthurus coeruleus* encompass only 1% detritus, and this species was also more abundant in closed than in open pools [58]. This reinforces the hypothesis of closed pools being feeding refuges for reef fishes against intense hydrodynamic conditions or even from predators that are more abundant in open pools and outside the atol rim [14, 17, 32; Longo, Morais, Silva & Floeter *pess obs*]. In the present study, lemon sharks (*Negaprion brevirostris*), potential predators of acanthurids, were only recorded in open pools, outside the atoll rim and also swimming towards the pools and the lagoon with the tide inflow [Longo, Morais, Silva & Floeter *pess obs*]. The presence of apex predators can reduce macroalgal consumption in coral reefs up to ten fold, as a consequence of increased risk-effect to herbivores [96]. Thus, the presence of sharks in open pools and outside the atoll might be leading herbivorous species to feed in closed pools, which contributes to the discrepant feeding pressure between open and closed pools at Rocas Atoll. The lower risk-effect caused by less abundant or less threatening predators can result in dramatic changes in fish behavior, potentially affecting the structure of reef fish assemblages and benthic communities [96-97].

Herbivory assays and diet of the main herbivores

Understanding the patterns of selection or avoidance of algae by fish is a challenging task, since it involves nutritional properties and chemical composition of algae, as well as the ability of fish to properly process the algal material. When seven distinct seaweed species were offered to herbivorous fishes at a closed pool, there was a clear selection of the red algae *Digenea simplex*. Along with *Dictyopteris jolyana,* this species presented the higher content of starches and lower of proteins and lipids among the seaweeds used in the experiment. The avoidance of *Caulerpa verticillata*, *Canistrocarpus cervicornis* and *Dictyopteris* spp. could be related to anti-herbivore chemical defenses in these algae. Caulerpine, caulerpicine and caulerpenyne produced by the genus *Caulerpa* may be feeding deterrent to fish [85, 98] and diterpenoid metabolites produced by *Canistrocarpus* sp. and *Dictyopteris* spp. also present different deterrent effects on fish, urchin and amphipods [99-101]. Although *Sargassum* sp. may have poliphenolics that in sufficient concentration may suppress herbivory by some groups [86], its structural defense may play an important role in diminishing susceptibility to herbivory [86, 102-103]. Conversely, *Padina* sp. is known as a palatable macroalgae both in the Pacific [23] and in the Caribbean, where a morphological plasticity in response to high herbivory pressure was documented [104]. This algae was avoided in our herbivory assays possibly because of a lower content of starches and proteins in comparison to *D. simplex,* or the presence of highly refractory carbohydrates typical of Phaeophyceae.

A previous study on herbivory at Rocas Atoll, demonstrated that *D. simplex* was among the most consumed alga but with no record of the identity of herbivores responsible for algal removal [33]. In our experiment, algal removal was integrally performed by two acanthurid species: *A. chirurgus* (95% of the bites) and *A. coeruleus*. When accounting for the number of bites, *A. chirurgus* was highly dominant generating low functional redundancy [15, 36]. Even considering differences in the abundance of these species (Fig S2), the contribution of *A. chirurgus* is still disproportionately higher than *A. coeruleus*. Regarding the proportion of bites on the algae, these species were fairly redundant, only differing in the proportion of bites taken from *D. simplex* and *Sargassum* sp. Although both *Acanthurus* species were important in terms of macroalgal consumption on the assays, a more detailed analysis of their diets revealed the items naturally targeted by these species.

The diet of *A. chirurgus* was heavily dominated by sediment and detritus with articulated coralline algae as the most important algal group. On the other hand, *A. coeruleus* diet was composed almost 80% with red corticated algae (which includes *D. simplex*). At a tropical reef in the Brazilian coast, the diet of *A. chirurgus* was dominated by detritus (44%), that only accounted for 1% of *A. coeruleus* diet [58]. The differences on food composition between these two species can be related to differences on their food processing modes. Herbivorous-detritivorous species (*Acanthurus chirurgus*) usually possess a thick-walled gizzard-like stomach to mechanically break down ingested material, while browser species (*A. coeruleus*) usually rely on endosymbiotic fermentation to digest algae [58, 84, 105]. These results indicate some feeding complementarity where *A. chirurgus* ingests more articulated calcareous algae, but also redundancy between these species since both ingest red corticated algae. In the Caribbean, *A. coeruleus* and *A. tractus* (former *A. bahianus*) were redundant within the genus but complementary to scarini labrids [106]. At Rocas Atoll, the elevated amount of sediment could be benefitting the abundance and feeding pressure of *A. chirurgus*. In such a dynamic system, the contribution of more versatile species to ecosystem function can be more important than species diversity itself. Our results indicate that few species dominate important and complex trophic pathways between algal turfs and reef fishes at Rocas Atoll, with different levels of complementarity and redundancy.

Conclusions

This is the first integrative approach encompassing patterns and processes in shallow reef habitats at Rocas Atoll and brings up the complexity of this ecosystem. While the patterns and processes observed in the open pools seems to be mostly driven by physical factors and the tolerance of organisms to such conditions, in closed pools there seems to be a synergy between physical factors and biotic interactions (*e.g.* reef fish feeding pressure and herbivory). Closed pools figure as important feeding refuges for reef fishes, both from harsh hydrodynamic conditions and predators, impacting the structure and functioning of these habitats.

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Supporting information

Table S1. Sample summary of the field effort across the four studied sites in Rocas Atoll, Brazil.

Table S2 Analysis of simmilarity (ANOSIM) testing the effect of day on the responses observed for algae biomass loss, and number of bites of *Acanthurus chirurgus* and *A. coeruleus* on each algae in the herbivory assays. Tests were based on Bray-Curtis Similarity on square-root transformed data.

Table S3 Mean density of reef fish species and families recorded across the four studied habitats in the Atoll (open pools, closed pools, lagoon and outer reef). (*) The species *Thalassoma noronhanum* is considered a diurnal planktivore , however regarding the feeding pressure on the benthos this species is acting as a mobile invertebrate feeders, reason why this species is assigned to two functional groups.

Table S4 Benthic groups recorded in the photoquadrats from open and closed pools of Rocas Atoll, Brazil.

Table S5 Summary of t-tests on percent cover of benthic organisms between closed and open pools. Data was square-root transformed prior to the test and significant differences are showed in bold. df = degree of freedom.

Table S6 Macroalgae groups identified in the algal turfs and their occurrence in the sampled habitats. Groups that polled accounted between 80 and 100% of the samples' dry weight in closed pools (*) and in open pools (†). Genera and species in bold correspond to the first record of occurrence at Rocas Atoll.

Table S7 Cryptofauna associated to algal turfs and their occurrence in the sampled habitats.

Table S8 Relative abundance of dietary items of the main roving herbivores at Rocas Atoll, *Acanthurus chirurgus* and *A. coeruleus*. Dominant items are displayed in bold.

Figure S1 Proportion of abundance and biomass for each reef fish functional group pooling the four studied habitats in Rocas Atoll, Brazil.

Figure S2 Biomass of the two most abundant herbivorous fishes in the Atoll, *Acanthurus chirurgus* and *A. coeruleus*, between closed and open pools. (*) indicate significant differences in the means between habitats (t-test for *A. chirurgus*: t=7.02, $p<0.001$; t-test for *A. coeruleus*: t= 2.16, $p<0.05$). Error bars represent standard error of the mean.

Figure S3. Mean concentration of soluble sugars, starch and protein in algal turfs of closed and open pools. (*) indicate significant differences (t-tests; Sugars, t = -2.89, p = 0.014; Starch, t = -7.476, p <0.001; Proteins, t = 0.628, p = 0.538). Error bars represent standard error of the mean.

Figure S4 Mean total reef fish feeding pressure on the benthos in closed and open pools. (*) indicate significant differences in the mean feeding pressure between these two habitats (t-test; t = 2.19, p = 0.03). (}) indicate the contribution of the specie *Acanthurus chirurgus* (90% from the total). Error bars represent standard error of the mean.

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Supporting Information

Table S 1 Sample summary of the field effort across the four studied sites in Rocas Atoll, Brazil.

Site	Abbreviation	Coordinates	Depth	N Videos	N Benthic surveys	N Algal turfs	N Fish surveys	Herbivory assays
Open Pools								
Barretinha	BAR	03°51’75’’ S 33°49’05’’ O	2-3m	-	-	-	5	-
Falsa Barreta	FBA	03°51’64’’ S 33°49’40’’ O	1-4m	15	18	5	5	-
Podes Crer	PCR	03°52’20’’ S 33°48’45’’ O	1-3m	16	16	5	8	-
Salão	SAL	03°52’29’’ S 33°48’33’’ O	8-10m	9	9	-	6	-
Sum of samples				**40**	**43**		**24**	
Closed Pools								
Âncoras	ANC	03°52’51’’ S 33°48’16’’ O	2-3m	15	16	-	17	-
Cemitério	CEM	03°52’18’’ S 33°49’02’’ O	1-2m	-	-	-	25	-
Tartarugas	TAR	03°52’43’’ S 33°48’59’’ O	2-3m	15	17	5	20	13
Rocas	ROC	03°51’86’’ S 33°47’49’’ O	1-2m	15	18	5	20	
Zulu	ZUL	03°52’33’’ S 33°47’89’’ O	1-2m	-	-	-	6	-
Sum of samples				**45**	**51**		**88**	
Other habitats								
Lagoon	LAG	03°51’64’’ S 33°47’60’’ O	1-2m	-	-	-	23	-
Outer reef	OUT	03°29’53’’ S 33°49’11’’ O	10-12m	-	-	-	21	-
Sum of samples				-	-	-	**44**	-
Total of samples				**85**	**94**	**20**	**153**	**13**

Table S 2 Analysis of similarity (ANOSIM) testing the effect of day on the responses observed for algal biomass loss, and number of bites of *Acanthurus chirurgus* and *A. coeruleus* on each algae in the herbivory assays. Tests were based on Bray-Curtis Similarity on square root transformed data.

Differences between days	**Global Test**	
	R Global	**p value**
Algae biomass loss	-0.003	0.475
***Acanthurus chirurgus* (bites)**	0.024	0.321
***Acanthurus coeruleus* (bites)**	0.052	0.280

Table S 1 Mean abundance ± standard error of reef fish species per family recorded across the four studied habitats in the Atoll (closed pools, lagoon, open pools and outer reef). Functional group abbreviations (in order of appearence) stand for: scrp = scrapers, fbrow = fine browsers, minv = mobile invertebrate feeders, npla = nocturnal planktivores, omni = omnivores, mcar = macrocarnivores, ther = territorial herbivores, sinv = sessile invertebrate feeders, dpla = diurnal planktivores, rbrow = rough browsers(*) The species *Thalassoma noronhanum* is considered a diurnal planktivore , however regarding the feeding pressure on the benthos it acts as a mobile invertebrate feeder, reason why it is assigned to two functional groups.

Family/Species	**Functional group**	**Closed pools**					**Lagoon**	**Open pools**				**Outer reef**
		Âncoras	**Cemitério**	**Rocas pool**	**Tartarugas**	**Zulu**	**Lagoon**	**Barretinha**	**Falsa barreta**	**Podes crer**	**Salão**	**Outer reef**
Acanthuridae												
Acanthurus bahianus	scrp	0.06 ± 0.06	-	-	-	-	-	-	-	-	-	-
Acanthurus chirurgus	scrp	68.41 ± 15.69	20.68 ± 6.26	68.2 ± 7.46	33 ± 7.19	82.67 ± 22.85	26.3 ± 5.09	24.4 ± 14.37	2.2 ± 1.11	4.5 ± 1.79	0.5 ± 0.34	19.67 ± 3.22
Acanthurus coeruleus	fbrow	10.47 ± 4	1.2 ± 0.51	4.65 ± 2.88	16.05 ± 4.71	4 ± 2.82	1.39 ± 0.85	2.6 ± 1.25	3.4 ± 0.93	0.63 ± 0.42	0.83 ± 0.48	9.9 ± 2.99
Albulidae												
Albula vulpes	minv	-	-	-	-	-	-	144 ± 66.98	-	-	-	-
Apogonidae												
Apogon americanus	npla	-	0.12 ± 0.09	0.05 ± 0.05	-	-	-	-	-	-	0.17 ± 0.17	-
Balistidae												
Balistes vetula	minv	-	-	-	-	-	0.17 ± 0.1	-	-	-	-	-
Melichthys niger	omni	-	-	-	0.05 ± 0.05	-	-	-	-	8.63 ± 2.23	9.83 ± 4.77	-
Belonidae												
Strongylura timucu	mcar	0.29 ± 0.29	0.16 ± 0.16	-	-	-	0.43 ± 0.31	-	-	0.25 ± 0.25	-	-
Blenniidae												
Ophioblennius trinitatis	ther	0.06 ± 0.06	-	0.15 ± 0.11	-	0.17 ± 0.17	0.39 ± 0.26	-	-	-	-	-

Carangidae												
Carangoides bartholomaei	mcar	1.06 ± 0.42	1.08 ± 0.73	0.6 ± 0.46	0.65 ± 0.31	-	0.61 ± 0.4	0.8 ± 0.49	-	0.25 ± 0.16	-	0.1 ± 0.07
Caranx crysos	mcar	-	-	-	-	-	-	-	-	-	-	0.1 ± 0.1
Caranx latus	mcar	-	-	-	0.1 ± 0.07	-	0.04 ± 0.04	-	-	-	-	-
Caranx lugubris	mcar	-	-	-	-	-	-	-	-	-	-	0.19 ± 0.11
Carcharhinidae												
Carcharhinus perezii	mcar	-	-	-	-	-	-	-	-	-	-	0.05 ± 0.05
Negaprion brevirostris	mcar	-	-	0.05 ± 0.05	-	-	-	0.2 ± 0.2	-	0.13 ± 0.13	-	-
Chaetodontidae												
Chaetodon ocellatus	sinv	1.71 ± 0.5	0.12 ± 0.07	1.35 ± 0.28	0.1 ± 0.1	1.83 ± 0.48	0.43 ± 0.14	-	-	-	-	0.1 ± 0.1
Diodontidae												
Diodon hystrix	minv	-	-	0.05 ± 0.05	-	-	-	-	-	-	-	-
Epinephelidae												
Cephalopholis fulva	mcar	1.88 ± 0.84	0.04 ± 0.04	2.9 ± 0.79	-	2.33 ± 1.17	4.74 ± 0.68	-	-	-	0.17 ± 0.17	0.05 ± 0.05
Dermatolepis inermis	mcar	-	-	-	-	-	-	-	-	-	0.17 ± 0.17	0.1 ± 0.07
Paranthias furcifer	dpla	-	-	-	-	-	0.39 ± 0.27	-	-	-	-	-
Ginglymostomatidae												
Ginglymostoma cirratum	mcar	-	0.16 ± 0.11	0.15 ± 0.15	-	0.17 ± 0.17	0.04 ± 0.04	-	-	-	-	-
Gobiidae												
Coryphopterus sp.	omni	40.88 ± 11.44	87.88 ± 8.73	40.5 ± 4.14	57.15 ± 11.1	20.67 ± 9.04	55.26 ± 9.18	-	6 ± 1.52	0.75 ± 0.75	1.83 ± 0.83	0.05 ± 0.05
Elacatinus phthirophagus	minv	-	-	-	0.05 ± 0.05	-	-	-	-	-	-	-
Gnatholepis thompsoni	omni	6.35 ± 1.87	71.52 ± 10.01	8.8 ± 1.73	30.8 ± 7.33	1.67 ± 1.67	10.43 ± 2.6	-	3.6 ± 0.81	7.25 ± 3.51	-	0.05 ± 0.05
Haemulidae												
Haemulon chrysargyreum	minv	12.94 ± 12.94	-	-	-	56.17 ± 37.4	-	-	-	-	-	0.52 ± 0.48

Haemulon parra	minv	-	-	3.7 ± 1.4	-	20.17 ± 10.89	0.3 ± 0.26	-	-	-	-	0.1 ± 0.1
Holocentridae												
Holocentrus adscensionis	minv	1.94 ± 1.27	9.16 ± 3.56	9.25 ± 3.58	0.85 ± 0.25	0.17 ± 0.17	3.87 ± 1.74	2.4 ± 1.03	9.8 ± 2.22	7 ± 2.57	2.33 ± 1.56	0.52 ± 0.15
Myripristis jacobus	npla	-	0.52 ± 0.44	-	-	0.17 ± 0.17	0.43 ± 0.31	-	-	-	-	0.48 ± 0.2
Kyphosidae												
Kyphosus spp.	rbrow	-	-	1.25 ± 1.1	-	-	-	-	0.4 ± 0.4	0.5 ± 0.5	-	1.38 ± 0.71
Labridae												
Halichoeres radiatus	minv	1.24 ± 0.3	1.52 ± 0.99	2.6 ± 0.46	0.15 ± 0.08	0.83 ± 0.4	1.39 ± 0.45	4 ± 2.59	2.4 ± 0.68	-	1.83 ± 0.65	7.43 ± 1.1
Sparisoma amplum	scrp	1 ± 0.39	-	-	0.05 ± 0.05	1.17 ± 0.6	-	-	-	-	-	-
Sparisoma axillare	scrp	1.29 ± 0.43	0.28 ± 0.24	17.7 ± 3.54	-	1.17 ± 0.83	0.87 ± 0.35	-	-	-	-	-
Sparisoma frondosum	scrp	0.06 ± 0.06	-	0.05 ± 0.05	0.05 ± 0.05	0.83 ± 0.83	-	-	-	-	-	0.1 ± 0.07
Sparisoma radians	scrp	-	-	-	-	-	-	-	-	-	-	0.24 ± 0.12
Sparisoma sp.	scrp	0.06 ± 0.06	-	-	-	-	-	-	-	-	-	0.05 ± 0.05
*Thalassoma noronhanum**	dpla/minv	141.12 ± 30.86	75.96 ± 9.51	14.2 ± 6.94	134.45 ± 20.91	57 ± 28.4	46.35 ± 7.88	157.6 ± 29.91	105.8 ± 13.04	202.25 ± 24.07	80.5 ± 20.3	171.86 ± 20.62
Lutjanidae												
Lutjanus jocu	mcar	0.18 ± 0.13	1.08 ± 0.62	1.6 ± 1.13	0.6 ± 0.22	0.17 ± 0.17	0.13 ± 0.07	-	0.2 ± 0.2	0.13 ± 0.13	0.17 ± 0.17	0.1 ± 0.07
Malacanthidae												
Malacanthus plumieri	mcar	0.29 ± 0.11	0.48 ± 0.13	0.1 ± 0.07	0.95 ± 0.2	-	0.26 ± 0.11	0.8 ± 0.37	-	0.25 ± 0.16	-	-
Monacanthidae												
Aluterus scriptus	sinv	-	-	-	0.05 ± 0.05	-	-	-	-	-	-	-
Mullidae												
Mulloidichthys martinicus	minv	0.12 ± 0.12	0.68 ± 0.48	-	1 ± 0.69	-	0.43 ± 0.43	-	-	-	0.17 ± 0.17	0.52 ± 0.22
Pseudupeneus maculatus	minv	-	-	0.1 ± 0.1	-	-	0.04 ± 0.04	-	-	-	0.17 ± 0.17	0.05 ± 0.05
Muraenidae												

Gymnothorax miliaris	mcar	-	-	0.05 ± 0.05	0.05 ± 0.05	-	-	-	-	-	-	-
Muraena pavonina	mcar	-	-	-	-	0.17 ± 0.17	-	-	-	-	-	-
Ostraciidae												
Acanthostracion polygonius	sinv	-	-	-	-	-	-	-	-	-	-	0.05 ± 0.05
Lactophrys trigonus	minv	-	-	0.05 ± 0.05	-	-	-	-	-	-	-	-
Pempheridae												
Pempheris schomburgkii	npla	-	-	-	-	-	-	-	-	-	-	3.81 ± 1.86
Pomacanthidae												
Pomacanthus paru	omni	0.06 ± 0.06	0.04 ± 0.04	0.05 ± 0.05	0.05 ± 0.05	-	0.04 ± 0.04	-	-	-	0.83 ± 0.48	0.33 ± 0.11
Pomacentridae												
Abudefduf saxatilis	omni	27.88 ± 13.27	17.36 ± 4.56	21.95 ± 6.38	69.15 ± 21.67	7.83 ± 1.78	9.52 ± 3.61	28.8 ± 9.32	3 ± 2.28	7.13 ± 3.5	4.5 ± 3.51	14.62 ± 2.79
Chromis multilineata	dpla	14.94 ± 8.88	-	8.1 ± 4.36	0.2 ± 0.16	1.83 ± 1.33	3.7 ± 1.87	-	-	-	0.33 ± 0.33	0.1 ± 0.1
Stegastes pictus	ther	-	-	-	-	-	0.26 ± 0.11	-	-	-	-	-
Stegastes rocasensis	ther	27.88 ± 4.46	39.76 ± 4.27	15.4 ± 3.16	50.3 ± 6.2	20.83 ± 5.56	28.3 ± 3.71	59.6 ± 14.25	87 ± 1.1	105.75 ± 14.62	61.17 ± 14.87	2 ± 0.38
Serranidae												
Rypticus saponaceus	mcar	-	0.04 ± 0.04	-	-	0.17 ± 0.17	-	-	-	-	-	0.05 ± 0.05
Sphyraenidae												
Sphyraena barracuda	mcar	0.06 ± 0.06	-	-	0.05 ± 0.05	-	-	-	-	-	-	-

Table S 4 Benthic groups recorded in the photoquadrats from open and closed pools of Rocas Atoll, Brazil.

	Closed Pools			Open Pools		
Benthic groups	**Âncoras**	**Rocas**	**Tartarugas**	**Falsa Barreta**	**Podes Crer**	**Salão**
Phylum Porifera						
Encrusting form	X	X	X	X	X	
Massive form	X	X				
Tubular form		X				
Phylum Cnidaria						
Class Anthozoa						
Order Zoanthidea						
Palythoa caribaeorum	X					X
Zoanthus sociatus	X			X	X	
Order Scleractinia						
Favia gravida		X				
Mussismilia hispida	X					
Porites astreoides	X	X	X			
Siderastrea stellata	X	X	X	X	X	X
Phylum Chordata						
Class Ascidiacea	X					
Algal turfs						
Calcareous turf	X	X		X	X	X
Non-calcified turf	X	X	X	X	X	X
Articulated Calcareous Algae		X		X		
Tricleocarpa cilyndrica						X
Galaxaura sp.	X			X		X
Cyanobacteria (microfilm)	X	X	X	X	X	
Corticated Macroalgae						
Champia parvula			X			

Codium spp.		X					X
Digenia simplex		X					
Hypnea musciformis				X	X		
Non-identified	X	X		X	X		
Crustose algae							
Crustose coralline algae	X	X		X	X		
Other non-calcified algae	X		X				
Filamentous algae							
Bryopsis pennata					X	X	
Caulerpa sp.				X			
Caulerpa verticillata				X		X	
Chaetomorpha sp.				X			
Non-identified	X	X		X	X		
Foliose macroalgae							
Canistrocarpus sp.				X	X	X	
Dictyopteris sp.				X	X		
Leathery macroalgae							
Lobophora variegata	X						
Padina sp					X		
Sargassum spp.		X		X	X		
Non-identified					X		
Sand and sediment	X	X	X	X	X	X	

Table S 5 Summary of t-tests on percent cover of benthic organisms between closed and open pools. Data was square root transformed prior to the test and significant differences are showed in bold. **df** = degree of freedom.

Benthic Group	**t-value**	**df**	**p value**	**Between pools**
Non-calcified turf	6.29	97	**< 0.001**	Closed > Open
Calcareous turf	-10.17	97	**< 0.001**	Closed < Open
Sediment	4.51	97	**< 0.001**	Closed > Open
Caulerpa verticilatta	-6.00	97	**< 0.001**	Closed < Open
Siderastrea spp.	-3.22	97	**0.001**	Closed < Open
Zoanthus sp.	-3.74	97	**< 0.001**	Closed < Open
Microfilm (cyanobacteria)	2.03	97	**< 0.05**	Closed > Open
Sargassum sp.	-3.80	97	**< 0.001**	Closed < Open
Canistrocarpus sp.	-4.64	97	**< 0.001**	Closed < Open
Calcareous Coralline Algae	2.42	97	**p< 0.05**	Closed > Open

Table S 6 Macroalgae groups identified in the algal turfs and their occurrence in the sampled habitats. Groups that polled accounted between 80 and 100% of the samples' dry weight in closed pools (*) and in open pools (†). Genera and species in bold correspond to the first record of occurrence at Rocas Atoll.

	Closed Pools		**Open Pools**	
Macroalgae groups	**Rocas**	**Tartarugas**	**Falsa Barreta**	**Podes Crer**
Division Rhodophyta				
Acrochaetium sp.	X			
Amphiroa sp. †			X	X
Bryothamnion triquetrum			X	
Ceramium gracilimum				X
***Chondria polyrhiza* ***	**X**	**X**	**X**	**X**
***Chondria* sp.**				**X**
Digenea simplex *	X	X	X	
Erythrocladia sp.				
Erythrotrichia sp.				
Gelidiella acerosa			X	
Gelidiella sp.	X			
Gelidium americanum			X	
***Gelidium crinale* ***	**X**	**X**	**X**	**X**
Gelidium pusillum	X	X		
Gelidium sp.	X			
Haliptilon subulatum			**X**	
Hypnea cenomyce			**X**	**X**
Hypnea musciformis	X		X	
Jania adhaerens	X	X		X
Jania capillacea				X
Jania verrucosa			**X**	
Jania prolifera		**X**		
Jania sp. †			X	X
Polysiphonia sp.		X		

Polysiphonia subtilissima		X		
Pterocladiella sanctarum		**X**	**X**	**X**
Division Chlorophyta				
Bryopsis sp.		X		
Caulerpa mexicana			X	
Caulerpa verticillata			X	
Caulerpella ambigua			**X**	**X**
Chaetomorpha spiralis			**X**	
Cladophora sp.	X	X		X
Derbesia marina	X			X
Valonia aegagropila †	X	X	X	
Division Heterokontophyta				
Class Phaeophyceae				
Canistrocarpus cervicornis				X
Dictyopteris delicatula		X	X	X
Dictyopteris plagiogramma	**X**	**X**		
Dictyopteris sp. 1			X	X
Dictyopteris sp. 2	X			
Dictyota mertensii				X
Dictyota pulchella			X	X
Ectocarpus sp.			X	
***Levringia* sp. ***	**X**			
Lobophora sp.			X	
Padina sp.			X	
Sargassum sp.			X	
Sphacelaria sp.		X	X	X

Table S 7 Cryptofauna associated to algal turfs and their occurrence in the sampled habitats.

Groups	Closed Pools		Open Pools	
	Rocas	**Tartarugas**	**Falsa Barreta**	**Podes Crer**
Phylum Annelida				
Class Polychaeta	X	X		X
Phylum Arthropoda				
Subphylum Crustacea				
Class Malacostraca				
Order Amphipoda				
Morpho 1		X	X	X
Morpho 2			X	X
Morpho 3			X	X
Morpho 4		X		X
Morpho 5	X		X	X
Order Decapoda				
Family Mithracidae				
Morpho 1	X		X	X
Morpho 2	X			X
Morpho 3				X
Super Family Xanthoidea				
Morpho 1	X			
Order Isopoda				
Morpho 1				X
Order Tanaidacea				
Morpho 1		X	X	X
Morpho 2		X	X	X
Subphylum Hexapoda				
Class Insecta				

Order Diptera				
Family Chironomidae				
Larvae	X	X	X	
Phylum Cnidaria				
Class Anthozoa				
Order Zoantharia				
Family Zoanthidae				
Zoanthus sociatus		X	X	X
Phylum Echinodermata				
Class Ophiuroidea				
Morpho 1				X
Morpho 2				X
Morpho 3				X
Phyllum Mollusca				
Class Gastropoda				
Morpho 1		X		
Morpho 2		X		
Morpho 3	X			

Table S 8 Relative abundance of dietary items, excluding sediment and detritus, of the main roving herbivores at Rocas Atoll, *Acanthurus chirurgus* and *A. coeruleus*. Dominant items are displayed in bold.

	Acanthurus chirurgus	***Acanthurus coeruleus***
Algae group	**Relative abundance in the diet (% ± SE)**	
Red calcareous algae	**48 ± 6**	3 ± 2
Red corticated algae	**27 ± 6**	**81 ± 3**
Green filamentous algae	12 ± 7	7 ± 1
Red filamentous algae	5 ± 3	0 ± 0
Invertebrates	6 ± 4	0 ± 0
Cyanophyceae	2 ± 1	6 ± 2
Green corticated algae	0 ± 0	0 ± 0
Brown corticated algae	0± 0	2 ± 1
Brown filamentous algae	0 ± 0	1 ± 1

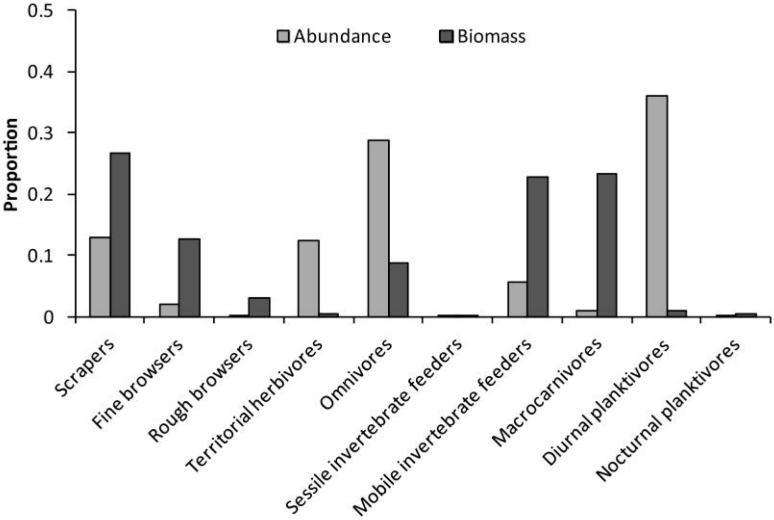

Figure S 1 Proportion of abundance and biomass for each reef fish functional group pooling the four studied habitats in Rocas Atoll, Brazil.

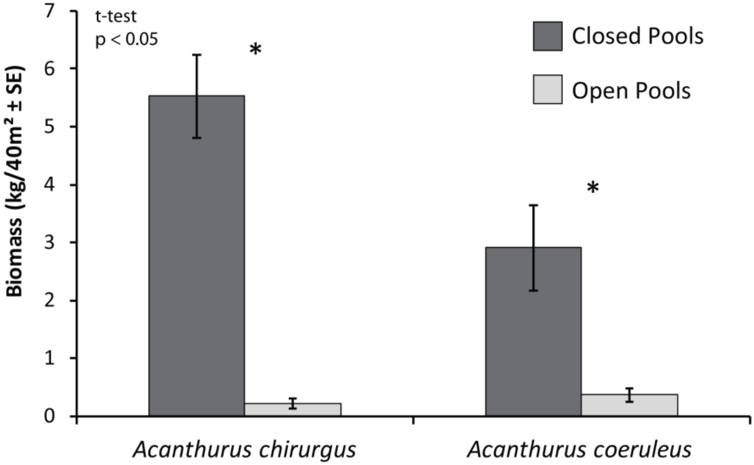

Figure S 2 Biomass of the two most abundant herbivorous fishes in the Atoll, *Acanthurus chirurgus* and *A. coeruleus*, between closed and open pools. (*) indicate significant differences in the means between habitats (t-test for *A. chirurgus*: t=7.02, p<0.001; t-test for *A. coeruleus*: t= 2.16, p<0.05). Error bars represent standard error of the mean.

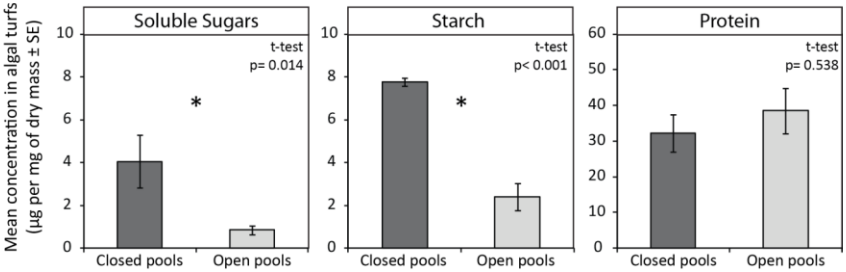

Figure S 3 Mean concentration of soluble sugars, starch and protein in algal turfs of closed and open pools. (*) indicate significant differences (t-tests; Sugars, t = -2.89, p = 0.014; Starch, t = -7.476, p <0.001; Proteins, t = 0.628, p = 0.538). Error bars represent standard error of the mean.

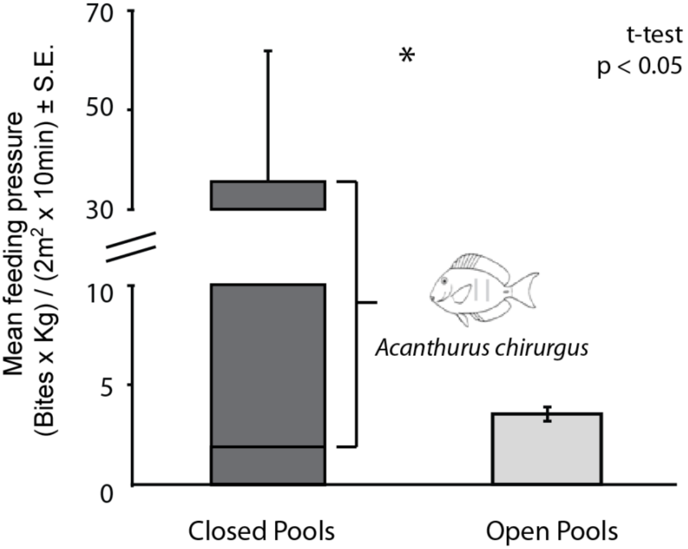

Figure S 4. Mean total reef fish feeding pressure on the benthos in closed and open pools. (*) indicate significant differences in the mean feeding pressure between these two habitats (t-test; t = 2.19, p = 0.03). (}) indicate the contribution of the specie *Acanthurus chirurgus* (90% from the total). Error bars represent standard error of the mean.

CAPÍTULO 3

Herbivory drives large-scale spatial variation in reef fish trophic interactions

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Herbivory drives large-scale spatial variation in reef fish trophic interactions

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Running headline: Large-scale spatial variation in fish trophic interactions

Abstract

Trophic interactions play a critical role in the structure and function of ecosystems. Given the widespread loss of biodiversity due to anthropogenic activities, understanding how trophic interactions respond to natural gradients (*e.g.* abiotic conditions, species richness) through large-scale comparisons can provide a broader understanding of their importance in changing ecosystems and support informed conservation actions. We explored large-scale variation in reef fish trophic interactions, encompassing tropical and subtropical reefs with different abiotic conditions and trophic structure of reef fish community. Reef fish feeding pressure on the benthos was determined combining bite rates on the substrate and the individual biomass per unit of time and area, using video recordings in three sites between latitudes 17°–27°S in the Brazilian Coast. Total feeding pressure decreased tenfold and the composition of functional groups and species shifted from the Northern to the Southernmost sites. Both patterns were driven by the decline in the feeding pressure of roving herbivores, particularly scrapers, while the feeding pressure of invertebrate feeders and omnivores were similar. The differential contribution to the feeding pressure across trophic categories, with roving herbivores being more important in the Northernmost and Southeastern reefs, determined changes in the intensity and composition of fish feeding pressure on the benthos among sites. It also determined the distribution of trophic interactions across different trophic categories, altering the evenness of interactions. Feeding pressure was more evenly distributed at the Southernmost than in the Southeastern and Northernmost sites, where it was dominated by few herbivores. Species and functional groups that performed higher feeding pressure than predicted by their biomass were identified as critical for their potential to remove benthic biomass. Fishing pressure unlikely drove the large-scale pattern, however it affected the contribution of some groups on a local scale (*e.g.* large-bodied parrotfish), highlighting the need to incorporate critical functions into conservation strategies.

Keywords feeding pressure; functional groups; geographic variation; critical functions; Brazil

Introduction

Trophic interactions are fundamental to the structure and function of ecosystems by altering patterns of species density and biomass across different trophic levels (Paine 1992). Anthropogenic activities are negatively affecting trophic interactions, causing severe changes in ecosystems, from biodiversity loss to shifts in abiotic conditions (Estes et al. 2011). Understanding the strength and distribution of trophic interactions in natural communities and their response to these changes is critical to support informed conservation actions (Duffy 2002).

Comparisons of trophic interactions along geographic scales can provide a broader understanding of their importance in changing ecosystems by benefitting from natural gradients, for example when there is variation in the species richness or abiotic conditions (Pennings & Silliman 2005). A recent large-scale study spanning a 32^o latitudinal gradient in seagrass beds demonstrated that predation on marine sessile invertebrate communities and resulting effects on species richness were stronger in the tropics compared to temperate regions (Freestone et al. 2011). However, in both terrestrial and marine systems, most large-scale comparisons of trophic interactions are focused on herbivory, without considering other trophic categories, and present inconsistent results (Moles et al. 2011; Poore et al. 2012).

In marine ecosystems, herbivory is widely recognized as a critical process (Poore et al. 2012), affecting the structure and functioning of different systems (*e.g.* rocky reefs-Sala & Bouderesque 1997; coral reefs-Mumby 2006; kelp forests-Carter, VanBlaricom &

Allen 2007). Although the large-scale geographic variation of plant chemical defences and susceptibility to herbivory have been investigated (*e.g.* Bolser & Hay 1996; Pennings, Siska & Bertness 2001), large-scale comparisons of the intensity of herbivory in marine systems through standardized methods are relatively uncommon (see Pennings & Silliman 2005; Pennings et al. 2009; Bennet & Bellwood 2011). A recent meta-analysis found little to no influence of temperature on herbivory in marine systems, but highlighted the strong effects herbivores have on producer's abundance (Poore et al. 2012).

A commonly referred hypothesis states that the ability of marine ectothermic herbivores to digest and assimilate plant material would decrease with lower temperatures (Gaines & Lubchenco 1982). This has been proposed as an explanation for the decrease in the species richness, abundance and bite rates of tropical herbivorous reef fishes as latitude increases in the Atlantic (i.e. towards colder areas; Floeter et al. 2005). Conversely, a recent large-scale study comprising three sites spanning 11^o of latitude on the coast of New Zealand argued that temperature is unlikely a constraint to temperate herbivorous fish because there were no differences in demographic patterns between herbivorous and carnivorous fishes from warmer and colder areas (Trip et al. 2013). Hence, there is still a debate on the interactive mechanisms between herbivory by reef fishes and temperature, with few studies going beyond patterns of species richness and abundance (see Bennet & Bellwood 2011).

Directly quantifying herbivory and predation as trophic interactions (*e.g.* rates of interaction) instead of inferring these rates through species richness and abundance across large spatial scales is challenging (Pennings & Silliman 2005; Freestone et al. 2011). Reef fishes feeding on the benthos comprise a good model to address such question, as these trophic interactions play an essential role in structuring benthic communities, for example through herbivory and predation on mesograzer crustaceans (Lewis 1986; Duffy & Hay 2000; Ceccarelli, Jones & McCook 2001; Kramer et al. 2013). To date, studies have mainly focused on macroalgal removal, relative richness and abundance of herbivores or trophic structure of communities, often neglecting other trophic interactions rather than herbivory (Ferreira et al. 2004; Floeter et al. 2005; Bennet & Bellwood 2011; Cheal et al. 2013). However, the per capita effects among species rather than differences in species richness and abundances may be driving shifts in interaction strength and thus need to be assessed (Pennings & Silliman 2005).

Food webs are generally structured by a few disproportionately strong and several weak to intermediate interactions (Paine 1992). The dominance of a few species in a given ecological process results in low ecological redundancy, commonly associated with less stability to disturbances (Duffy 2002; Hoey & Bellwood 2009). As a result, higher species diversity may not equate to higher system stability when species perform functions unevenly (Duffy 2002; Hooper et al. 2005). Consumers that impact the ecosystem disproportionately to their abundances can play central roles in the structure and function of communities (Power et al. 1996). A reduction in functionally dominant trophic links can prompt declines in biodiversity, therefore identifying these central species across geographic scales could guide the conservation of key ecological processes they mediate (Paine 1992; Duffy 2002; Green & Bellwood 2009).

We explored the large-scale variation of reef fish feeding pressure on the benthos in three sites spanning 10° of latitude, encompassing tropical and subtropical reefs along the Brazilian coast (Fig. 1). Feeding pressure was determined combining bite rates on the substrate and the individual biomass per unit of time and area. This study aims to determine: (i) how total feeding pressure and the contribution of different fish functional groups within distinct trophic categories vary across large spatial scales; and (ii) identify species and functional groups that perform higher feeding pressure than predicted by their abundances, highlighting their importance to the ecosystem and the need for incorporating functional approaches into conservation strategies.

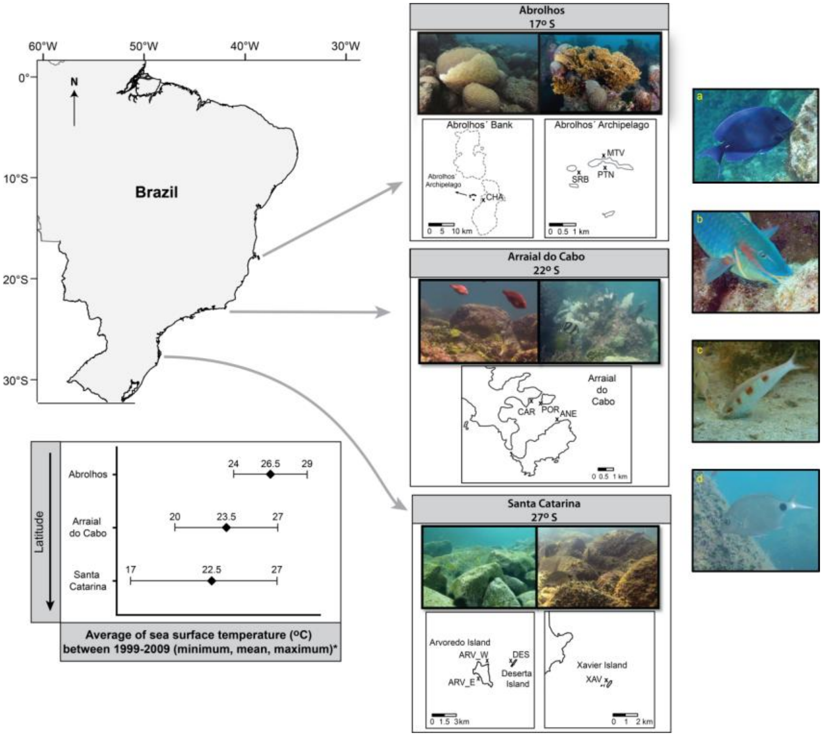

Figure 1 Studied reef areas along the Brazilian coast. Abbreviations in the maps indicate the locations within sites: CHAP = Chapeirão; MTV = Mato Verde; SRBA = Siriba; PTN = Portinho Norte; CAR = Cardeiros; POR = Porcos; ANE = Anequim; ARV_W = Western Arvoredo; Arv_E = Eastern Arvredo; DES =Deserta; XAV = Xavier. * Sea surface temperature data from NOAA (http://www.nodc.noaa.gov/sog/cortad).

Materials and methods

STUDY AREA

This study was conducted in three reef sites along the Brazilian coast, encompassing tropical and subtropical reefs from 17°S to 27°S, with mean annual sea surface temperature varying from 26.5°C to

22.5^{o}C, respectively (Fig. 1; average annual temperatures from 1999–2009 available in http://www.nodc.noaa.gov/sog/cortad/; NOAA). In each site, a minimum of three locations were sampled during the austral summer to account for local heterogeneity and all fieldwork was staggered between 09:00–15:00h to ensure data were comparable within and between sites (see Table S1 in Supporting Information).

The Northernmost site is within the Abrolhos Bank, approximately 60 km off the coast of Bahia state, north-eastern Brazil (17°58’S; 38°42’W), considered the largest and richest coral reefs in the South Atlantic (Francini-Filho et al. 2013). Three fringing reefs were sampled at the Abrolhos’ Archipelago (Portinho Norte, Siriba and Mato Verde) and one additional reef at the top of coral pinnacles of the Parcel dos Abrolhos (Chapeirão), with depth varying from 3–10 m. All sampled areas are within the Abrolhos Marine National Park, established in 1983, but due to the inconsistent enforcement there is occasional poaching in the areas (Francini-Filho & Moura 2008a; Francini-Filho et al. 2013). The fringing reefs of the Archipelago are not massive coral formations and may be regarded as rocky reefs with a developing reef-building community (Francini-Filho et al. 2013). Benthic cover at the studied sites at Abrolhos was mainly epilithic algal community, coralline and fleshy algae, hydrocorals and scleractinian corals (see details in Appendix S1). Mean annual sea surface temperature at Abrolhos was 26.5^{o}C, varying from 24^{o}–29^{o}C and water temperature during fieldwork ranged from 27^{o}–29^{o}C.

The Southeastern study sites were subtropical rocky reefs located at the leeward side of the bay of Arraial do Cabo, Rio de Janeiro state (22^{o}58’S; 41^{o}59’W), South-Eastern Brazil. Three rocky reefs protected from winds and high waves, with depth varying between 3–11 m, were sampled: Anequim, Cardeiros and Porcos (Fig. 1). Despite having restrictions for fisheries since 1997, including a small no-take zone, the effectiveness of enforcement in these reefs is compromised. These reefs are composed of granite boulders ending in a sand bottom around 10 m (Ferreira, Peret & Coutinho 1998). Benthic cover was primarily epilithic algal community, sponges, zoanthids and gorgonians (Appendix S1). This region is influenced by coastal upwelling events during the austral summer and spring, however as the studied reefs are located in the leeward side of bays and inlets, this cold and nutrient-enriched water only bathes them for short periods and generally in deeper zones (Ferreira, Peret & Coutinho 1998). Mean annual sea surface temperature at Arraial do Cabo was 23.5°C, varying from 20°–27°C, and water temperature during fieldwork ranged from 23.5°–25°C.

The Southernmost study sites were subtropical rocky reefs of coastal islands in Santa Catarina state (27 °36’S; 48°23’W), South Brazil, lying from 3–13 km from the coast and depths varying between 3–12 m (Fig. 1). Four rocky reefs were studied: two with no protection from fisheries (Xavier and Western Arvoredo) and two legally protected by the Arvoredo Marine Reserve since 2003 (Eastern Arvoredo and Deserta), although with insufficient enforcement. These reefs are similar to the studied reefs in Arraial do Cabo, with granite boulders ending in sand bottoms around 10 m. Benthic cover was predominantly epilithic algal community and fleshy algae, in addition to sponges in deeper and zoanthids in shallower areas (Appendix S1). Mean annual sea surface temperature at Santa Catarina was 22.5°C, varying from 17°–27°C, and water temperature during fieldwork ranged from 23°–25°C. Although the mean temperatures between the Southernmost and the Southeastern sites were similar, 59% of the temperatures recorded between 1999-2009 at the Southernmost site were below 23.5 ^{o}C and 28% below 20^{o}C, respectively the annual mean and minimum temperatures of the Southeastern site in the same period. Therefore, water temperature in the studied sites could be described as higher at Abrolhos (Northernmost site), intermediate at Arraial do Cabo (Southeastern site) and lower at Santa Catarina (Southernmost site; Fig. 1).

REEF FISH FEEDING PRESSURE AND ABUNDANCE

Reef fish feeding pressure on the benthos was assessed with remote underwater video recordings. A video camera on a weighted tripod was placed on the reef substratum and a 2 m transect tape was used to demarcate the recorded area and removed after one minute. Each area was recorded for 15 min with the central 10 min of each video analysed (*sensu* Longo & Floeter 2012). A minimum of three locations within each study site were sampled; an average of 15 replicated 2 m^2 reef areas were haphazardly selected and video recorded (Table S1). This effort resulted in 290 video samples: 79 at Abrolhos, 90 at Arraial do Cabo and 121 at Santa Catarina.

Each fish recorded feeding on the benthos was identified and assigned to a functional group; the total length estimated based on the transect tape initially deployed; and the number of bites on the reef substratum were counted. A bite was considered every time a fish stroke the benthos with its jaws opened, closing its mouth subsequently, regardless of ingestion (Hoey & Bellwood 2009; Longo & Floeter

2012). Feeding pressure was determined by the total bites taken and body mass (kg) of each fish, to account for potential body size variation in the bite impact (Hoey & Bellwood 2009). The estimated biomass of fish was obtained from length–weight relationships from the literature (Froese & Pauly 2013). This method allowed fish feeding pressure to be evaluated from the perspective of several functional groups within different trophic categories, accounting for body size variation, per unit of time and area [(Bites x kg) / (2 m^2 x 10 min)]. Here, feeding pressure is used as a metric of interaction strength *sensu* Paine (1992).

Fish density and biomass were estimated using 20 x 2 m strip transects (40 m^2), where the diver swam identifying, counting and estimating the size (total length) of larger (> 5cm) and shoaling fishes. The fishes were assigned to functional groups and the density and biomass of each species was obtained for each transect. These surveys were conducted at the same sites and period of day where video recording were taken and in the same or adjacent days to minimize differences in the assessed community. A total of 412 replicated transects were conducted: 148 at Abrolhos, 68 at Arraial do Cabo and 200 at Santa Catarina.

FUNCTIONAL GROUPS

Despite potential problems associated with combining reef fishes into trophic and functional groups (Halpern & Floeter 2008), the functional perspective can provide a better understanding of ecosystems (*e.g.* Bellwood, Hughes & Hoey 2006; Hoey & Bellwood 2009). In this study, fishes were assembled into eight functional groups based on trophic categories and feeding behaviour from the literature (*e.g.* Ferreira et al. 2004; Halpern & Floeter 2008; Green & Bellwood 2009; Longo & Floeter 2012), complemented by extensive field observations by the authors.

Particularly for nominally herbivorous fishes (*sensu* Choat, Clements & Robbins 2004), we combined feeding modes and mobility, incorporating nutritional ecology into the discussions (Ferreira et al. 2004; Clements, Raubenheimer & Choat 2009). Herbivorous fishes were divided in two major categories: roving herbivores, comprising four functional groups according to their feeding mode, but intrinsic divergent nutritional ecology: scrapers, excavators, fine browsers and rough browsers; and territorial herbivores (Ferreira et al. 2004). Scrapers and excavators can ingest a rich mass of detritus and animal matter trapped on the epilithical algal matrix and macroalgae they feed on, and can occasionally predate live corals (Choat, Clements & Robbins 2004). However, scrapers remove less reef substratum than excavators, implying different contributions in reef bioerosion (Green & Bellwood 2009). Scrapers and excavators usually exhibit low ability for digesting algal carbohydrates, both endogenously and exogenously (Choat & Clements, 1998). As a result, they rely on protein-rich detritus to meet their nutritional requirements (Crossman, Choat & Clements 2005; Ferreira & Gonçalves 2006). Thus, while we are referring to scrapers and excavators simply as herbivores, in the Brazilian province they possess similar proportions of plant material and sediment/detritus in their diets (Ferreira & Gonçalves 2006), and thus could be regarded as herbivorous-detritivorous species. In this study, scrapers included two acanthurids (surgeonfishes) and five scarinae labrids (parrotfishes), while excavator was comprised by a single species, the parrotfish *Scarus trispinosus* (following Ferreira & Gonçalves 2006; Francini-Filho et al. 2008; Longo & Floeter 2012). Other Brazilian parrotfish species (*Sparisoma amplum*) may act as excavators at larger sizes (Ferreira & Gonçalves 2006; Francini-Filho et al. 2008b), but only small individuals of this species (< 30 cm) were observed and thus classified as scrapers.

Browsers consistently feed on macroalgae by selecting and cropping individual algal components without removing the reef substratum or large amounts of detritus (Green & Bellwood 2009). Once they ingest primarily and almost exclusively macroalgae (i.e. algivorous), browser species can rely on endosimbiotic bacteria to ferment the highly complex algal carbohydrates they ingest (Choat & Clements, 1998). Here, browsers were also separated by feeding mode; those that crop small pieces of algae, were labelled fine browsers (one acanthurid), whereas those that remove large pieces of algae (kyphosids), were labelled rough browsers. Apart from feeding rates, diet and isotopic niche (*e.g.* Lewis 1986; Ferreira & Gonçalves 2006; Dromard et al. 2014), very little is known about the nutrient assimilation of the fine browser species in the present study, *Acanthurus coeruleus*, but it is likely to be an intermediate between those described to scrapers and browser (Choat & Clements, 1998).

Territorial herbivores, namely damselfishes, feed primarily on the epilithical algal matrix they farm within a defended territory, having a critical role in structuring benthic community through grazing and territoriality (Ceccarelli, Jones & McCook 2001). The nutritional ecology of these fishes is poorly understood, but most species ingest large amounts of filamentous algae, animal material and detritus (Wilson

& Bellwood 1997; Ferreira, Peret & Coutinho 1998). Thus, although territorial herbivores are likely to exhibit intermediate levels of gut fermentation between detritivores and herbivores (Choat, Clements & Robbins 2004), here they were conservatively classified as a single group of territorial herbivores, comprising two damselfish species of the genus *Stegastes*.

The classification of fishes into the groups of mobile invertebrate feeders (i.e. feed on small benthic crustaceans, worms, molluscs), sessile invertebrate feeders (i.e. feed on cnidarians, molluscs, sponges) and omnivores (i.e. diversified diet including plankton, animal and plant material) followed Ferreira et al. (2004). The nutritional ecology, and physiology of omnivores can vary as a response to temperature (Behrens & Lafferty 2007) and although there might be a wide variation in feeding mode and mobility of reef fishes grouped as omnivores in the present study (Ferreira et al. 2004), they were conservatively classified as a single group.

DATA ANALYSIS

A permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) design was created based on the hierarchical sampling of localities (each reef) nested within sites (latitudes). Thus, “sites” were treated as a fixed factor and “locality” as random factors nested within “sites”. Such design was used to investigate both the variation in the intensity and composition of feeding pressure (response variables) across the sites and localities. The use of PERMANOVA on Euclidian Distance matrices calculated from only one variable yields an equivalent to

Fisher's test, using permutations to calculate pseudo-F distributions and p-values (Anderson 2001). Thus, differences in the total feeding pressure (response variable) were investigated using this PERMANOVA design (999 iterations) on an Euclidean distance matrix obtained from square root transformed data. Similarly, this was also used to evaluate the total feeding pressure excluding the contribution of roving herbivores (response variable), and for the feeding pressure of each functional group independently (response variables). Differences in the total non-mass-standardized bite rates (response variable) were also explored with and without roving herbivores to hold the consistency of the observed patterns for feeding pressure. Compositional changes in the feeding pressure of species and functional groups were assessed with the same PERMANOVA design (999 iterations), on Euclidean Distance matrices obtained from square root transformed data. This procedure was repeated excluding the contribution of roving herbivores for both species' and functional groups' matrices. Pairwise comparisons were conducted only when the fixed factor was significant. Such tests were performed in the software Primer 6 & PERMANOVA+ (Anderson & Gorley 2007).

To investigate how uniformly the feeding pressure was distributed among species and functional groups, an evenness measure was adapted from Hurlbert's (1971) probability of inter-specific encounter. This index calculates the probability of two randomly sampled individuals from the assemblage represent different species, where 0 indicates that all individuals belong to the same species and 1 that all individuals differ. As applied in the present study, it represents the probability of two randomly sampled units of feeding pressure within a pool being performed by different species or functional groups. This is measured in probability units and, different from other indices is not prejudiced by sample size (Gotelli 2008). Cumulative rarefaction curves based on this index were performed with ECOSIM 7.0 (Gotelli & Entsminger 2007), providing confidence intervals for each curve through 1000 iterations. Thus, if the observed evenness and confidence intervals for a given site, do not overlap the confidence interval generated to another site, the null hypothesis that the evenness of communities do not significantly differ can be rejected at $\alpha = 0.05$ (Gotelli 2008). A flat pattern is expected in such rarefaction curves because of the index's independence to sample sizes (Gotelli 2008), but this approach was chosen over other methods because it standardizes the evenness measure to a common number of feeding pressure among sites and provides confidence intervals for hypothesis testing (Gotelli & Colwell 2001). The relationship between the mean feeding pressure, mean abundance and biomass from visual censuses were assessed through Pearson's correlations, applied on log(x+1) transformed data by species and functional groups pooled from all studied sites. For significant correlations, 95% confidence intervals were generated through 1000 iterations. Combining data from video recordings and visual censuses was possible because there is evidence of a limited difference in species detection between both techniques in the studied areas, with video recording having more advantages to assess feeding pressure and visual census to assess fish density (Longo & Floeter 2012). Combining mean fish biomass with the feeding pressure metric illustrate a compensation between bite rates and density of different sized individuals within and between species. Where more abundant but smaller individuals with higher bite rates could have a similar contribution to less abundant but bigger individuals with lower bite rates.

Results

There was a significant reduction in the total feeding pressure from the Northern to the Southernmost site (PERMANOVA, P < 0·05; Fig. 2), with values declining roughly ten times between them (Abrolhos= 28·06, Arraial do Cabo= 6·35 and Santa Catarina= 3·69; Table 1). This was consistent with the decreasing pattern observed in the contribution of roving herbivores, particularly scrapers, whose feeding pressure significantly varied among the three sites (PERMANOVA; P = 0·001; Table S2). However, total feeding pressure did not vary among sites when all roving herbivores were excluded from the analysis (PERMANOVA; P = 0·001; Table 1). Similarly, non-mass-standardized total bite rates followed the same pattern with and without roving herbivores (see Figure S1 in Supporting Information; Table S3).

Scrapers were the most representative functional group at the Northernmost and Southeastern sites contributing 61% and 57% of the total feeding pressure and accounting for approximately 70% and 98% of the feeding pressure exerted by roving herbivores, respectively. The feeding pressure of this group at the Southernmost site was 4% of the total. Excavators and fine browsers were only recorded at the Northernmost reefs (Abrolhos) while rough browsers were rarely observed along the three studied sites, even though it was the most notable roving herbivore in the Southernmost reefs (Santa Catarina). Omnivores, in turn, presented an inverse pattern, acting as the main group in the Southernmost site with 40% of the feeding pressure, decreasing to 18% at the Southeastern and 4% at the Northernmost sites. The relative functional contribution of scrapers decreased around 15 times from the Northern to the Southernmost site while omnivores' increased 10 times (Fig. 2). Feeding pressure of territorial herbivores and mobile invertebrate feeders also increased towards the Southernmost site, being respectively 2% and 3% at Abrolhos and 21% and 18% in Santa Catarina, while sessile invertebrate feeders were always below 5%.

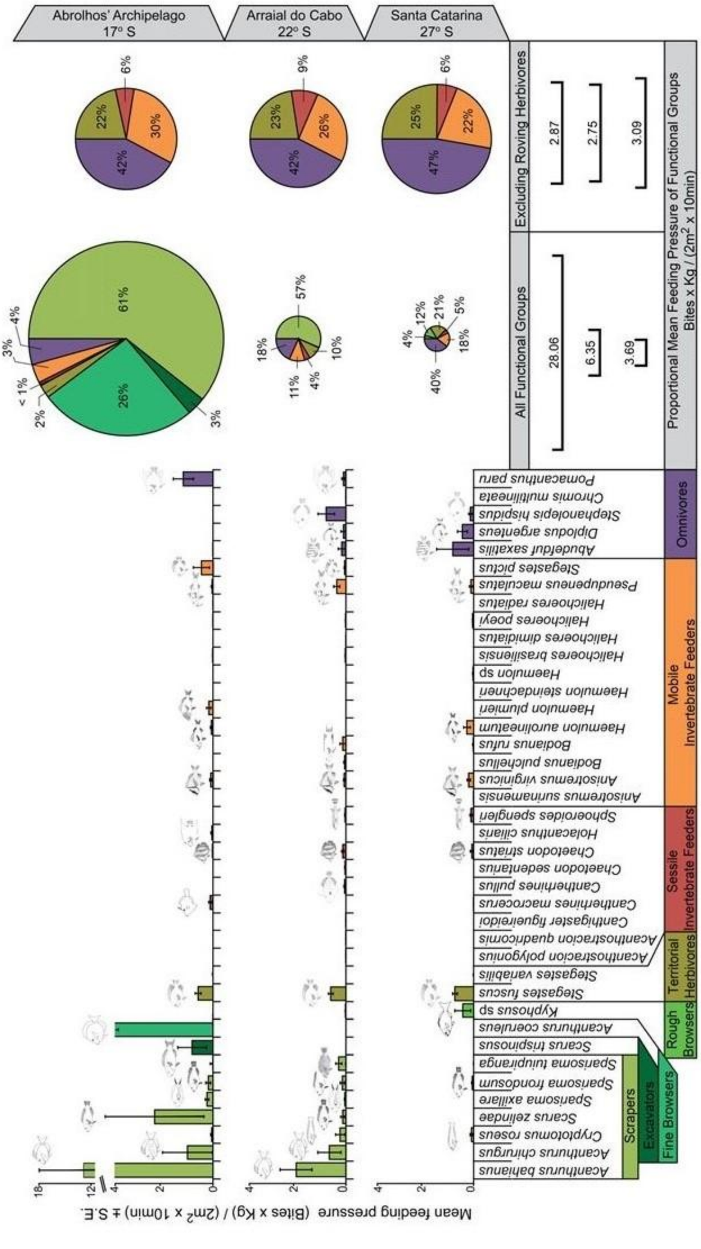

Figure 2 Mean feeding pressure of species (bar plots ± S.E.) and proportional mean feeding pressure of functional groups across the studied sites (pie charts). Circle sizes are proportional to the total feeding pressure.

Table 1 Summary of permutational multivariate analysis of variance (PERMANOVA) for total feeding pressure of all functional groups and excluding roving herbivores, with site as a fixed factor and locality as a random factor nested within sites. Pairwise comparisons are only provided for the fixed factor. Pseudo-F distribution and p-values obtained through 999 iterations. Significant differences are presented in bold ($p < 0.05$). df = degrees of freedom; MS = mean squares.

Variable	**Source of variation**	**df**	**MS**	**Pseudo-F**	***p*-value**
Total feeding pressure of the entire community					
Main Test	Site	2	14.585	8.454	**0.014**
	Locality (Site)	8	1.756	1.422	0.181
Pairwise comparisons	**t**	***p*-value**			
Abrolhos vs. Arraial	2.069	0.099			
Abrolhos vs. Santa Catarina	4.556	**0.018**			
Arraial vs. Santa Catarina	1.897	0.078			
Total feeding pressure excluding roving herbivores	**Source of variation**	**df**	**MS**	**Pseudo-F**	***p*-value**
Main Test	Site	2	0.445	0.309	0.729
	Locality (Site)	8	1.492	2.412	**0.016**

Most feeding pressure at the Northernmost site (Abrolhos) was performed by acanthurid species of two functional groups (the scraper *Acanthurus bahianus* and the fine browser *A. coeruleus*) and at the Southeastern site (Arraial do Cabo) by two scraper acanthurid species (*A. bahianus* and *A. chirurgus*). In the Southernmost study area (Santa Catarina), the rough browser *Kyphosus* sp. was the roving herbivore performing higher feeding pressure, while the territorial herbivore *Stegastes fuscus* and the omnivorous species *Abudefduf saxatilis* were the major contributors (Fig. 2).

The composition of species and functional groups performing feeding pressure significantly varied among studied sites (PERMANOVA, P < 0·05; Table 2). However, excluding all roving herbivores, the composition of functional groups did not vary among the sites, but species within these groups did (Fig. 2; Table 2). Feeding pressure was more evenly distributed among the functional groups in the Southernmost site (Table 3; Figure S2a), with an evenness of 0·75, followed by the Southeastern site, with 0·63, and the Northernmost site, with 0·56. A similar pattern was observed in the species level; Abrolhos displayed a lower evenness (0·70) in comparison to Arraial do Cabo (0·85) and Santa Catarina (0·86) in the presence of all roving herbivores (Fig. S2c). However, when all roving herbivores were excluded from both analyses, the evenness of feeding pressure did not vary among the study sites (Table 3; Fig. S2b and S2d).

Feeding pressure was not correlated to either abundance of functional groups (r = 0·22, p = 0·37) or species (r = 0·20, p=0·11, Fig.3a and 3b). However, there was a significant and positive correlation between feeding pressure and biomass of both functional groups (r =

0·52, p = 0·02; Fig. 3c) and species (r = 0·41, p = 0·001; Fig. 3d). Two functional groups presented a higher feeding pressure than predicted by their biomass: scrapers at Abrolhos and Arraial do Cabo, and fine browsers at Abrolhos. Also, the feeding pressure of all acanthurid species was disproportionate to their biomass at Abrolhos and Arraial do Cabo (Fig. 3). The territorial herbivore *Stegastes fuscus*, the mobile invertebrate feeder *S. pictus* and the omnivore *Pomacanthus paru* at Abrolhos in addition to the omnivore *Stephanolepis hispidus* at Arraial do Cabo, also performed a higher feeding pressure than predicted by their biomass.

Table 2 Summary of permutational multivariate analysis of variance (PERMANOVA) and pairwise comparisons on the composition of feeding pressure, with site as a fixed factor and locality as a random factor nested within sites. Pairwise comparisons are only provided for the fixed factor. Significant differences are presented in bold ($p < 0.05$). Pseudo-F distribution and p-values obtained through 999 iterations. Significant differences are presented in bold ($p < 0.05$). df = degrees of freedom; MS = mean squares.

Variables	**Source of Variation**	**df**	**MS**	**pseudo-F**	***p*-value**
Entire Community					
Functional groups					
Main Test	Sites	2	90.081	7.678	**0.002**
	Locality (Site)	8	11.889	1.317	0.136

Pairwise Comparison (Site)	**t**	***p***
Abrolhos vs. Arraial	2.291	**0.006**
Abrolhos vs. Santa Catarina	2.209	**0.033**
Arraial vs. Santa Catarina	3.499	**0.008**

	Source of Variation	**df**	**MS**	**pseudo-F**	***p*-value**
Species					
Main Test	Sites	2	77.687	5.919	**0.002**
	Locality (Site)	8	13.316	1.351	0.087

Pairwise Comparison (Site)	**t**	***p***
Abrolhos vs. Arraial	2.077	**0.036**
Abrolhos vs. Santa Catarina	3.066	**0.006**
Arraial vs. Santa Catarina	2.024	**0.021**

	Source of Variation	**df**	**MS**	**pseudo-F**	***p*-value**
Excluding roving herbivores					
Functional groups					
Main Test	Sites	2	1.175	0.169	0.994
	Locality (Site)	8	7.226	3.354	**0.001**
Species					
Main Test	Sites	2	11.516	2.029	**0.016**
	Locality (Site)	9	5.860	2.370	**0.001**
Pairwise Comparison (Site)	**t**	***p***			
Abrolhos vs. Arraial	1.451	**0.048**			
Abrolhos vs. Santa Catarina	1.434	**0.052**			
Arraial vs. Santa Catarina	1.469	0.097			

Table 3 Evenness (Hurlbert's PIE) of feeding pressure within functional groups and species, with and without roving herbivores, and comparisons among the three sites. The evenness resulted from cumulative rarefaction curves generated for each site and comparisons are based on the 95% confidence intervals (1000 iterations; Figure S1). Significant differences are presented in bold

Variables	**Abrolhos (17°S)**	**Arraial do Cabo (22°S)**	**Santa Catarina (27°S)**	**Comparison (95% CI)**
Functional Groups				
All	**0.559**	**0.625**	**0.749**	**AB = AC ≠ SC**
Except Roving Herbivores	0.682	0.696	0.665	AB = AC = SC
Species				
All	**0.704**	**0.849**	**0.861**	**AB ≠ AC = SC**
Except Roving Herbivores	0.746	0.835	0.823	AB = AC = SC

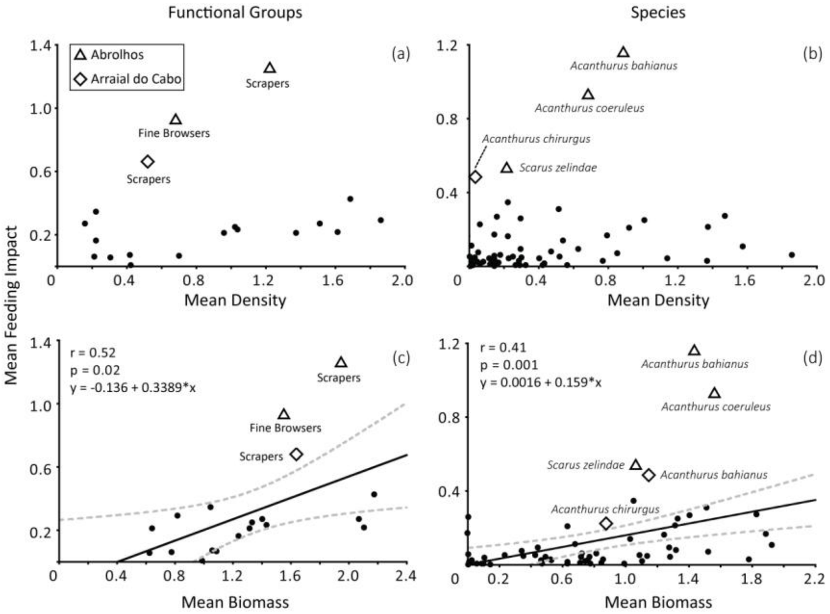

Figure 2 Pearson's correlation between mean feeding pressure, mean density and biomass of species and functional groups. Data from the three study sites were pooled in this analysis and log(x+1) transformed. Triangles indicate data from Abrolhos and diamonds from Arraial do Cabo. Only herbivore's functional groups and species identified as critical are indicated. Gray dashed lines indicate 95% confidence intervals generated through 1000 iterations.

Discussion

The decline in the total feeding pressure (pooling all trophic categories) from the Northern to the Southernmost sites was mostly driven by the reduction in the feeding pressure of roving herbivores whose richness and abundance decline beyond the latitude 23^{o}S (i.e. Arraial do Cabo) in the Western Atlantic (Ferreira et al. 2004; Floeter et al. 2005). The feeding pressure of roving herbivores also determined changes in the composition and distribution of the feeding pressure among the studied areas.

The distinct patterns of feeding pressure between roving herbivores and other trophic categories suggest that an herbivory-related constraint could be taking place. The potential physiological constraints on tropical herbivorous fishes (*e.g.* acanthurids, scarids) to digest and assimilate plant material in lower temperatures (Gaines & Lubchenco 1982) has already been used as an explanatory hypothesis for declining bite rates, richness and abundance of herbivorous fish in the South Atlantic (Ferreira et al. 2004; Floeter et al. 2005). Although the difference in the mean sea surface temperature between the South-eastern and the Southernmost sites was 1^{o}C, the minimum temperature varied 3^{o}C between the areas (20^{o} and 17^{o}C, respectively). Additionally, temperatures below 20^{o}C, a range that can affect the distribution and bite rates of herbivorous fishes in the Western Atlantic (Floeter et al. 2005), were only recorded at the Southernmost site. Thus, fish could be responding more to long-term temperature patterns than to the instantaneous temperature (see Bennet & Bellwood 2011). Because most roving herbivores in the present study (scrapers) are in fact herbivorous-detritivorous and rely on a higher protein ingestion from detritus, associated microbiota and benthic invertebrates (Choat, Clements & Robbins 2004; Ferreira & Gonçalves 2006; Dromard et al. 2014), the herbivory-related constraint related to this functional group should be reconsidered. Additionally, it is still poorly understood how the relative contribution of detritus, invertebrates and plant material in the diet of these species may vary across geographic scales. Hence directly assigning the observed declining feeding pressure to constraints in their digestive ability or only to temperature would be inaccurate.

A recent study comparing demographic traits (eg. growth rates, life span) and abundance of two reef fish species with distinct nutritional ecology (herbivore vs. carnivore) found a consistent pattern for both species along a temperature gradient despite their different feeding strategies (Trip et al. 2003). However, the herbivorous fish in that study, *Odax pullus*, consistently feeds on macroalgae (*i.e.* algivore) and belong to a temperate related clade, being distributed among subtropical and temperate reefs of New Zealand and Australia (Clements et al. 2004). Thus, the lower temperatures do not constrain their ability to digest and assimilate plant material as it could potentially do to tropical originated herbivorous fish that inhabit warmer habitats and also rely on detritus in their diet (*e.g.* scarinis and some acanthurids). Studies applying consistent methods across a large spatial scales, comprising tropical and subtropical originated herbivorous fishes, with distinct nutritional ecology, are needed before a precise conclusion may be drawn on this matter.

Alternatively, characteristics of the reefs, rates of primary production, algal biomass, chemical defences and nutritional quality of algae among the studied areas could also be important explanatory factors for the feeding pressure patterns of roving herbivores (Hay 1997; Cebrian et al. 2009; Poore et al. 2012). The reefs at the Northernmost area, for example, present more tropical characteristics in comparison to the other studied sites, comprising twenty species of scleractinian corals and higher coral cover (Leão, Kikuchi & Testa 2003; Appendix S1). Conversely, the rocky reefs of the Southeastern and Southernmost areas comprise fewer coral species (five and two, respectively; Leão et al. 2003), and are more similar in terms of reef composition (*e.g.* granite boulders with low coral cover; Appendix S1; see pictures in Fig. 1) and trophic structure of reef fish assemblages (Ferreira et al. 2004). Thus, one could expect that the feeding pressure of roving herbivores would be higher at the Northernmost site but similar between the two other areas. However, there was an abrupt decline in the feeding pressure of this group between the Southeastern to the Southernmost areas, coinciding with the decline in the abundance of roving herbivores in the same areas, primarily attributed to temperature-related factors (Ferreira et al. 2004; Floeter et al. 2005). Differences in the macroalgal availability are also unlikely to be the explanatory factor to the patterns in the present study because: (1) macroalgal cover did not significantly vary between the three studied sites (Appendix S1); (2) the richness of macroalgae did not decline from the Northern to the Southernmost studied sites; and (3) when the macroalgal composition by genera and species was compared along the Brazilian coast, the Northernmost site was more similar to tropical areas, while the Southeastern and Southernmost sites belonged to the warm temperate group (Horta et al. 2001).

Macroalgal removal by reef fishes at the Great Barrier Reef declined ten times between the Northern and Southernmost sites across a 7^o latitudinal gradient, pooling macroalgae browsers and scrapers (Bennet & Bellwood 2011). This was consistent with the tenfold reduction in herbivory across the three sites spanning 10^o of latitude in the present study, also pooling browsers, scrapers and excavators. Another common outcome was the dominance of a few species comprising most of macroalgal removal (browsers and scrapers) and feeding pressure (mainly scrapers), generating low functional redundancy.

The dominance of all roving herbivores combined, also affected the composition and distribution of feeding pressure among different trophic categories. The evenness pattern of trophic interactions within functional groups and species was determined by a few strong (scrapers) and several weak interactions (territorial herbivores, mobile invertebrate feeders and omnivores). Manipulation of grazing by invertebrates in an intertidal habitat also revealed a skewed distribution of trophic interactions towards dominant species (Paine 1992). In kelp forests, the combination of weak interactions from different species has important effects on food webs (Sala & Graham 2002). If the dominance of trophic interactions by few species can result in less stability (*sensu* Duffy 2002), the higher evenness of trophic interactions observed in Santa Catarina could translate into a higher functional redundancy of trophic links and would provide more stability and resistance to the loss of biodiversity (Duffy 2002).

The incongruence between feeding pressure and density of species and functional groups can be reflecting the fact that fish from different trophic groups and nutritional strategies present different bite rates (Choat, Cements & Robbins 2004). However, from a general perspective, it may be also interpreted in the notion that species performing more function than would be predicted based on their biomass, have the potential to be critical species to ecosystems (Power et al. 1996). Even though we did not assess the amount of removed substratum and the effects of fish feeding pressure on the benthos, scrapers and fine browsers adding up to three *Acanthurus* and a *Scarus* species (Fig. 3) can be suggested as critical because: (1) they performed most of the total feeding pressure; (2) their contribution was greater than would be predicted based on their biomass (Power et al. 1996); (3) their feeding pressure and its consequent benthic biomass removal, can be critical ecosystem processes in reef systems (*e.g.* Lewis 1986; Hoey & Bellwood 2009); and (4) these functional groups and mainly acanthurid species determined the large-scale spatial variation in fish feeding pressure.

There is a widespread notion, mostly associated to herbivores and top predators, that the removal of critical species and functional groups by overfishing may strongly impact the functioning of reefs often resulting in phase-shifts (Mumby 2006; Hoey & Bellwood 2009; Estes et al. 2011; Cheal et al. 2013). Despite being the most species rich functional group in reef systems, invertebrate feeders and their relative contribution to ecosystem function are poorly discussed and seldom regarded as critical (Jones, Ferrel & Sale 1991). Omnivores are also commonly overlooked, especially considering that this category often comprises species with different feeding modes that can perform important functional roles in the reefs. While the consequences of loosing these groups are still to be understood, fishing pressure is increasingly affecting different trophic levels including herbivores, invertebrate feeders and omnivores (Floeter, Halpern & Ferreira 2006; Estes et al. 2011; Bender et al. 2013).

On a large scale, it is unlikely that fishing pressure drove the decline in the feeding pressure of roving herbivores because the exploitation of this group does not occur in the Southernmost studied area where they presented the lower feeding pressure, but it is intense between the Northeastern coast of Brazil and the Southeastern studied sites where they comprised most of the feeding pressure (see Floeter, Halpern & Ferreira 2006; Nóbrega & Lessa 2007; Cunha et al. 2012;; Bender et al. 2014). Thus, if the differences in the fishing pressure were the main drivers of the observed large-scale patterns, a completely opposite scenario would be expected, where roving herbivores would be more important in the Southernmost reefs. Conversely, on a local scale, the patterns of feeding pressure are likely influenced by the decline or disappearance of large herbivores. For example, large-bodied scarids, such as the greenbeak parrotfish *Scarus trispinosus,* has been historically under strong fishing pressure at Abrolhos and Arraial do Cabo (Floeter, Halpern & Ferreira 2006; Bender et al. 2013, 2014). This species was recently categorized as endangered in the IUCN red list given its 50% population decline over the past 20-30 years caused by overfishing (Ferreira et al. 2012). At the Southeastern site (Arraial do Cabo), both local ecological knowledge and underwater visual census data shows an historical decline in this species populations (Bender et al. 2014). Thus, the absence of feeding pressure by *S. trispinosus* at Arraial do Cabo (Fig. 2) probably result from overfishing limiting species functional roles, while their feeding pressure at Abrolhos could have been even higher in the past. Acanthurids identified as critical at the reefs of Abrolhos and Arraial Cabo, are also under fishing pressure in the northeastern Brazilian coast (Nóbrega & Lessa 2007; Cunha et al. 2012), which could be affecting their functional roles in the reefs. Invertebrate feeders (*e.g. Pseudupeneus maculatus*) and omnivores (*e.g. Diplodus argenteus*) also demand urgent attention since both are under fishing pressure in the Brazilian reefs (Floeter, Halpern & Ferreira 2006; Cunha et al. 2012) and the consequences of their potential ecological extinction are difficult to predict. Even though some of these species do not fit the criteria to be in most red lists, their ecological roles are threatened and must be protected.

The remarkable changes in the intensity and composition of fish feeding pressure on the benthos across the studied sites was driven by the declining contribution of roving herbivores. Comparing how species with different feeding ecology affect the strength and distribution of trophic interactions across large spatial scales can shed light to new interaction-based approaches to functional redundancy and conservation of reef ecosystems.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

AppendixS1. Information on the benthic cover at the studied sites.

Table S1. Sample summary of the field effort at the study sites.

Table S2. Summary of PERMANOVA of total feeding pressure per functional group between the studied sites.

Table S3. Summary of PERMANOVA for total non-mass-standardized bite rates between the studied sites, with and without roving herbivores.

Figure S1. Mean feeding pressure and non-mass-standardized bite rates between the studied sites.

Figure S2. Cumulative rarefaction curves of the evenness of feeding pressure within functional groups and species, with and without roving herbivores, and comparisons between the studied sites.

Supporting Information

Table S1 Sample summary of the field effort at the study sites along the Brazilian Coast. UVC= underwater visual census.

Site	Abbreviation	Coordinates	Depth	N (Videos)	N (UVC)	Month	Year
Abrolhos (17° S)							
Chapeirão	CHA	17°58’38.62’’ S 38°43’19.40’’ W	6-12m	15	28	March	2010
Mato Verde	MTV	17°57’53.78’’ S 38°42’04.69’’ W	4-10m	8	25	March	2010
Portinho Norte	PTN	17°57’43.52’’ S 38°41’52.51’’ W	3-10m	40	50	March	2010
Siriba	SRB	17°58’10.63’’ S 38°42’38.19’’ W	4-10m	16	45	March	2010
Sum of samples				**79**	**148**		
Arraial do Cabo (22° S)							
Anequim	ANE	22°58’51.81’’ S 41°59’03.34’’ W	3-12m	30	20	April	2011
Cardeiros	CAR	22°57’55.27’’ S 42°00’06.34’’ W	3-12m	30	20	April	2011
Porcos	POR	22°58’03.27’’ S 41°59’39.11’’W	3-12m	30	20	April	2011
Sum of samples				**90**	**64**		
Santa Catarina (27° S)							
Eastern Arvoredo	ARV_E	27°17’34.15’’ S 48°21’27.66’’ W	3-12m	25	25	Feb-Apr	2011
Western Arvoredo	ARV_W	27°17’06.23’’ S 48°22’17.16’’ W	3-12m	33	51	Feb-Apr	2010/2011
Deserta	DES	27°16’09.23’’ S 48°19’49.13’’ W	3-12m	33	44	Feb-Apr	2011
Xavier	XAV	27°36’32.35’’ S 48°23’09.27’’ W	3-12m	30	80	Feb-Apr	2010/2011
Sum of samples				**121**	**200**		
Total of samples				**290**	**412**		

Table S2 Summary of permutational multivariate analysis of variance (PERMANOVA) for total feeding pressure of each functional group with site as a fixed factor and locality as a random factor nested within sites. Pairwise comparisons are only provided for the fixed factor. PERMANOVA was applied on Log (x+1) transformed data and using Euclidean Distance and thus yields an equivalent to Fisher's test using permutations (Anderson 2001). Pseudo-F distribution and p-values obtained through 999 iterations. Significant differences are presented in bold ($p < 0.05$). df = degrees of freedom; MS = mean squares.

Functional Group	**Source of variation**	**df**	**MS**	**Pseudo-F**	***p*-value**
Scrapers					
Main Test	Site	2	18.899	33.498	**0.001**
	Locality (Site)	9	0.436	0.407	0.930
Pairwise comparisons	**t**	***p*-value**			
Abrolhos vs. Arraial	11.555	**0.007**			
Abrolhos vs. Santa Catarina	2.478	**0.031**			
Arraial vs. Santa Catarina	5.869	**0.004**			
Territorial herbivores	**Source of variation**	**df**	**MS**	**Pseudo-F**	***p*-value**
Main Test	Site	2	0.122	0.231	0.729
	Locality (Site)	9	0.607	2.820	**0.003**
Sessile Invertebrate Feeders	**Source of variation**	**df**	**MS**	**Pseudo-F**	***p*-value**
Main Test	Site	2	0.772	1.669	0.219
	Locality (Site)	9	0.558	6.731	**0.003**
Mobile Invertebrate Feeders	**Source of variation**	**df**	**MS**	**Pseudo-F**	***p*-value**
Main Test	Site	2	0.849	0.123	0.890
	Locality (Site)	9	0.786	2.502	**0.027**
Omnivores	**Source of variation**	**df**	**MS**	**Pseudo-F**	***p*-value**
Main Test	Site	2	1.731	0.940	0.463
	Locality (Site)	9	2.183	4.467	**0.003**

Table S3 Summary of permutational multivariate analysis of variance (PERMANOVA) for total non-mass-standardized bite rate of all functional groups and excluding roving herbivores, with site as a fixed factor and locality as a random factor nested within sites. Pairwise comparisons are only provided for the fixed factor. Pseudo-F distribution and p-values obtained through 999 iterations. Significant differences are presented in bold ($p < 0.05$). df = degrees of freedom; MS = mean squares.

Variable	**Source of variation**	**df**	**MS**	**Pseudo-F**	***p*-value**
Total bite rate of the entire community					
Main Test	Site	2	810.05	10.479	**0.014**
	Locality (Site)	8	80.61	3.295	0.181
Pairwise comparisons	**t**	***p*-value**			
Abrolhos vs. Arraial	2.203	0.062			
Abrolhos vs. Santa Catarina	4.592	**0.003**			
Arraial vs. Santa Catarina	2.972	**0.038**			
Total bite rate excluding roving herbivores	**Source of variation**	**df**	**MS**	**Pseudo-F**	***p*-value**
Main Test	Site	2	58.784	1.525	0.270
	Locality (Site)	8	40.324	3.985	**0.001**

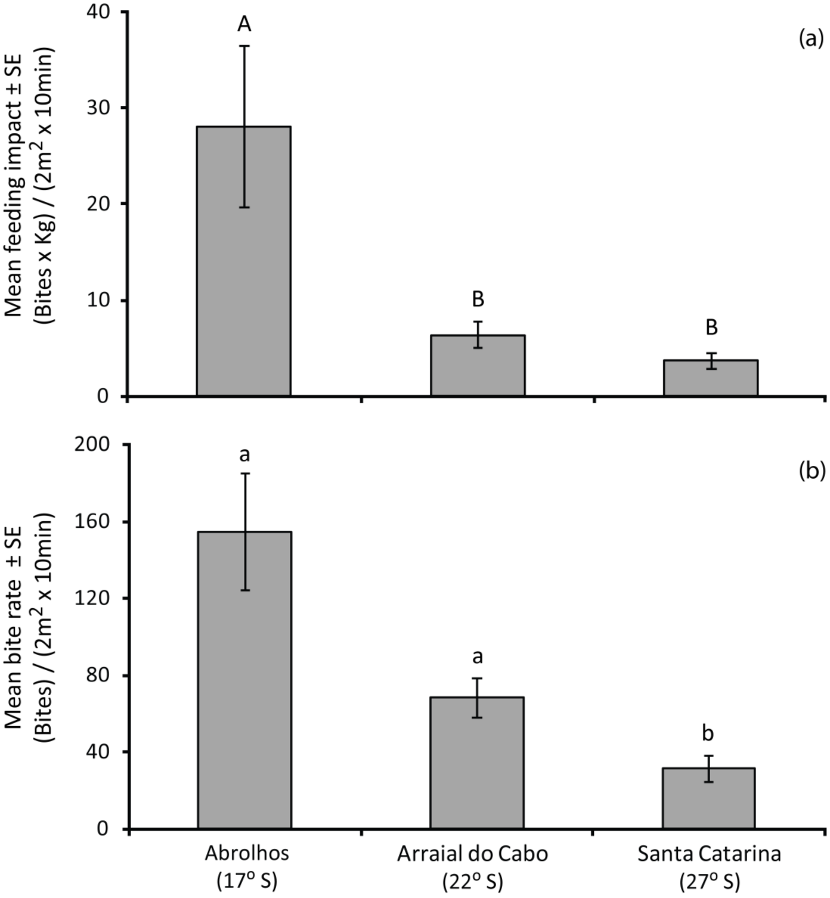

Figure S1 Mean feeding pressure (a) and non-mass-standardized bite rates (b) between the studied sites. Letters above the bars refers to pairwise comparisons from PERMANOVA tests, with upper case letters referring to the results in Table 1 and lower case letters to Table S3.

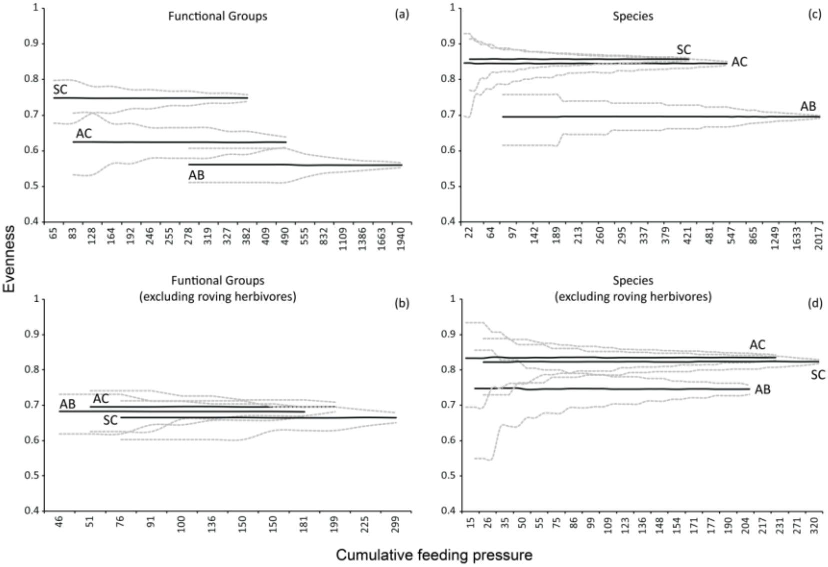

Figure S2 Cumulative rarefaction curves of the evenness of feeding pressure by functional groups (a, b) and species (c,d), accounting for all functional groups (a,c) and excluding roving herbivores (b,d). Gray dashed lines indicate 95% confidence intervals generated through 1000 iterations. AB = Abrolhos (17° S); AC = Arraial do Cabo (22° S); SC = Santa Catarina (27° S).

Ecology and Evolution

Appendix S1: Information on the benthic cover at the studied sites

Benthic cover at the studied sites was assessed through sets of five photoquadrats taken inside the recorded areas right after the recording period. A total of 78 areas were surveyed at Abrolhos (Chapeirão= 15; Mato Verde= 7; Portinho Norte= 40; Siriba=16), 86 at Arraial do Cabo (Anequim= 27; Cardeiros= 35; Porcos= 24) and 33 at Santa Catarina (Arvoredo West= 17; Xavier=16). All images were analysed in the software CPCE version 4.1 (Kohler & Gill 2006), randomly positioning points over the images and identifying benthic organisms below each of them. Organisms were classified in seven broad categories based on the dominant groups: macroalgae, coralline crustose algae, scleractinian corals, other anthozoans, sponges and others. Percent cover of each benthic group (relative abundance) was obtained for each set of five images (sample) and averaged to describe the sites. Differences in the overall benthic cover composition (response variable) were investigated through permutational multivariate analysis of variance (PERMANOVA; Anderson 2001), according to our hierarchical sampling of localities (each reef) nested within sites (latitudes). Thus, “sites” were treated as a fixed factor and “locality” as a random factor nested within “sites”. Differences in the percent cover of each benthic group were also assessed through the same PERMANOVA design, but applied on each benthic group separately. All benthic cover data was transformed through the arc sine of the square root and PERMANOVA tests were performed on Euclidian Distance matrices using the software Primer 6 & PERMANOVA+ (Anderson & Gorley 2007). The use of PERMANOVA on Euclidean Distance matrix obtained for one single variable yields an equivalent to Fisher’s test using permutations and generates pseudo-F distribution and p-values (Anderson 2001). The category “others” was excluded from the analysis because it lacks biological meaning, once organisms grouped in this category are not necessarily the same in the three sites. The overall benthic cover significantly varied between sites and localities within sites (Table AS1 and AS2). Macroalgal cover did not significantly vary between the sites, but the cover of scleractinian corals, sponges and sand did vary (Table AS3).

Table AS 1 Mean percent cover (± S.E.) of benthic groups in each site. Percent cover values that varied between sites are displayed in bold. * Detailed results of the test on differences between sites are presented in Table AS3.

Benthic groups	**Sites**			**Difference between sites***
	Abrolhos (17^{o}S)	**Arraial do Cabo (22^{o}S)**	**Santa Catarina (27^{o}S)**	
Macroalgae	61.53% (±2.44)	53.49% (±2.18)	59.23% (±2.75)	n.s.
Crustose coralline algae	11.64% (±1.00)	7.43% (±0.75)	20.63% (±1.92)	n.s.
Scleractinian Corals	**11.29%** (±1.28)	**2.63%** (±0.45)	**0.00** (±0.00)	AB ≠ AC AB ≠ SC AC = SC
Other Anthozoans	6.29% (±1.44)	18.14% (±2.27)	0.90 (±0.42)	n.s.
Sponges	**1.23%** (±0.19)	**3.92%** (±0.82)	**0.82** (±0.31)	AB ≠ AC AB = SC AC = SC
Sand	**2.55%** (±0.60)	**10.48%** (±1.16)	**13.28** (±1.92)	AB ≠ AC AB ≠ SC AC = SC
Others	5.85% (±1.06)	6.63% (±1.09)	5.27 (±1.47)	not tested

Table AS 2 Summary of permutational multivariate analysis of variance (PERMANOVA) for the overall benthic cover composition, with site as a fixed factor and locality as a random factor nested within sites. Pairwise comparisons are only provided for the fixed factor. PERMANOVA was applied on an Euclidean Distance matrix obtained from arc sine of the square root transformed data. Pseudo-F distribution and p-values obtained through 999 iterations. Significant differences are presented in bold ($p < 0.05$). df = degrees of freedom; MS = mean squares.

Variable	**Source of variation**	**df**	**MS**	**Pseudo-F**	***p*-value**
Overall benthic cover composition					
Main Test	Site	2	3.55	2.893	**0.031**
	Locality (Site)	6	1.36	8.997	**0.001**
Pairwise comparisons	**t**	***p*-value**			
Abrolhos vs. Arraial	1.561	0.094			
Abrolhos vs. Santa Catarina	2.039	**0.015**			
Arraial vs. Santa Catarina	0.168	0.108			

Table AS 3 Summary of permutational multivariate analysis of variance (PERMANOVA) for each benthic group (response variable) with site as a fixed factor and locality as a random factor nested within sites. Pairwise comparisons are only provided for the fixed factor. The test was applied on Euclidean Distance matrices obtained from arc sine of square root transformed data (999 iterations). Significant differences are presented in bold (p < 0.05). df = degrees of freedom; MS = mean squares.

Functional Group	**Source of variation**	**df**	**MS**	**Pseudo-F**	***p*-value**
Macroalgae					
	Site	2	0.005	0.113	0.881
	Locality (Site)	6	0.540	16.594	**0.001**
Crustose Coralline Algae	**Source of variation**	**df**	**MS**	**Pseudo-F**	***p*-value**
	Site	2	0.572	5.385	0.071
	Locality (Site)	6	0.117	7.523	**0.001**
Scleractinian Corals	**Source of variation**	**df**	**MS**	**Pseudo-F**	***p*-value**
	Site	2	0.838	7.948	**0.016**
	Locality (Site)	6	0.116	5.900	**0.001**
Pairwise comparisons	**t**	***p*-value**			
Abrolhos vs. Arraial	2.550	**0.045**			
Abrolhos vs. Santa Catarina	3.765	**0.017**			
Arraial vs. Santa Catarina	2.273	0.113			
Other Anthozoans	**Source of variation**	**Df**	**MS**	**Pseudo-F**	***p*-value**
	Site	2	1.083	2.702	0.158
	Locality (Site)	6	0.444	8.887	**0.001**
Sponges	**Source of variation**	**df**	**MS**	**Pseudo-F**	***p*-value**
	Site	2	0.188	12.802	**0.007**
	Locality (Site)	6	0.016	2.689	**0.017**
Pairwise comparisons	**t**	***p*-value**			
Abrolhos vs. Arraial	3.671	**0.021**			

Abrolhos vs. Santa Catarina	1.801	0.194			
Arraial vs. Santa Catarina	3.419	0.089			

Sand	**Source of variation**	**df**	**MS**	**Pseudo-F**	***p*-value**
Main Test	Site	2	0.816	7.047	**0.043**
	Locality (Site)	6	0.127	4.599	**0.001**

Pairwise comparisons	**t**	***p*-value**
Abrolhos vs. Arraial	3.381	**0.011**
Abrolhos vs. Santa Catarina	4.359	**0.046**
Arraial vs. Santa Catarina	0.617	0.594

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CAPÍTULO 4

Latitudinal variation in reef fish-benthos trophic interactions

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Latitudinal variation in reef fish trophic interactions on the benthos

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ABSTRACT

Aim Evaluate how the intensity of trophic interactions between fishes and the benthos change with latitude along the eastern coasts of North and South America between about 30 degrees N and S due to changes in activity and composition of reef fishes across these biogeographic regions.

Location A 60° latitudinal gradient in the Western Atlantic.

Methods Reef fish feeding pressure on the benthos was determined from video recordings combining bite rates on the substrate and the individual biomass per unit of time and area. To our knowledge, this is the first study to quantify trophic interactions along such wide latitudinal amplitude using a standardized method. We used linear mixed effects models to assess ecological and human-related factors that explain variation in the mean feeding pressure of all functional groups combined along the latitudinal gradient. Compositional changes of the feeding pressure, both from the functional and taxonomic perspectives, were evaluated using cluster analysis.

Results Feeding intensity was higher in the tropical region and decreased towards extratropical regions in both hemispheres. Ecological drivers (temperature) appeared more important to determine this trend than human-related factors. There was a consistent shift in the predominance of feeding pressure by herbivorous functional groups in the tropics to feeding pressure by omnivores in extratropical regions. Composition of feeding pressure by functional group was more similar within regions with similar temperature than biogeography. Conversely, in terms of species, there was a clear biogeographic footprint in feeding pressure composition.

Main conclusion Our results support the prediction of higher intensity of biotic interactions in the tropics decreasing towards extratropical regions, which was mostly driven by temperature. Human-related factors probably alter the amplitude of variations but not the direction of the latitudinal trend. The identity of species within functional groups was a combination of biogeographic and ecological factors.

Keywords Western Atlantic, latitudinal gradient, herbivory, biogeography

INTRODUCTION

Trophic interactions are critically important in both terrestrial and marine ecosystems (Estes et al. 2011). Among marine systems, there are clear examples of how predation strongly affect community organization and ecosystem function, such as: in the intertidal rocky shores where predation by the seastar *Pisaster ochraceus* enhances species diversity (Paine 1966); in kelp forests, where loss of sea otters allows herbivorous sea uchins to escape control and collapse kelp populations (Estes et al. 1998); and in coral reefs where loss of top predators and herbivores can result in phase-shifts from coral to algae-dominated reefs (Jackson et al. 2001). Differences in the strength of trophic interactions can be linked to abiotic conditions (*e.g.*, temperature), interespecific variation of feeding ecology (*e.g.*, different species within trophic groups), trophic structure of assemblages (*e.g.*, predominant feeding modes) and human-related impacts (*e.g.*, removal of key predators; Jackson et al. 2001; Burkepile and Hay 2008, 2010; Longo et al. 2014). Thus, to enhance understanding of trophic interactions and their consequences, it is necessary to combine macroecology and biogeography which may best be achieved through comparisons across large geographic scales using consistent methods (Pennings & Silliman 2005; Poore et al. 2012; Longo et al. 2014).

There is a commonly accepted prediction that biotic interactions are more intense in the tropics and decrease towards higher latitudes (reviewed by Schemske 2009). This has been challenged by meta-analyses that question the idea of higher herbivory in the tropics, both in terrestrial and marine ecosystems (Moles et al. 2011; Poore et al. 2011). Apart from these meta-analyses, experimental comparisons of trophic interactions across latitudes are scarce in the literature (but see Pennings & Silliman 2005; Bennet & Bellwood 2011; Freestone et al. 2011). Additionally, there have been comparative studies of plant palatability, with most suggesting greater herbivory on, and documenting diminished palatability and greater chemical defenses of, tropical versus temperate plants (Coley and Aide 1991; Bolser and Hay 1996; Siska et al. 2002; Moles et al. 2011; Morrison and Hay 2012). This divergence of findings may be related to difficulties in finding or producing datasets with groups that have a good taxonomic resolution, information on species biogeography and trophic interactions.

Reef fishes have a well established taxonomy and biogeography (Briggs 1974; Floeter et al. 2008), their trophic interactions with benthic organisms, particularly herbivory, are known to be critical to the reef ecosystems and can be relatively easily quantified (Hay 1997; Poore et al. 2012; Longo et al. 2014). The trophic and functional structure of reef fish assemblages are well established and indicate more herbivores in tropical versus extratropical assemblages in the Western Atlantic (Floeter et al. 2004; Bender et al. 2013), with a decrease in the richness, abundance and biomass of herbivorous reef fishes with latitude (Floeter et al. 2005). Reef fish trophic interactions are also affected by abiotic conditions that are expected to vary with latitude, such as temperature (Floeter et al. 2005; Bennet & Bellwood 2011; Poore et al. 2012; Longo et al. 2014). Because fish have a thermo-dependent metabolism (Clarke & Johnston 1999), their feeding behavior may also vary with temperature. Grazing rates of herbivorous fishes, for instance, were known to be positively correlated to water temperature in the Caribbean, Eastern Brazil, and the Tropical Eastern Pacific (Carpenter 1986; Ferreira et al. 1998; Smith 2008). Reef fishes also comprise a wide variety of feeding modes, diets and nutritional strategies by exploring very diversified food sources across trophic levels (*e.g.*, Harmelin-Vivien 2002; Clements et al. 2009; Bellwood et al. 2014). As a consequence of diet and feeding behavior, fish of different trophic categories can exert different feeding pressure on the benthos (Longo et al. 2014). The quality of food sources explored by each functional group (protein and energy contents) could determine bite rates due to changing metabolic needs, particularly when the same species is exposed to different temperatures (*e.g.*, seasonal variations or species with a wide geographic distribution; Harmelin-Vivien 2002; Floeter et al. 2004). Reef habitat and depth also influence herbivory by reef fishes, usually with higher herbivory rates in shallow waters (Hay 1981; Fox & Bellwood 2007). Thus, reef fishes are a good model to investigate large-scale variation in trophic interactions.

Reef fishes are threatened by a variety of human activities, from the direct impact of overfishing to habitat loss, pollution, ocean acidification and warming, that affect over 75% of the worlds'coral reefs (Jackson et al. 2001; 2014; Mora et al. 2011). For example, fishing of important herbivores in coral reefs in the Pacific and Caribbean causes significant structural and functional changes in these ecosystems that shifted from a coral to an algal-dominated state (Bellwood et al. 2004; Rasher et al. 2013; Jackson et al. 2014). The negative relation between human density and standing biomass of reef fishes (Mora et al. 2011) combined with the historical loss of grazers (Mumby 2006) could be shaping the patterns of reef fish feeding pressure across multiple spatial scales.

We addressed latitudinal variation of important trophic interactions in reef ecosystems (reef fish feeding on the benthos) in terms of intensity, functional and taxonomic composition in 16 locations between latitudes 34°N and 27°S in the Western Atlantic. We evaluated latitudinal gradients in biotic interactions (see Schemske 2009) by quantifying total fish feeding pressure at each location. We hypothesized that because fish have a thermo-dependent metabolism and tend to feed more in the tropics (Clarke & Johnston 1999), reef fish feeding pressure on the benthos would be higher in warmer tropical region than in cooler subtropical regions. Apart from temperature, human-related impacts could also be driving significant changes across ecosystems and altering grazing rates (Mumby 2006). Thus, we tested how environmental (depth and temperature) and human-related factors (human population density and biomass of commercially important fish) were related to the latitudinal variation in the intensity of reef fish feeding pressure. Based on the interaction between quality of food sources and temperature (Harmelin-Vivien 2002), we also hypothesized that functional groups within herbivores would feed more in warmer regions (tropical reefs), while feeding by other functional groups that explore food sources with higher protein and energy contents (*e.g.*, invertivores) would vary less with latitude. Feeding pressure, and the composition of feeders, were evaluated between 34^{o}N and 27^{o}S as a function of both species and functional groups of fishes. Our goal was to describe and test the notion of latitudinal trends in biotic pressures from the functional and taxonomic perspectives in the context of ecological drivers and the biogeography of reef fishes in the Western Atlantic.

METHODS

Field procedures and dataset

We assessed reef fish feeding pressure on the benthos as a metric of trophic interactions (see Longo et al. 2014) in 16 locations along 60^{o} of latitude (from 32^{o}N to 27^{o}S) comprising tropical and subtropical sites in both hemispheres (Fig. 1; Table S1). Data were obtained through video recordings of 2 m^{2} reef areas for 10 min, where every fish feeding on the benthos was identified, had its total length estimated, and the number of bites on the reef substratum counted (Longo & Floeter 2012; Longo et al. 2014). Feeding pressure was estimated as the product of the number of bites taken and the body mass (Kg) of the fish - obtained through length–weight relationships from the literature (Froese & Pauly 2014). The inclusion of fish biomass accounts for body size variation, per unit time and area [(Bites x kg)/(2 m^{2} x 10 min)]. All fieldwork was conducted during the summer of each hemisphere between 2011 and 2014. At each location (Fig. 1), we sampled 2-6 sites separated by 500 m to 90 Km and at depths ranging from 1-30 m (but most in the 3-12m range). At each site, we videoed 5-40 replicated 1 x2 m areas – each separated from its nearest neighbor by 5-10 m. Samples were haphazardly positioned across the reef to encompass a good representation of the variety of substratum available at each site. In total, we evaluated 1,201 10 min videos, with a mean of 12 videos per site (Table S1). Reef fish were assigned to functional groups based on a combination of diet and feeding modes (*sensu* Longo et al. 2014; Table S2). Fish that feed on macroalgae, filamentous algae and associated detritus were categorized as herbivores even in the cases when most of the species nutrition comes out of detritus (see Clements et al. 2009). Herbivores were separated into functional groups based on their feeding modes (scrapers, excavators, fine browsers, rough browsers) and behavior (territorial herbivores; Table S2). Invertivores were separated into either mobile invertebrate feeders (*e.g.*, feeding on small crustaceans and/or mollusks; Haemulidae) or sessile invertebrate feeders (*e.g.*, feeding on corals, gorgonians and/or sponges; Chaetodontidae). Species with diversified diet, including plankton and benthic animals and plants were grouped as omnivores (Table S2).

Average annual mean and minimum sea surface temperatures (2005–2010) were obtained for each location from the online Bio-ORACLE database (ca. 9km spatial resolution; see Tyberghein et al. 2012) using the bilinear method with the ‘raster’ package in R software (R Core Team 2014). Two metrics were used to estimate the human impact at each location: human population density and total biomass of selected fish species with commercial importance (Table S3). These metrics were chosen because it has been shown that human population density has a negative correlation with fish standing biomass (Mora et al. 2011) and that the biomass of selected commercially important fish was negatively related to fishing pressure in the Caribbean (Vallès & Oxenford 2014). Human population density was described as the average density within a 25 km radius as in Mora et al. (2011) (data at 0.25u cells for the year 2000: http://sedac.ciesin.columbia.edu/gpw/global.jsp). The biomass of selected species of commercial importance were obtained from 20 x 2 m strip transects (40 m^2), where all fish were identified, counted, and sized by divers (Floeter et al. 2007; Table S1). Biomass was obtained through length–weight relationships from the literature (Froese & Pauly 2014). For the analysis of feeding pressure composition by functional group, locations were assigned *a priori* into three major categories: extratropical (34°N, 31°N, 22°S, 23°S and 27°S), transitional (26°N and 20°S) and tropical reefs (between 24°N and 17°S). These categories were based on physical characteristics (*e.g.*, temperature, reef construction; see Fig. 1), reef structure and benthic cover (*e.g.*, coral cover; see Castro & Pires 2001), and the structure of reef fish assemblages (Ferreira et al. 2004; Floeter et al. 2008; Bender et al. 2013).

Data analyses

Because feeding pressure (mass-standardized bites) and non-mass standardized bite rates were correlated (r=0.75) all analysis were based on feeding pressure, as it allows a better comparison within individuals of the same species and among different functional groups (Longo et al. 2014; Fig. S1). A linear mixed effects model assessed factors that explained the variation in the mean feeding pressure of all functional groups combined along the latitudinal gradient. Mean feeding pressure in each location (response variable), depth, mean sea surface temperature, mean human density and biomass of commercially important fish (fixed factors) were square root transformed prior to the test and location was included in the model as a random factor. The model selection procedure was based on creating a model with the combination of all fixed factors and a reduced model excluding the factors of interest (human-related variables). The comparison between the fit of both models, inform if including human impact in the model improves its fit. Because we did not get data on the biomass of commercially important fish for Central Florida (26^{o}N), models were fitted on the entire data set but without this explanatory variable (Scenario 1) and on a data set excluding Central Florida from the response variables but including all explanatory variables (Scenario 2). Two different models were fitted within Scenario 1: (1) a full model containing depth, sea surface temperature and human density as fixed factors; and (2) an environmental model excluding human density from the fixed factors. For Scenario 2, the fitted models were: (1) a full model containing depth, sea surface temperature, human density, and biomass of commercially important fish as fixed factors; and (2) an environmental model excluding human density and biomass of commercially important fish. The models were compared for each scenario through the Akaike information criteria (AIC) and AIC weight, which indicates the probability that the model is the best among the whole set of candidate models. Models were fitted using the “lme” function in the package “nlme” and compared using the function “model.sel” in the package “MuMIn” in the software R (R Core Team

2014). Compositional changes in the reef fish feeding pressure across locations, both from the functional and taxonomic perspectives, were evaluated using cluster analysis (Bray-curtis similarity; UPGMA) with a profile similarity analysis to evaluate the significance of the observed groups (SIMPROF) and a SIMPER analysis to evaluate the contribution of functional groups and species to the observed clustering pattern (Clarke et al. 2008). The significance of the three groups defined *a priori* (extratropical, transitional and tropical reefs) were tested based on the composition of feeding pressure by functional group through a permutational analysis of variance considering the three categories as fixed factors and locations nested within categories as random factors (PERMANOVA, Anderson 2001). These tests were run in the software Primer 6 & PERMANOVA+ (Anderson & Gorley 2007), on Bray-curtis similarity matrix obtained from data standardized by the total of samples and square-root transformed (response variables). Because feeding pressure data from Costa dos Corais (8^{o}S) was heavily dominated by a single species of damselfish (*Stegastes fuscus*), likely as a result of strong human impact on these reefs, we treated it as an outlier and removed it from these analyses.

RESULTS

Reef fish feeding on the benthos was variable but of higher intensity in the tropical region (from 24°N to 17°S) than in extratropical reefs both northern (24°N–34°N) and southern (20°S–27°S) hemispheres (Fig. 1). These differences were associated with mean sea surface temperatures of 26–28°C in the tropical region and 21–24°C in the extratropical regions. Whereas minimum temperatures ranged from 23-27°C in the tropical areas but as low as 14°C (31°N and 34°N) and 18°C–22°C in the regions of highest latitudes we surveyed (Fig. 1). The two tested scenarios (with and without Central Florida; see Methods) were consistent regarding the influence of environmental (depth and mean sea surface temperature) and human-related factors (human density and biomass of commercially important fish). In both cases, the environmental model generated the lower AICc values, with weights of

94% and 99%, respectively (Table 1), compared to the other tested model (full model). Weights can be interpreted as the probability of that model being the best among the whole set of candidate models. Therefore our results indicate that environmental factors, particularly temperature, played a more important role in comparison to human-related factors (Table1).

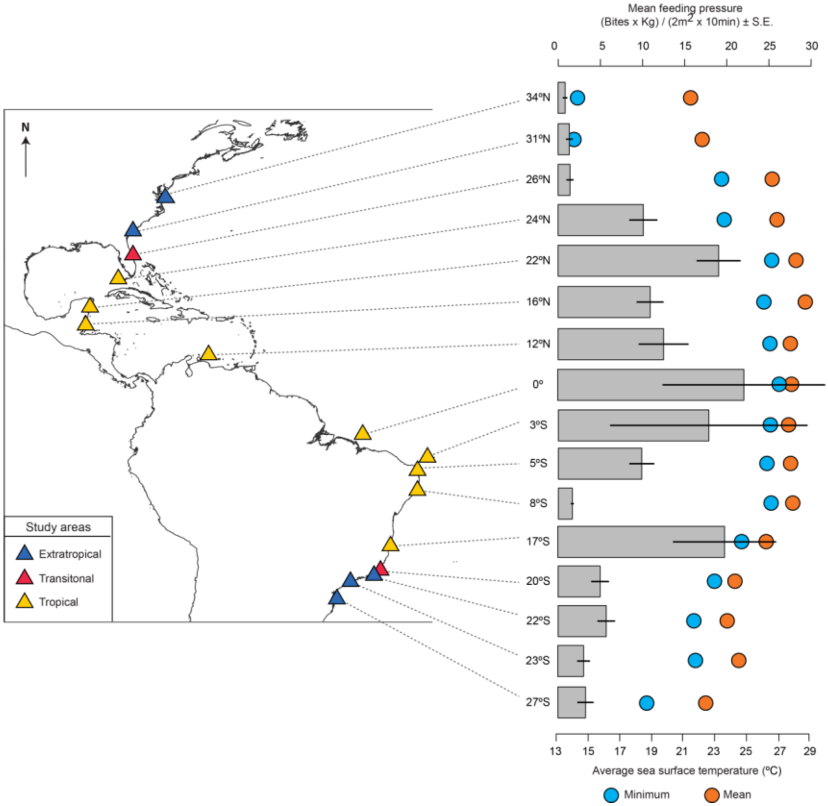

Figure 1: Latitudinal trend of reef fish feeding pressure on the benthos in the Western Atlantic and its relation to average minimum and mean sea surface temperature (http://sedac.ciesin.columbia.edu/gpw/global.jsp).

Table 1. Model selection and fixed effects' coefficients of the fitted models to assess the influence of environmental and human-related variables in the mean feeding pressure of all functional groups combined along the latitudinal gradient. Best fitted models of each scenario are highlighted in gray. Scenario 1: entire data set of feeding pressure without the biomass variable. Scenario 2: data set of feeding pressure, excluding Central Florida (26°N) and including all factors (see Methods). (SST) Sea surface temperature. (d.f.) degrees of freedom. *Biomass of commercially important fish (see Table S3).

Scenario/Model	Intercept	Depth	Mean SST	Human density	Biomass*	d.f.	AICc	Δ AIC	Weight
Scenario1									
Environmental	**-10.970**	**-0.181**	**2.663**	-		**5**	**4922.8**	**0**	**0.943**
Full model	-10.720	-0.182	2.628	-0.006		6	4930.6	7.76	0.019
Scenario 2									
Environmental	**-11.650**	**-0.134**	**2.782**	-	-	**5**	**4756.5**	**0**	**0.995**
Full model	-12.030	-0.152	2.816	0.008	0.125	7	4767.3	10.79	0.005

In the tropical areas, the feeding pressure of herbivorous functional groups combined was between 10 and 25-fold higher in comparison to all the other functional groups combined (Fig.S2). Thus, the latitudinal trend in the intensity of feeding pressure was mostly related to heavy feeding by herbivores in the tropics (Fig 2). Feeding by scrapers dominated the herbivorous functional group, particularly in the tropical region. Feeding pressure of excavators occurred most notably in the Florida Keys (24°N), Mexico (22°), Belize (16°N) and at Parcel do Manoel Luís (0°), with a striking scarcity along the Brazilian coast. There was no clear pattern in the feeding pressure of fine browsers along the studied gradient, however feeding pressure of rough browsers was mostly recorded in higher latitudes. Feeding pressure by territorial herbivores was higher along the Brazilian coast in comparison to the Caribbean. Omnivores were the most important functional group in transitional and subtropical reefs. Feeding pressure of mobile invertebrate feeders was similar throughout the latitudinal range whereas the contribution of sessile invertebrate feeders was higher in the Caribbean.

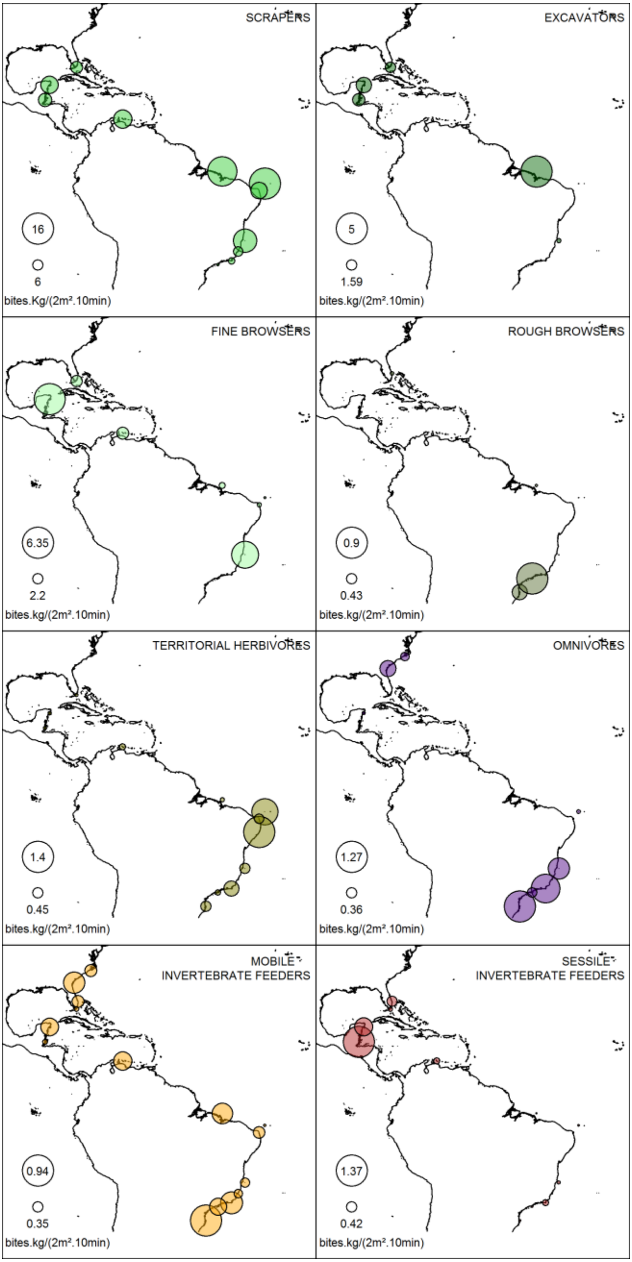

Figure 2. Feeding pressure on the benthos of different reef fish functional groups along the Western Atlantic. Note the different scales.

Proportional contribution to total feeding pressure from different functional groups changed with latitude (Fig 3). The regions we defined *a priori* as extratropical, transitional, and tropical differed significantly in relative feeding pressure among functional groups (PERMANOVA; Pseudo-$F_{2,16}$= 11.646, p= 0.001), with transitional reefs presenting 62% and 46% similarity to tropical and extratropical reefs, respectively. These levels of similarities are reflected in the cluster analysis, where extratropical reefs formed a separate cluster and the transitional reefs clustered more closely with the tropical reefs. While Central Florida (26°N) showed ~50% similarity to tropical reefs, the similarity between Espírito Santo (20°S) and tropical reefs ranged from 70–80% (Fig. 3; see details in Fig. S3). Thus, the composition of feeding pressure by functional group was similar within regions with similar temperature conditions, irrespective of their biogeographic history.Omnivores and mobile invertebrate feeders combined generated 68% of the similarity within the extratropical group, scrapers and fine browsers showed 70% similarity within the tropical group, and scrapers and mobile invertebrate feeders contributed 80% to the group of transitional reefs (Table 2; dissimilarities between groups are shown in Table S4).

In contrast to the analyses considering functional groups, based on a cut of 50% of similarity from the cluster analysis of feeding pressure by species (dendrogram, Fig. 3), six groups could be distinguished: extratropical reefs of the Northern Hemisphere (34°N and 31°N), transitional reefs of the Northern hemisphere (26°N), Caribbean (24°N–12°N), Northeastern Brazil (0°–5°S), Eastern Brazil (17°N–22°N) and extratropical reefs of the Southern Hemisphere (23°S and 27°S). Species that most contributed to the extratropical North group were *Halichoeres bivittatus*, *Archosargus probatocephalus* and *Diplodus holbrooki*; *Aluterus scriptus* contributed to the transitional group; different Acanthuridae species contributed to the Caribbean, Northeastern and Eastern Brazil, while *Kyphosus* spp. and *Diplodus argenteus* contributed to the extratropical South group (Table S5). Thus, this analysis indicates that, within the tropical region, the same functions can be performed by different species (Fig. 3). For example, the contribution of the Acanthuridae family and the Tribe Scarini to the feeding pressure varied considerably between the Caribbean and Brazilian province. In the Brazilian province, feeding pressure of Acanthuridae species is higher than Scarini species, but the opposite occurs in most of the Caribbean (Fig. 4). Within Acanthuridae, the sister species pair *Acanthurus tractus* in the Northern hemisphere and *Acanthurus bahianus* in the Southern hemisphere were frequently among the most actively feeding species along with *Acanthurus chirurgus* and *Acanthurus coeruelus*, which were common to both hemispheres. Within Scarini, feeding pressure in most sites was dominated by *Sparisoma* spp. except for Curaçao (12°N), Parcel do Manoel Luís (0°) and Abrolhos (17°S), where feeding pressure by *Scarus* spp. prevailed.

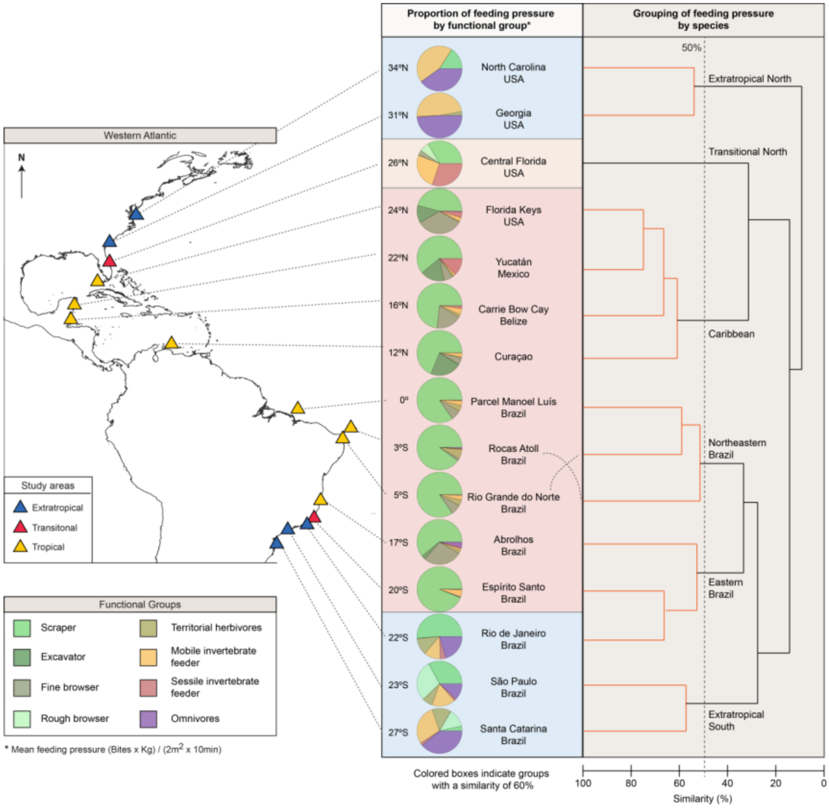

Figure 3. The composition of reef fish feeding pressure by functional group, and a cluster analysis of the feeding pressure composition by species (Bray-curtis; UPGMA). Colored boxes around the pie charts indicate locations showing 60% similarity when analyzed by functional group (Bray-Curtis; UPGMA; see Fig. S3). The dendrogram on the right depicts results from analyses using species (instead of functional groups); clusters in red represent those with significant results in the SIMPROF test - the gray dashed line indicates clusters of 50% similarity. Please note the dashed lines indicating a shift in the relation between the pie charts and cluster branch for Rocas Atoll (3^{o}S) and Rio Grande do Norte (5^{o}S).

Table 2. Results of SIMPER analyses indicating the contribution of functional groups to within groups similarities of feeding pressure composition.

Groups	**Overall average similarity**	**Functional groups**	**Average similarity**	**Contribution (%)**	**Cummulative contribution (%)**
Extratropical reefs	67.25	Omnivores	23.61	35.11	35.11
		Mobile invetebrate feeders	22.17	32.96	68.08
		Scrapers	9.35	13.9	81.98
		Territorial herbivores	6.67	9.92	91.9
Tropical reefs	76.5	Scrapers	41.09	53.71	53.71
		Fine browsers	13.78	18.01	71.72
		Mobile invetebrate feeders	6.06	7.92	79.64
		Territorial herbivores	5.74	7.51	87.15
		Excavators	5.3	6.93	94.08
Transitional reefs	55.04	Scrapers	32.8	59.59	59.59
		Mobile invertebrate feeders	12.79	23.24	82.83
		Fine browsers	4.48	8.14	90.97

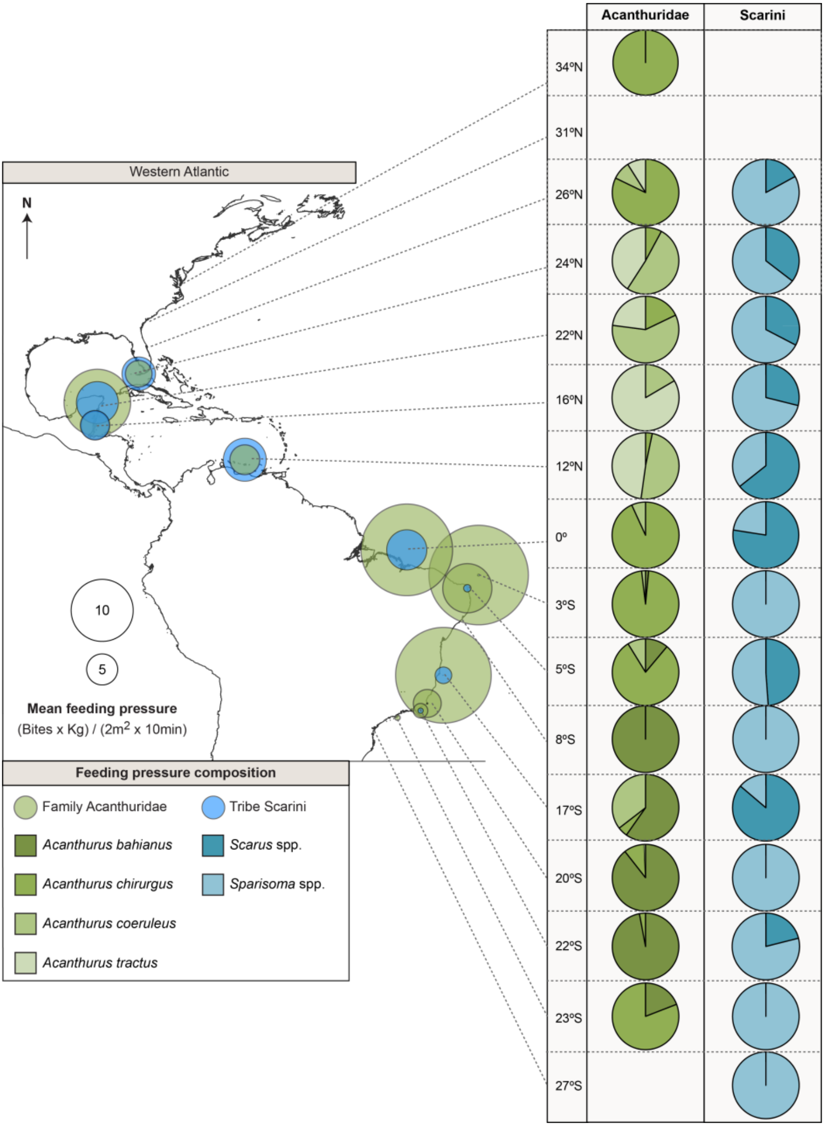

Figure 4. Feeding pressure of the two most representative herbivorous groups in the Western Atlantic (the family Acanthuridae and the Tribe Scarini). Pie charts on the right indicate relative feeding pressure for species or genera in that group. The absence of pie charts indicate the group was not recorded in the respective location.

DISCUSSION

There were consistent latitudinal trends in the intensity of feeding pressure on the benthos and remarkable compositional changes in terms of fish functional groups and species along the Western Atlantic. Feeding pressure was higher in the tropics and decreased towards extratropical reefs in both hemispheres, with higher temperature being strongly associated with the increased feeding pressure in the tropics. Although human-related factors (nearby human density and the abundance of fishes harvested commercially) showed only a weak association with this large-scale pattern, humans can influence feeding pressure on a local scale (Mumby 2006; Longo et al. 2014). At Costa dos Corais (8°S), for example, feeding pressure was surprisingly low given its geographic location. Studied reefs in this area were mostly dominated by algal turfs, territories of the damselfish *Stegastes fuscus* and some small-sized herbivores, which can be seen when comparing feeding pressure and non-mass standardized bite rates (Fig. S1). This pattern is likely a response to direct human impact on these shallow and coastal reefs, with overfishing removing most of large-bodied roving herbivores (Ceccarelli et al. 2006). The composition of feeding pressure by functional group among sites concurred with the temperature conditions, where herbivorous functional groups were more representative in the tropics, and mobile invertebrate feeders and omnivores in the extratropic. Conversely, the identity of species in these functional groups varied within regions, according to biogeographic history.

The latitudinal trend in the instensity of feeding pressure was mostly related to temperature, which can have profound effects on fish metabolism. It has been estimated that fish living at 30°C (tropical) consumes roughly six times more oxygen than a fish living at 0°C (polar), and thus need six times as much food per unit of time to meet resting metabolic needs (Clarke & Johnston 1999). Differences in the metabolic needs between tropical and extratropical fish at the scale of the present study are much lower, however the effect of temperature on fish metabolism can influence their feeding pressure on the benthos. At lower temperatures, for instance, herbivorous reef fishes feed more slowly (Carpenter et al. 1986; Ferreira et al. 1998; Smith et al 2008), remove less macroalgae (Bennet & Bellwood 2011), and thus generate a lower feeding pressure (Longo et al. 2014).

Herbivorous functional groups, particularly scrapers, were the most strongly representative among all functional groups, and are thus directly linked to this temperature-related latitudinal trend. Species within this group ingest macroalgae and epilithical algal matrix, but also detritus and sediments. Based on the fermentation profiles and diet described for Pacific herbivorous fish, most species classified as scrapers in the present study could be regarded as detrital feeders (Choat et al. 2002). Pacific species within this dietary group have higher bite rates in comparison to other herbivores that avoid or ingest lower amounts of detritus, and usually retain food in the digestive tract for longer (*e.g.* Kyphosidae; Choat et al. 2004). Feeding pressure by herbivores that ingest considerable amounts of detritus (scrapers) decreased from warmer towards colder regions; this was not the case for rough browsers that ingest minimal detritus. Thus, dietary groups and nutritional strategies (*sensu* Choat et a. 2002, 2004) of these herbivores need to be better understood in terms of how temperature may affect metabolic efficiency.

In the present study, feeding pressure of excavating herbivorous fishes was recorded in few of the studied sites, highlighting its low contribution along the Brazilian coast, which could be related to local fishing pressure on excavating species (Bender et al. 2014; Longo et al. 2014). Two excavating species occur in Brazil, but both are targeted by artisanal fisheries in Northeastern Brazil (Ferreira & Gonçalves 2006; Francini-Filho & Moura 2008; Cunha et al. 2012) - large individuals of *Sparisoma* amplum and the greenbeack parrotfish *Scarus trispinosus*, respectively sister species of *Sparisoma viride* and *Scarus guacamaia* from the Caribbean. There has been an historical decline in the abundance and size of *S. trispinosus* at the site we studied in Rio de Janeiro (22°S; Bender et al. 2014), which probably also happened at other sites along the Brazilian coast. The latitude with higher feeding pressure of excavators (mostly *S. trispinosus*), Parcel do Manoel Luís

(0°), is approximately 90 km off the coast and contains coral pinnacles between 1 and 30 m deep. Because this site is more expensive and risky for fishers to visit, it is likely that they do not fish or fish less herbivores, which are of lower commercial value than large carnivores (*e.g.*, groupers and jacks). Feeding pressure of rough browsers was higher in extratropical reefs, where this group is also more abundant and constitute greater biomass (Ferreira et al. 2004; Floeter et al. 2005). However, feeding pressure of kyphosids might be underestimated in this study as they frequently feed on very shallow areas of the reefs (Welsh & Bellwood 2014; usually less than 2m deep Longo, Ferreira & Floeter *pers. obs.*), where data collection was frequently not possible due to hydrodynamic conditions.

Feeding pressure of territorial herbivores was higher along the Brazilian coast than in the Caribbean. Lower abundances of the territorial herbivore *Stegastes planifrons* in the Caribbean were related to the loss of their prefered microhabitat associated with the staghorn coral *Acropora cervicornis* that experienced a severe decline in the past decades (Precht et al. 2010). Such pattern could be resulting in the observed lower feeding pressure of territorial herbivores in the Caribbean region. Also, the removal of medium and large fishes from reefs has a positive effect on damselfish abundance by reducing predation and also competition with other herbivores (Ceccareli et al. 2006), which might be the case for the reefs at 8°S. Territorial damselfish can alter algal succesional pathways to favor more suitable algal assemblages within their territories preventing the stablishment of fleshy macroalgae (Ceccareli et al. 2011). At present, Brazilian reefs are heavily dominated by algal turfs (between 40–80% of benthic cover; SISBIOTA-Mar *unpublished data* – www.sisbiota.ufsc.br; Figueiredo et al. 2009), which could favor or result from high abundances of damselfish. It is unclear whether Brazilian reefs were dominated by algal turfs in the past, or whether this occurred after over-exploitation of other fishes, or other threats related to pollution and altered sedimentation. However, this hypothetical phase-shift to turf-dominated reefs with high abundances of damselfish deserves further attention. Feeding pressure by mobile invertebrate consumers was common throughout the entire latitudinal gradient we assessed; but feeding by sessile invertebrate consumers was more concentrated in the Caribbean. This was probably due to higher number of species within this group, particularly butterflyfish (Chaetodontidae), for which density and feeding behavior are linked to the availability of corals and gorgonians (Pitt 1991), which are more abundant in the Caribbean than in Brazil.

The distinct pattern between functional groups of different trophic categories could be related to the relative nutritional quality of food resources. Although plasticity of feeding and digestive strategies can jeopardize simple categorical classifications, reef fishes could be viewed as those utilizing high-quality (*i.e.*, protein-rich invertebrates, or high quality filamentous algae in territories) versus low-quality foods (detritus and sparse filaments; Harmelin-Vivien 2002; Floeter et al. 2004; Bender et al. 2013). This could be reflected in species' bite rates, since those using lower quality foods would need to compensate by ingesting larger amounts of food (Carpenter 1986; Cruz-Rivera and Hay 2000; Floeter et al. 2004). For example, feeding rates of the scraper *Acanthurus chirurgus* in Northeastern Brazil, where mean temperature is around 26.5°C, were roughly 20-25 bites.min^{-1} (Francini-Filho et al. 2009), whereas feeding rates of the mobile invertebrate feeder *Haemulon aurolineatum* in a close area in Northeastern Brazil with similar temperature (27°C) was 1.4 bites.min^{-1} (Pereira & Ferreira 2013). Thus, regardless of temperature variation, fish that explore relatively lower quality food (*e.g.*, the herbivorous *A.* chirurgus) present higher bite rates than those exploring relatively higher quality food (*e.g.*, the invertivorous *H.* aurolineatum).

The feeding pressure of herbivorous scrapers, excavators, and fine browsers, that explore relatively lower quality food in comparison to invertivores, was ~5–16 greater than the other groups (*e.g.*, omnivores, mobile and sessile invertebrate feeders; Fig. 2). The strategy of substituting quantity for quality may also limit the temperature ranges (and thus latitudes) over which such strategies are viable (Harmelin-Vivien 2002). It is interesting that the rapidly feeding scrapers, excavators, and fine browsers that consume lower quality foods were restricted to tropical areas, while territorial herbivores, omnivores, and fishes feeding on mobile invertebrates extended well into the extratropical areas. If warmer and more stable temperatures in the tropics enhance the ability of species to use low-quality food sources (Harmelin-Vivien 2002), this could aid diversification of important reef fish families (Lobato et al. 2014) and alter the trophic structure of reef fish assemblages across latitudes (Floeter et al. 2004).

The composition of feeding pressure by functional groups showed similar changes with latitude in both the Northern and Southern hemispheres, with groups that utilize low-quality food being well represented in the tropics, while fishes using higher-quality foods were more prevalent in extratropical areas. Transitional reefs clustered closer to tropical reefs, likely because of the contribution of herbivores and their paucity in extratropical reefs. When we evaluated by species instead of functional groups, there was a clear biogeographic footprint in the composition of feeding pressure. Species generating feeding pressure in extratropical reefs on the Northern hemisphere were strikingly different from those in the other regions. For example, feeding pressure by the omnivores *Archosargus probatocephalus* and *Diplodus holbrooki* were only recorded in this region. Interestingly, feeding pressure by the congeneric omnivore *Diplodus argenteus* was among the most representative in the extratropical reefs of the Southern hemisphere (Longo et al. 2014). Both species are omnivores (~50% plants and ~30% invertebrates) and shift towards a more carnivorous diet in colder seasons (Pike & Lindquist 1994; Dubiaski & Masunari 2004). This mirrored pattern of congeneric species in both hemispheres demonstrates the biogeographic footprint and a consistent shift from lower-quality plant to higher-quality animal diets associated to declining temperatures.

Regarding tropical groups, different species within the family Acanthuridae marked the differences between sites within this region, with the regional endemics *Acanthurus tractus* characterizing the Caribbean, *Acanthurus bahianus* (sister species of *A. tractus*) the Eastern Brazil, and the widely distributed *Acanthurus chirurgus* the Northeastern Brazil (Table S5; Fig. 5). The predominance of feeding pressure of the tribe Scarini over the family Acanthuridae in the Caribbean in comparison to Brazil agrees with patterns of density and biomass, and can be associated with a greater degree of reef development in the Caribbean (Floeter et al. 2005). Within Scarini, the genus *Scarus* tend to be more associated to coral reef habitats while *Sparisoma* can be found in a wide variety of habitats, even with lower coral cover (Streelman et al. 2002). Feeding pressure by the genus *Scarus* was higher than *Sparisoma* in only three studied locations Curaçao (12°N), Parcel do Manoel Luís (0°) and Abrolhos (17°S), habitats with the highest coral cover in each of the regions (*i.e.*, Caribbean, Northeastern Brazil and Eastern Brazil, respectively). These shifts in Acanthuridae–Scarini ratios and species within these groups between the Caribbean and Brazil, suggest that the same functional groups are composed by different species as a result of combination between biogeographic (*e.g.* regional endemics) and ecological factors (*e.g.* tolerance to different conditions). This could have profound effects for functional redundancy because: (1) there might be different levels of complementarity and redundancy within and between genera, with functions of species from different genera being more similar than function of con-generic species (Burkepille & Hay 2011); (2) species of the same group can explore different microhabitats (Fox & Bellwood 2013) or present different capacities of nutrient assimilation (Drommard et al. 2015); and (3) species within a functional group can perform functions unevenly (Duffy 2002; Longo et al. 2014). Thus, more accurate functional approaches should go beyond taxonomic relatedness, defining and quantifying the function and the contribution of each species within the group.

We showed a latitudinal gradient, in the intensity and composition of trophic interactions (reef fish feeding pressure), through a standardized method across a broad geographical scale encompassing North and South hemispheres. Our results of feeding pressure (trophic interaction) support the prediction of higher intensity of biotic interactions in the tropics decreasing towards extratropical regions, which was mostly related with temperature variations. Human-related factors, such as overfishing, are probably altering the amplitude of variations on a local scale but not its direction on the latitudinal scale, and thus showed a weak relation with the latitudinal trend of feeding pressure. The composition of feeding pressure by functional groups was linked to temperature by differently affecting functional groups within different trophic categories. There was a clear biogeographic footprint on the species within functional groups across latitudes. Thus, the functional approach was consistent between the different biogeographic regions with shifts in species identity and their relative contribution within functional groups, which should be accounted in global scale studies on functional redundancy and ecosystem function.

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BIOSKETCHES

Guilherme Longo is a PhD candidate with a broad interest in the ecology of reef ecosystems, particularly trophic interactions, ecosystem functioning and conservation.

Supporting Information

Table S1 Sample summary of the field effort at the study sites along the Western Atlantic Ocean. UVC= underwater visual census.

Site	Abbreviation	Coordinates	Depth	N (Videos)	N (UVC)	Month	Year
North Carolina, USA (34°N)							
SW Knuckle Buoy	SW	34°24’828’’ N 76°30’499’’ W	12m	20	6	September	2013
Station Rock	SR	34°35’160’’ N 77°03’618’’ W	12-14m	12	6	September	2013
Sum of samples				**32**	**12**		
Gray’s Reef, USA (31°N)							
Monitoring Site	MS	31°23’791’’ N 80°53’419’’ W	18m	13	5	July	2013
BP06N	BP	31°22’392’’ N 80°51’999’’ W	18m	9	5	July	2013
Ledge4	L4	31°23’819’’ N 80°53’999’’ W	18m	6	5	July	2013
FS15	FS15	31°22’588’’ N 80°50’372’’ W	20m	7	5	July	2013
FS17	FS17	31°23’943’’ N 80°54’127’’ W	18m	4	5	July	2013
Sum of samples				**40**	**25**		

Central Florida, USA (26°N)							
Bluffs	BL	26°54’179’’ N 80°01’106’’ W	23m	12	n.a.	September	2013
Captain Mikes	CM	26°52’245’’ N 80°00’875’’ W	24m	11	n.a.	September	2013
Spadefish	SF	26°53’665’’ N 80°00’933’’ W	25m	12	n.a.	September	2013
Area 51	A51	26°53’665’’ N 80°00’933’’ W	26m	12	n.a.	September	2013
Sum of samples				**47**	-		
Florida Keys, USA (24°N)							
Conch Reef	CR	24°57’011’’ N 80°27’030’’ W	5-17m	15	9	September	2013
Molasses	MOL	25°00’050’’ N 80°22’015’’ W	5-14m	20	12	September	2013
Picles	PI	24°59’015’’ N 80°24’052’’ W	5-17m	20	10	September	2013
Sum of samples				**55**	**31**		
Yucatán, Mexico (22°N)							
Playa del Carmen							
Moche	MOC	20°38’419’’ N 84°18’474’’ W	6-8m	5	13	October	2013

Jardines	JAR	20°37’272’’ N 87°01’553’’ W	6-8m	10	12	October	2013
Barracudas	BAR	20°38’419’’ N 87°02’915’’ W	7-8m	11	9	October	2013
Sabalos	SAB	20°34’872’’ N 87°06’586’’ W	6-7m	10	27	October	2013
Cozumel							
Chankannaack	CHN	20°34’869’’ N 87°06’589’’ W	12m	13	10	October	2013
Paraiso	PAR	20°28’121’’ N 86°59’019’’ W	12m	15	9	October	2013
Sum of samples				**65**	**80**		
Carrie Bow Cay, Belize (16°N)							
Carrie Bow 1	CBC1	16°48’130’’ N 88°04’724’’ W	10m	11	4	November	2013
Carrie Bow 2 (SouthWater)	CBSW	16°48’965’’ N 88°04’596’’ W	14m	12	5	November	2013
Carrie Bow 3	CBC3	16°47’241’’ N 88°04’585’’ W	10m	10	5	November	2013
Carrie Bow 4	CBC4	16°46’632’’ N 88°04’530’’ W	10m	12	6	November	2013
Curlew Bank	CUR	16°46’417’’ N 88°04’523’’ W	4-9m	24	15	November	2013
Sum of samples				**57**	**35**		
Curaçao (12°N)							
Oostpunt1	OO1	12°02’140’’ N 68°47’853’’ W	9-12m	11	12	October	2013

Oostpunt2	OO2	12°02’249’’ N 68°48’319’’ W	9-12m	11	11	October	2013
Snake Bay	SNB	12°08’392’’ N 68°59’825’’ W	9-12m	12	19	October	2013
Water Factory	WAF	12°06’320’’ N 68°57’150’’ W	9-12m	12	13	October	2013
Westpunt	WEP	12°22’552’’ N 69°09’490’’ W	9-12m	11	19	October	2013
Sum of samples				57	**74**		
Parcel Manoel Luís, Brazil (0°)							
Anacris	ANA	00°52’11.5’’ S 44°15’51.4’ W	9-12m	11	61	April	2013
Basil	BAS	00°52’11.5’’ S 44°15’51.4’ W	25-27m	3	22	April	2013
Sum of samples				**14**	**83**		
Rocas Atoll, Brazil (3° S)							
Âncoras	ANC	03°52’51’’ S 33°48’16’’ W	2-3m	15	17	January	2012
Falsa Barreta	FBA	03°51’64’’ S 33°49’40’’ W	1-4m	15	5	January	2012
Podes Crer	PCR	03°52’20’’ S 33°48’45’’ W	1-3m	16	8	January	2012
Rocas	ROC	03°51’86’’ S 33°47’49’’ W	1-2m	15	20	January	2012
Salão	SAL	03°52’29’’ S 33°48’33’’ W	8-10m	9	6	January	2012

Tartarugas	TAR	03°52’43’’ S 33°48’59’’ W	2-3m	15	20	January	2012
Sum of samples				**85**	**76**		
Rio Grande do Norte, Brazil (5° S)							
Barreirinha	BAA	05°57’22’’ S 35°02’21’’ W	11-15m	23	25	October-March	2011-2013
Batente das Agulhas	BAT	05°33’52’’ S 35°04’21’’ W	9-23m	8	17	March	2013
Cabeço do Leandro	CAB	05°57’00’’ S 35°02’14’’ W	14-17m	8	17	March	2013
Maracajaú	MAR	05°23’39’’ S 35°15’32’’ W	1.5-3.5m	15	28	October	2011
Pedra do Siva	PSI	05°33’52’’ S 35°05’24’’ W	13-21m	12	24	March	2013
Rio do Fogo	RFG	05°15’44’’ S 35°21’48’’ W	1-2m	10	17	March	2013
Sum of samples				**76**	**128**		
Costa dos Corais, Brazil (8-9°S)							
Tamandaré, Pernambuco							
Ilha do Meio	IME	08°45’42’’ S 35°05’16’’ W	2-3m	15	10	March	2012
Perua Preta	PEP	08°43’31’’ S 35°05’19’’ W	1-2m	8	8	March	2012
Pirambu	PIR	08°45’28’’ S 35°05’09’’ W	7-8m	16	-	March	2012

Maragogi, Alagoas							
Barra das Galés	BAG	09°01’58’’ S 35°11’34’’ W	1.5-3m	20	9	March	2012
Galés	GAL	09°01’27’’ S 35°11’29’’ W	1.5-3m	16	6	March	2012
Taocas	TAO	08°59’54’’ S 35°10’50’’ W	1.5-3m	18	9	March	2012
Sum of samples				**93**	**42**		
Abrolhos, Brazil (17° S)							
Chapeirão	CHA	17°58’38.62’’ S 38°43’19.40’’ W	6-12m	15	28	March	2010
Mato Verde	MTV	17°57’53.78’’ S 38°42’04.69’’ W	4-10m	8	25	March	2010
Portinho Norte	PTN	17°57’43.52’’ S 38°41’52.51’’ W	3-10m	40	50	March	2010
Siriba	SRB	17°58’10.63’’ S 38°42’38.19’’ W	4-10m	16	45	March	2010
Sum of samples				**79**	**148**		

Guarapari, Brazil (20°S)							
Escalvada	ESC	20°41’59’’ S 40°24’27’’ W	4-12m	24	60	February	2014
Rasa	RAS	20°40’36’’ S 40°21’58’’ W	4-12m	25	-	February	2014
Três Ilhas	TRI	20°36’44’’ S 40°22’44’’ W	4-12m	23	43	February	2014
Sum of samples				72	**103**		
Arraial do Cabo, Brazil (22° S)							
Anequim	ANE	22°58’51.81’’ S 41°59’03.34’’ W	3-12m	30	20	April	2011
Cardeiros	CAR	22°57’55.27’’ S 42°00’06.34’’ W	3-12m	30	20	April	2011
Porcos	POR	22°58’03.27’’ S 41°59’39.11’’ W	3-12m	30	20	April	2011
Sum of samples				**90**	**64**		

São Paulo, Brazil (23° S)							
Ilha dos Búzios (Saco do Urubu)	BUZ	23°48’21’’ S 45°09’29’’ W	3-11m	19	20	February	2013
Ilha das Cabras	CAB	23°49’49’’ S 45°23’38’’ W	3-11m	19	19	February	2013
Diogo	DIO	23°56’07’’ S 45°17’01’’W	3-11m	22	20	February	2013
Alcatrazes (Portinho Sul)	ALC	24°06’19’’ S 45°42’09’’W	3-11m	21	20	February	2013
Saco do Sombrio	SOM	23°53’36’’ S 45°14’39’’W	3-11m	20	21	February	2013
Sum of samples				**101**	**100**		
Santa Catarina (27° S)							
Eastern Arvoredo	ARVE	27°17’34.15’’ S 48°21’27.66’’ W	3-12m	25	25	Feb-Apr	2011
Western Arvoredo	ARVW	27°17’06.23’’ S 48°22’17.16’’ W	3-12m	33	51	Feb-Apr	2010/2011
Deserta	DES	27°16’09.23’’ S 48°19’49.13’’ W	3-12m	33	44	Feb-Apr	2011
Xavier	XAV	27°36’32.35’’ S 48°23’09.27’’ W	3-12m	30	80	Feb-Apr	2010/2011
Sum of samples				**121**	**200**		
Total of samples				**1085**	**1201**		

Table S2 List of species assigned to each functional groups across all studied sites.

	North Carolina, USA	**Gerogia, USA**	**Central Florida, USA**	**Florida Keys, USA**	**Yucatán, Mexico**	**Carrie Bow Cay, Belize**	**Curaçao**	**Parcel Manoel Luís, Brazil**	**Rio Grande do Norte, Brazil**	**Atol das Rocas, Brasil**	**Costa do Corais, Brazil**	**Abrolhos, Brazil**	**Espírito Santo, Brazil**	**Rio de Janeiro, Brazil**	**São Paulo, Brazil**	**Santa Catarina, Brazil**
Latitude	**34° N**	**31° N**	**26° N**	**24° N**	**22° N**	**16° N**	**12° N**	**0°**	**5° S**	**3° S**	**8° S**	**17° S**	**20° S**	**22° S**	**23° S**	**27° S**
Scrapers	**X**		**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**
Acanthurus bahianus								X	X	X	X	X	X	X	X	
Acanthurus chirurgus	X		X	X	X		X	X	X	X		X	X	X	X	
Acanthurus tractus			X	X	X	X	X									
Cryptotomus roseus												X		X		X
Scarus coelestinus				X												
Scarus iseri				X	X	X	X									
Scarus taeniopterus			X	X	X	X	X									
Scarus vetula					X	X	X									
Scarus zelindae								X	X			X		X		

	North Carolina, USA	Gerogia, USA	Central Florida, USA	Florida Keys, USA	Yucatán, Mexico	Carrie Bow Cay, Belize	Curaçao	Parcel Manoel Luís, Brazil	Rio Grande do Norte, Brazil	Atol das Rocas, Brasil	Costa do Corais, Brazil	Abrolhos, Brazil	Espírito Santo, Brazil	Rio de Janeiro, Brazil	São Paulo, Brazil	Santa Catarina, Brazil
Scarus sp.					X							X				
Sparisoma amplum								X	X	X	X				X	
Sparisoma atomarium			X													
Sparisoma aurofrenatum			X	X	X	X	X									
Sparisoma axillare								X	X	X	X	X	X	X	X	
Sparisoma chrysopterum				X	X	X										
Sparisoma frondosum								X	X	X	X	X	X	X	X	X
Sparisoma rubripinne				X	X	X										
Sparisoma tuiupiranga												X		X	X	
Sparisoma sp.								X	X		X	X		X		X
Excavators				**X**	**X**	**X**		**X**				**X**				
Scarus trispinosus								X				X				

	North Carolina, USA	**Gerogia, USA**	**Central Florida, USA**	**Florida Keys, USA**	**Yucatán, Mexico**	**Carrie Bow Cay, Belize**	**Curaçao**	**Parcel Manoel Luís, Brazil**	**Rio Grande do Norte, Brazil**	**Atol das Rocas, Brasil**	**Costa do Corais, Brazil**	**Abrolhos, Brazil**	**Espírito Santo, Brazil**	**Rio de Janeiro, Brazil**	**São Paulo, Brazil**	**Santa Catarina, Brazil**
Sparisoma viride				X	X	X										
Fine browsers			X	X	X	X	X	X	X	X	X	X	X		X	X
Acanthurus coeruleus			X	X	X	X	X	X	X	X		X	X			
Sparisoma radians								X	X		X				X	X
Rough browsers			X					X						X	X	X
Kyphosus sectatrix															X	
Kyphosus vaigiensis			X					X						X	X	X
Kyphosus sp.															X	
Territorial herbivores		**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**
Microspathodon chrysurus				X	X	X	X		X		X					
Stegastes adustus					X	X	X									
Stegastes fuscus									X		X	X	X	X	X	X

	North Carolina, USA	Gerogia, USA	Central Florida, USA	Florida Keys, USA	Yucatán, Mexico	Carrie Bow Cay, Belize	Curaçao	Parcel Manoel Luís, Brazil	Rio Grande do Norte, Brazil	Atol das Rocas, Brasil	Costa do Corais, Brazil	Abrolhos, Brazil	Espírito Santo, Brazil	Rio de Janeiro, Brazil	São Paulo, Brazil	Santa Catarina, Brazil
Stegastes leucostitus			X			X	X									
Stegastes partitus			X	X			X									
Stegastes pictus									X			X		X		X
Stegastes planiforns						X	X									
Stegastes rocasensis										X						
Stegastes variabilis		X	X	X	X			X	X		X	X			X	X
Mobile invertebrate feeders	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**
Anisotremus virginicus			X	X	X			X	X			X	X	X	X	X
Balistes capriscus		X														
Bodianus pulchellus														X	X	
Bodianus rufus			X	X	X				X		X		X	X	X	X
Calamus calamus	X	X														

	North Carolina, USA	**Gerogia, USA**	**Central Florida, USA**	**Florida Keys, USA**	**Yucatán, Mexico**	**Carrie Bow Cay, Belize**	**Curaçao**	**Parcel Manoel Luís, Brazil**	**Rio Grande do Norte, Brazil**	**Atol das Rocas, Brasil**	**Costa do Corais, Brazil**	**Abrolhos, Brazil**	**Espírito Santo, Brazil**	**Rio de Janeiro, Brazil**	**São Paulo, Brazil**	**Santa Catarina, Brazil**
Calamus pena	X	X		X												
Centropristis striata	X	X														
Haemulon aurolineatum	X	X							X			X			X	X
Haemulon flavolineatum					X											
Haemulon parra					X				X							
Haemulon plumieri	X		X	X				X	X			X				
Haemulon sciurus					X											
Haemulon squamipinna									X							
Haemulon sp.																X
Halichoeres bivittatus	X	X			X			X	X							
Halichoeres brasiliensis									X		X	X		X		

	North Carolina, USA	**Gerogia, USA**	**Central Florida, USA**	**Florida Keys, USA**	**Yucatán, Mexico**	**Carrie Bow Cay, Belize**	**Curaçao**	**Parcel Manoel Luís, Brazil**	**Rio Grande do Norte, Brazil**	**Atol das Rocas, Brasil**	**Costa do Corais, Brazil**	**Abrolhos, Brazil**	**Espírito Santo, Brazil**	**Rio de Janeiro, Brazil**	**São Paulo, Brazil**	**Santa Catarina, Brazil**
Halichoeres caudalis	X	X														
Halichoeres dimidiatus								X						X	X	
Halichoeres garnotti			X	X	X	X	X									
Halichoeres maculipina			X	X		X	X									
Halichoeres penrosei									X							
Halichoeres poeyi								X	X		X	X	X	X	X	X
Halichoeres radiatus					X					X		X				
Halichoeres sp.							X									
Holocentrus adscencionis			X							X						
Hyporthodus indiglo						X										
Hyporthodus unicolor							X									
Lactophrys triqueter				X	X		X									

	North Carolina, USA	**Gerogia, USA**	**Central Florida, USA**	**Florida Keys, USA**	**Yucatán, Mexico**	**Carrie Bow Cay, Belize**	**Curaçao**	**Parcel Manoel Luís, Brazil**	**Rio Grande do Norte, Brazil**	**Atol das Rocas, Brasil**	**Costa do Corais, Brazil**	**Abrolhos, Brazil**	**Espírito Santo, Brazil**	**Rio de Janeiro, Brazil**	**São Paulo, Brazil**	**Santa Catarina, Brazil**
Malacanthus plumieri										X					X	
Mulloidichthys martinicus							X									
Pseudupeneus maculatus	X	X	X	X	X	X		X	X		X	X	X	X	X	X
Rhomboplites aurorubens																X
Sessile invertebrate feeders	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**		**X**	**X**	**X**	**X**	**X**
Acanthostracion polygonius					X									X		
Acanthostracion quadricornis		X												X		
Aluterus scriptus			X													
Canthigaster figueiredoi														X		X

	North Carolina, USA	Gerogia, USA	Central Florida, USA	Florida Keys, USA	Yucatán, Mexico	Carrie Bow Cay, Belize	Curaçao	Parcel Manoel Luís, Brazil	Rio Grande do Norte, Brazil	Atol das Rocas, Brasil	Costa do Corais, Brazil	Abrolhos, Brazil	Espírito Santo, Brazil	Rio de Janeiro, Brazil	São Paulo, Brazil	Santa Catarina, Brazil
Canthigaster rostrata				X	X		X									
Cantherhines macrocerus												X				
Cantherhines pullus													X	X		
Chaetodon capistratus				X	X	X	X									
Chaetodon ocellatus			X	X				X		X						
Chaetodon sedentarius			X	X	X									X		
Chaetodon striatus				X	X	X			X			X	X	X	X	X
Holacanthus ciliaris			X			X			X			X				
Holacanthus tricolor			X	X	X	X	X		X							
Monacanthus tuckeri			X													
Sphoeroides greeleyi														X		
Sphoeroides spengleri	X	X			X								X	X	X	X

	North Carolina, USA	Gerogia, USA	Central Florida, USA	Florida Keys, USA	Yucatán, Mexico	Carrie Bow Cay, Belize	Curaçao	Parcel Manoel Luís, Brazil	Rio Grande do Norte, Brazil	Atol das Rocas, Brasil	Costa do Corais, Brazil	Abrolhos, Brazil	Espírito Santo, Brazil	Rio de Janeiro, Brazil	São Paulo, Brazil	Santa Catarina, Brazil
Omnivores	X	X			X		X		X	X	X	X	X	X	X	X
Abudefduf saxatilis					X				X	X	X	X		X	X	X
Archosargus probatocephalus	X	X														
Diodon histrix													X			
Diplodus argenteus													X	X	X	X
Diplodus holbrooki	X	X														
Melichtys niger					X					X						
Pomacanthus arcuatus						X										
Pomacanthus paru					X		X									
Stephanolepis hispidus		X												X	X	X

Table S3 List of commercially important species at each sampling location. (*) Central Florida did not have available data.

Local	Species
North Carolina, USA (34°N)	
	Archosargus probatocephalus
	Caranx crysos
	Centropristis ocyurus
	Centropristis striata
	Chaetodipterus faber
	Mycteroperca bonaci
	Mycteroperca microlepis
	Mycteroperca phenax
	Seriola rivoliana
Georgia, USA (31°N)	
	Archosargus probatocephalus
	Balistes capriscus
	Caranx bartholomei
	Centropristis ocyurus
	Centropristis striata
	Chaetodipterus faber
	Lutjanus analis
	Lutjanus griseus
	Mycteroperca microlepis
	Mycteroperca phenax
	Sphyraena barracuda
	Sphyraena guanacho
	Sphyraena picudilla
Central Florida, USA (26°N)*	
	Data unavailable
Florida Keys, USA (24°N)	
	Caranx ruber
	Cephalopholis fulva
	Epinephelus adscencionis

	Epinephelus cruentata
	Lutjanus analis
	Lutjanus apodus
	Lutjanus mahogany
	Mycteroperca bonaci
	Negaprion brevirostris
	Ocyurus chrysurus
	Sphyraena barracuda
Yucatán, Mexico (22°N)	
	Caranx bartholomei
	Caranx lugubris
	Caranx ruber
	Cephalopholis cruentata
	Cephalopholis fulva
	Epinephelus adscencionis
	Epinephelus guttatus
	Lutjanus analis
	Lutjanus apodus
	Lutjanus griseus
	Lutjanus synagris
	Mycteroperca interstitialis
	Mycteroperca phenax
	Mycteroperca venenosa
	Sphyraena barracuda
Carrie Bow Cay, Belize (16°N)	
	Caranx bartholomei
	Caranx ruber
	Cephalopholis fulva
	Epinephelus cruentata
	Epinephelus guttata
	Epinephelus striata
	Mycteroperca phenax
	Ocyurus chrysurus
	Sphyraena barracuda

Curaçao (12°N)	
	Caranx ruber
	Cephalopholis cruentata
	Cephalopholis fulva
	Lutjanus analis
	Lutjanus apodus
	Lutjanus mahogany
	Lutjanus synagris
	Mycteroperca interstitialis
	Sphyraena barracuda
Parcel Manoel Luís, Brazil (0°)	
	Caranx bartholomei
	Caranx crysos
	Caranx ruber
	Chaetodipterus faber
	Dermatolepis inermis
	Epinephelus adscencionis
	Epinephelus itajara
	Lutjanus jocu
	Mycteroperca bonaci
	Sphyraena barracuda
Atol das Rocas, Brazil (3°S)	
	Caranx bartholomei
	Caranx latus
	Cephalopholis fulva
	Dermatolepis inermis
	Lutjanus jocu
	Negaprion brevirostris
	Sphyraena barracuda
Rio Grande do Norte, Brazil (5°S)	
	Caranx bartholomei
	Caranx hippos
	Caranx ruber
	Cephalopholis fulva

	Chaetodipterus faber
	Epinephelus adscencionis
	Epinephelus itajara
	Lutjanus alexandrei
	Lutjanus cyanopterus
	Lutjanus jocu
	Lutjanus synagris
	Mycteroperca bonaci
	Pseudocaranx dentex
	Seriola rivoliana
	Sphyraena barracuda
Costa dos Corais, Brazil (8°S)	
	Caranx bartholomei
	Cephalopholis fulva
	Epinephelus adscencionis
Abrolhos, Brazil (17°S)	
	Caranx latus
	Caranx ruber
	Epinephelus morio
	Lutjanus jocu
	Mycteroperca bonaci
Espírito Santo, Brazil (20°S)	
	Caranx crysos
	Caranx latus
	Cephalopholis fulva
	Dermatolepis inermis
	Mycteroperca bonaci
Rio de Janeiro, Brazil (22°S)	
	Caranx latus
	Caranx ruber
	Epinephelus marginata
	Lutjanus analis
	Lutjanus jocu
	Mycteroperca acutirostris

	Mycteroperca interstitialis
São Paulo, Brazil (23°S)	
	Caranx crysos
	Chaetodipterus faber
	Epinephelus marginata
	Epinephelus morio
	Hyporthodus niveatus
	Lutjanus analis
	Mycteroperca acutirostris
	Mycteroperca bonaci
	Mycteroperca interstitialis
	Pseudocaranx dentex
	Seriola rivoliana
Santa Catarina, Brazil (27°S)	
	Caranx crysos
	Caranx latus
	Chaetodipterus faber
	Epinephelus marginata
	Hyporthodus niveatus
	Lutjanus analis
	Mycteroperca acutirostris
	Mycteroperca bonaci
	Mycteroperca interstitialis
	Pseudocaranx dentex
	Seriola rivoliana

Table S4 Results of SIMPER analyses indicating the contribution of sfunctional groups to observed differences the composition of feeding pressure among the groups.

Group contrast	**Overall average dissimilarity**	**Functional groups**	**Average dissimilarity**	**Contribution (%)**	**Cummulative contribution (%)**
Tropical vs. Extratropical	60.88	Omnivores	13.01	21.37	21.37
		Scrapers	11.94	19.62	40.99
		Mobile invertebrate feeders	10.25	16.83	57.82
		Fine browsers	9.1	14.95	72.77
		Excavators	5.71	9.38	82.15
		Rough browsers	4.62	7.58	89.73
		Territorial herbivores	3.86	6.34	96.08
Tropical vs. Transitional	37.79	Sessile invertebrate feeders	6.51	17.22	17.22
		Fine browsers	6.47	17.13	34.35
		Excavators	6.09	16.12	50.48
		Mobile invertebrate feeders	5.81	15.38	65.86
		Scrapers	5.25	13.9	79.76
		Rough browsers	3.28	8.69	88.45
		Territorial herbivores	2.93	7.77	96.22

Transitional vs. Extratropical	53.48	Omnivores	14.56	27.23	27.23
		Scrapers	12.2	22.81	50.04
		Sessile invertebrate feeders	6.38	11.94	61.97
		Mobile invertebrate feeders	6.21	11.61	73.58
		Territorial herbivores	5.42	10.14	83.72
		Rough browsers	5.36	10.02	93.73

Table S5 Results of SIMPER analyses indicating the contribution of species to within groups similarities of feeding pressure composition.* The transitional reef of the North hemisphere was not included in this analysis because it contained only one location (Central Florida).

Region	**Overall average similarity**	**Functional groups**	**Average similarity**	**Contribution (%)**	**Cummulative contribution (%)**
Extratropical North	53.94	*Halichoeres bivittatus*	14.3	26.51	26.51
		Arcosargus probatocephalus	10.84	20.1	46.6
		Diplodus holbrooki	8.51	15.78	62.38
		Calamus penna	7.76	14.38	76.76
		Calamus calamus	6.1	11.31	88.07
		Pseudupeneus maculatus	3.29	6.09	94.17
Caribbean	65.12	*Acanthurus tractus*	11.22	17.23	17.23
		Sparisoma viride	10.19	15.65	32.88
		Acanthurus coeruleus	10.07	15.46	48.34
		Sparisoma aurofrenatum	8.41	12.92	61.26
		Scarus taeniopterus	5.47	8.4	69.66
		Scarus iseri	3.14	4.83	74.49
		Holacanthus tricolor	2.25	3.45	77.93
		Stegastes adustus	2.13	3.28	81.21
		Acanhturus chirurgus	1.9	2.91	84.12

		Chaetodon capistratus	1.9	2.91	87.03
		Sparisoma rubripinne	1.65	2.53	89.56
		Halichoeres garnotti	1.22	1.87	91.43
NE Brazil	46.02	*Acanhturus chirurgus*	1.42	42.62	42.62
		Acanthurus coeruleus	4.47	14.84	57.46
		Acanthurus bahianus	0.9	7.53	64.99
		Sparisoma axillare	2.82	7.38	72.37
		Sparisoma frondosum	2.39	6.29	78.66
		Scarus zelindae	0.62	4.28	82.94
		Anisotremus virginicus	0.89	2.54	85.48
		Scarus trispinosus	0.41	2.3	87.78
		Stegastes fuscus	0.41	1.85	89.63
		Sparisoma sp.	0.77	1.68	91.31
E Brazil	66.37	*Acanthurus bahianus*	38.24	57.63	57.63
		Acanthurus coeruleus	6.82	10.28	67.9
		Pseudupeneus maculatus	5.04	7.6	75.5
		Sparisoma frondosum	3.11	4.69	80.19
		Bodianus rufus	2.91	4.38	84.58
		Chaetodon striatus	2.2	3.32	87.9
		Anisotremus virginicus	2.19	3.3	91.2
Extratropical South	57.32	*Kyphosus* sp.	10.76	18.78	18.78
		Diplodus argenteus	8.83	15.4	34.18
		Stegastes fuscus	7.92	13.81	47.99
		Anisotremus virginicus	5.84	10.18	58.17
		Haemulon aurolineatum	5.49	9.57	67.74
		Abudefduf saxatilis	4.59	8	75.74
		Sparisoma frondosum	3.58	6.24	81.99
		Pseudupeneus maculatus	3.5	6.1	88.09
		Stephanolepis hispidus	2.5	4.37	92.46

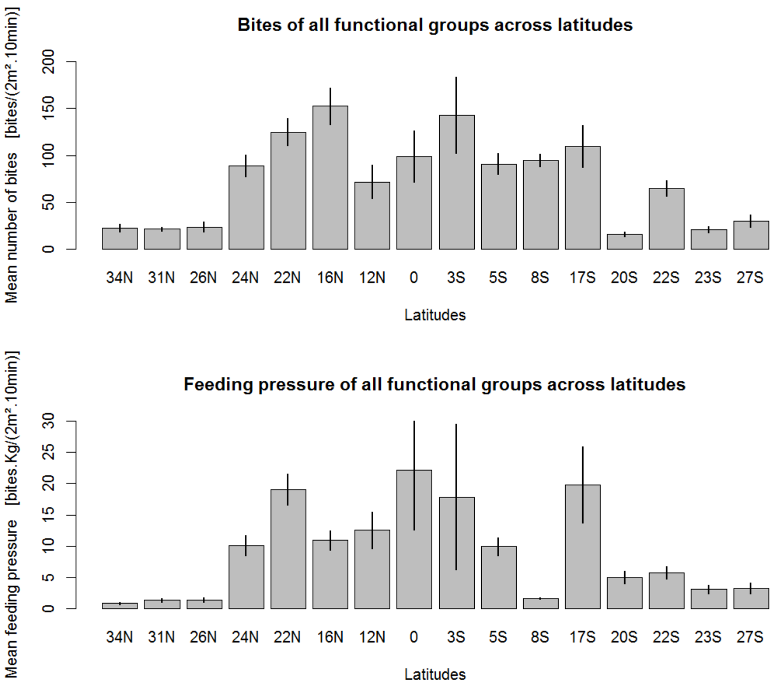

Figure S1 Latitudinal trends in reef fish feeding pressure on the benthos. (a) mass-standardized bites; (b) non-mass standardized bites.

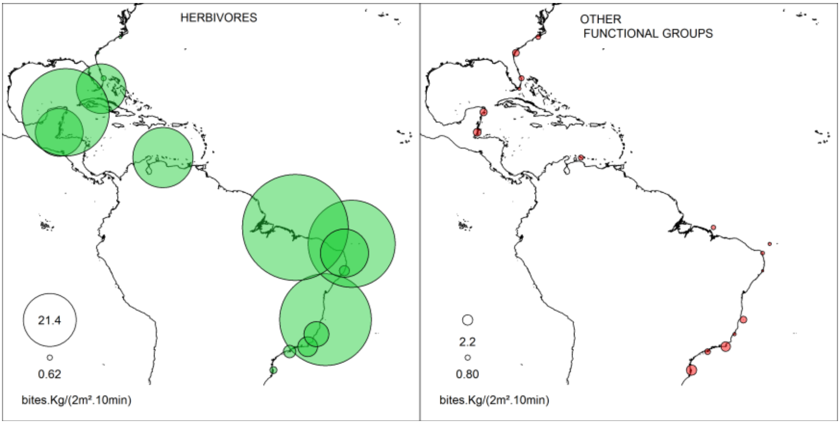

Figure S2 Reef fish feeding pressure of herbivorous functional groups combined (*i.e.*, scrapers, excavators, fine browsers, rough browsers and territorial herbivores; left) and of other functional groups combined (mobile invertebrate feeders, sessile invertebrate feeders and omnivores; right).

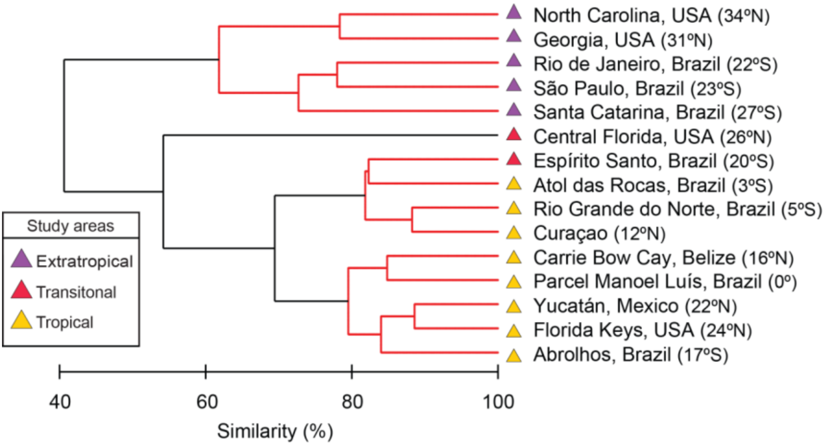

Figure S3 Cluster analysis (Bray-Curtis Similarity; UPGMA) of the relationship between sites based on the composition of feeding pressure by functional groups. Clusters colored in red represent those with significant results in the SIMPROF test.

CONCLUSÃO GERAL

Diante dos resultados apresentados ao longo dos quatro capítulos desta tese, conclui-se que estudos sobre o funcionamento de ecossistemas recifais devem ir além da quantificação de padrões de diversidade, abundância e biomassa, já que as interações tróficas em ambientes recifais e, consequentemente, os processos mediados por tais interações são moldados por múltiplos fatores ao longo de diferentes escalas espaciais. Demonstrou-se através do efeito das interações de contato entre corais e macroalgas sobre a herbivoria de ouriços (Capítulo 1), que a intensidade das interações bióticas podem ser moduladas na escala de centímetros, enquanto seus efeitos podem atingir escalas maiores como de habitat (centenas de metros) ou mesmo região. A sinergia entre fatores bióticos e abióticos demonstrada através das variações nas assembleias de peixes, cobertura bentônica e interações tróficas de peixes sobre o bentos em diferentes habitats do Atol das Rocas (Capítulo 2), indicaram a complexidade do funcionamento de ecossistemas e dificuldade de compreendê-los, sobretudo sem abordagens abrangentes e multidisciplinares. Ainda que se compreenda a distribuição e diferentes tolerâncias e respostas de organismos em relação à fatores abióticos, é necessário que a contribuição das interações bióticas diretas (*e.g.*, predação) e indiretas (*e.g.*, efeito de risco ou “*risk-effect*”), bem como seus potenciais efeitos, sejam considerados no funcionamento dos ecossistemas. Aumentando a escala para variações espaciais de centenas de quilômetros (Capítulo 3), a redução na contribuição dos herbívoros de recifes mais quentes em direção a mais frios e a contribuição desproporcional de algumas espécies e grupos funcionais, indicam que o funcionamento dos ambientes recifais pode variar e depender de espécies e grupos distintos de acordo com condições locais específicas (*e.g.*, temperatura, abundância). Esta abordagem permitiu também a identificação de grupos-chave, com contribuição desproporcional baseado em sua abundância, o que pode ser utilizado para direcionar ações de manejo e conservação sobre processos críticos mediados por esses grupos. Por fim, através da abordagem latitudinal de ampla escala no Atlântico Ocidental, que incluiu recifes tropicais e extratropicais em ambos os hemisférios (Capítulo 4), ressaltou-se a importância combinada de aspectos ecológicos (*e.g.*, temperatura) e biogeográficos (*e.g.*, endemismo regional) como determinantes das interações tróficas. Embora recifes em diferentes regiões compartilhem funções semelhantes, as espécies compondo os grupos funcionais bem como a contribuição relativa de cada uma dessas espécies, pode afetar aspectos importantes como redundância funcional e o funcionamento dos ecossistemas. A combinação dessas abordagens desde a escala do centímetro até a escala latitudinal permitiu avanços importantes em diversos aspectos da ecologia, sobretudo: (1) demonstrando a complexidade das interações tróficas e chamando atenção para potenciais dificuldades de entendimento do funcionamento de ecossistemas a partir dos tradicionais modelos de padrões de riqueza, abundância e biomassa, o que deve ser levado em conta em estudos desses descritores em escala global; e (2) indicando abordagens iniciais possíveis pra que a compreensão de interações tróficas possa ser usada em ações de manejo de processos críticos mediados por essas interações.