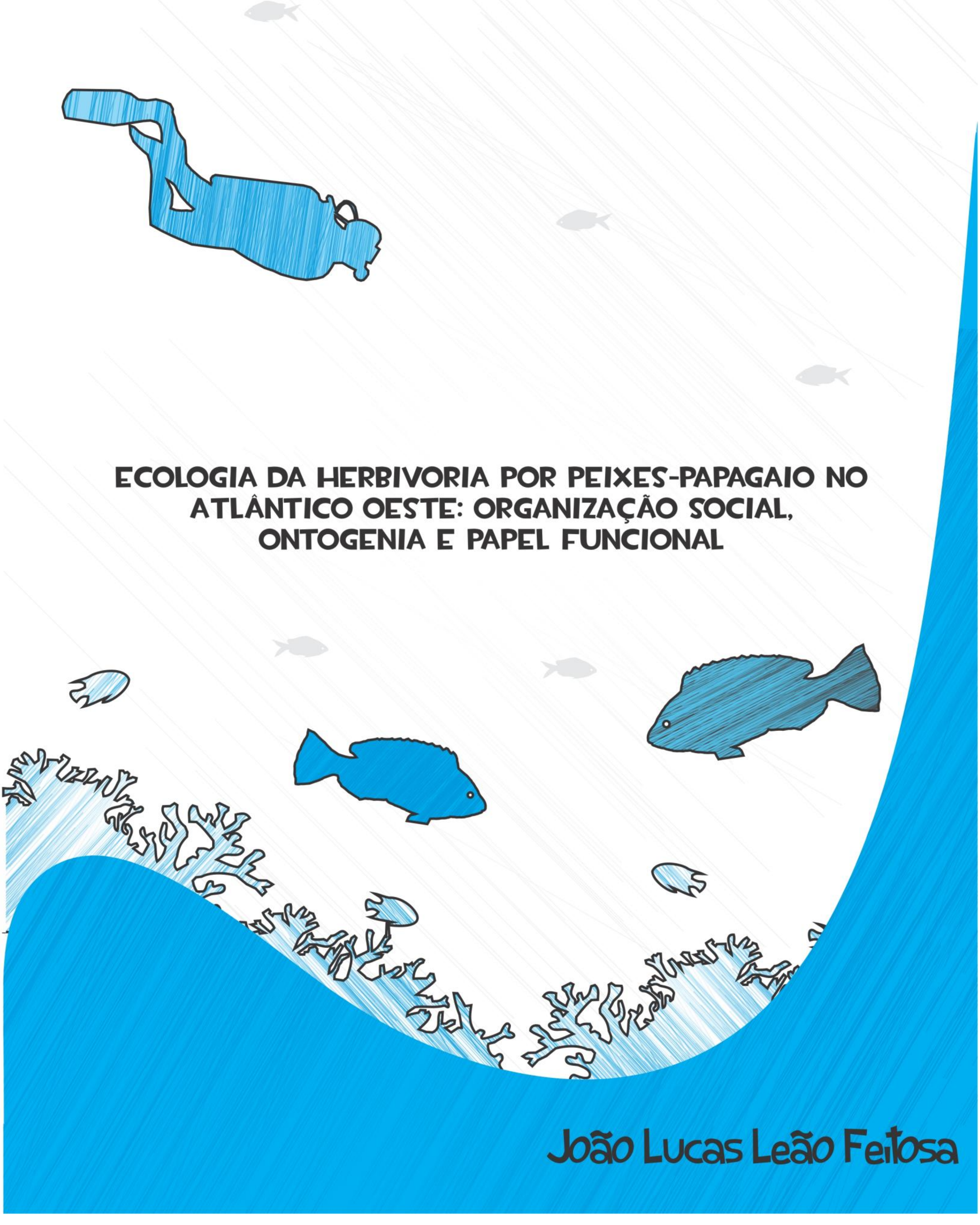

ECOLOGIA DA HERBIVORIA POR PEIXES-PAPAGAIO NO ATLÂNTICO OESTE: ORGANIZAÇÃO SOCIAL, ONTOGENIA E PAPEL FUNCIONAL

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Tese apresentada ao Programa de Pós-Graduação em Oceanografia da Universidade Federal de Pernambuco, Centro de Tecnologia e Geociências como parte dos requisitos para obtenção do grau de Doutor em Oceanografia Biológica.

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“Na beira do rio, na proa da maré
Tinha xié, tinha caranguejo,
Tinha aimoré, tinha guaiamum,
Tinha?
Tinha!
Dentro do mangue
tinha guará, tinha guaxinim
Socó e inhanum
Tinha?
Tinha!
Tinha aratu.
Professor, tem guarú? Tem!
Tinha gato, tinha siri
Tinha saúna, tinha camurim
Tinha?
Tinha!"

Erasto Vasconcelos e Banda Eddie

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Resumo Geral

A herbivoria é um dos fatores responsáveis pelo controle da biomassa e cobertura de algas, bem como molda a composição específica de suas assembleias. Vários organismos são herbívoros, dentre eles os peixes-papagaio (família Scaridae), que através do consumo de algas abrem espaço para o assentamento e crescimento de corais juvenis, realizando um papel central na manutenção dos recifes de coral. Estudos recentes têm associado a diminuição da cobertura viva de recifes de coral à diminuição da abundância de peixes herbívoros da família Scaridae, causada pela intensa pesca dirigida a estas espécies, várias ja classificadas como ameaçadas ou quase ameaçadas segundo critérios da IUCN. Vários trabalhos têm sido desenvolvidos abordando a função dos peixes-papagaio, porém a maioria das teorias que envolvem a herbivoria por peixes recifais foi desenvolvida no Indo-Pacífico e no Caribe. Entretanto, tais estudos geralmente tratam a alimentação como uma característica de cada espécie, negligenciando potenciais efeitos da organização social e ontogenia em sua composição alimentar. Nesse âmbito, a presente tese teve como objetivo elucidar três pontos principais, que resultaram na composição de três capítulos, analisando: (1) a influência de distintas organizações sociais na alimentação de peixes-papagaio; (2) a influência de mudanças ontogenéticas e no uso de distintos habitats na alimentação de peixes-papagaio; (3) o efeito da herbivoria por peixes-papagaio nos recifes de coral brasileiros. Para o primeiro capítulo, a espécie *Scarus iseri*, uma das espécies de peixe-papagaio mais abundantes do Caribe, foi selecionada tendo em vista que a maioria dos estudos abordando a ecologia social de peixes-papagaio foram realizados com esta espécie. Durante o presente trabalho, foram identificadas duas distintas organizações sociais para esta espécie, os grupos estacionários e os territoriais, ambos consistindo de poucos indivíduos que usam uma área limitada, mas agressivamente defendida por seus membros apenas no último grupo. Foi observado que indivíduos em diferentes grupos sociais se distribuíram de forma distinta no ambiente recifal e que possuíam estruturas de tamanho diferenciadas, sendo os indivíduos jovens mais abundantes nos ambientes de grupos estacionários, devido a exclusão competitiva por indivíduos territoriais. As agressões intraespecíficas, mais frequentes nos grupos territoriais, foram utilizadas para defender habitats com maior disponibilidade de alimento preferido por *S. iseri*. Os indivíduos em grupos territorialistas se alimentaram principalmente de algas filamentosas, um item de maior palatabilidade e alta produção, enquanto que a dieta de indivíduos em grupos estacionários foi composta por detritos presentes no substrato e sobre esponjas. Foi possível observar que os peixes-papagaio podem mudar sua ecologia alimentar de acordo com sua organização social, alterando por conseguinte sua função do ambiente recifal. No segundo capítulo a espécie estudada foi *Sparisoma axillare*, o peixe-papagaio mais abundante na maioria dos recifes de coral brasileiros. Este estudo focou sua ecologia alimentar na fase jovem em quatro diferentes habitats dos recifes de Tamandaré: (1) os bancos de algas, (2) o back reef, (3) o topo recifal e (4) o fore reef. Os indivíduos menores de 5 cm preferiram habitar os bancos de macroalgas e o topo recifal, enquanto os indivíduos maiores que 5 cm habitaram em maior número o back e o fore reef, diferença devida a distintas condições pós-assentamento entre estes habitats. Interações agressivas com o peixe-donzela *Stegastes fuscus* foram o principal fator influenciando essa distribuição e as taxas de alimentação de *S. axillare*. Indivíduos menores ocorreram em habitats dominados por *S. fuscus* por apresentar comportamento críptico e se alimentaram em baixa frequência, ao crescer estes indivíduos aumentaram suas taxas de alimentação e passaram ao comportamento vagueador. A preferência alimentar dos jovens foi determinada pela disponibilidade de alimento em cada habitat, entretanto algas filamentosas foram o principal alimento de indivíduos menores, enquanto que para indivíduos maiores de 10 cm uma maior ingestão de areia foi constatada. Através deste estudo foi observado que uma espécie de peixe-papagaio pode variar sua dieta de acordo com a disponibilidade de alimento em cada ambiente, o que pode ser dependente do seu tamanho e sua interação com outras espécies. No terceiro capítulo foi abordado o efeito da herbivoria por peixes-papagio nos recifes de coral costeiros do Brasil. Para tal, três experimentos utilizando a exclusão da herbivoria com gaiolas foram realizados, observando: (1) a influência da herbivoria na biomassa de algas; (2) a influência da herbivoria na percentual de cobertura bentônica; (3) a influência da herbivoria na sucessão ecológica da cobertura bentônica. Foi observado que a exclusão da herbivoria não resultou em um aumento da biomassa de algas, como observado na literatura. Entretanto, foi registrado um aumento na cobertura e riqueza das algas filamentosas nos tratamentos de exclusão da herbivoria, que ocorreram de forma elítica e epifítica. Com o aumento da cobertura de algas filamentosas, foi observado uma diminuição na cobertura de algas folhosas e calcárias articuladas, onde o último grupo apresentou uma relação positiva com a temperatura ao longo do experimento. As algas filamentosas também apresentaram uma relação positiva com a temperatura e em períodos de maior turbidez o crescimento de sua cobertura foi interrompido. No experimento de sucessão, a exclusão da herbivoria resultou em uma maior continuidade das espécies pioneiras na sucessão ecológica, as algas filamentosas. Entretanto, apesar da remoção da herbivoria a asesembleia de algas retornou a um estado de dominância de algas calcárias articuladas, um estado sucessional avançado. Os achados obtidos no presente estudo resultaram da baixa densidade de herbívoros raspadores (i.e. peixes-papagaio), capazes de retirar grandes porções de algas calcárias articuladas com sua alimentação, abrindo espaços no substrato para o assentamento de corais. Através da presente tese, se salienta e embasa a prioridade da criação de estratégias de manejo voltadas para a preservação de tal grupo, para que a saúde dos ambientes recifais seja garantida.

Palavras-chave: Oceanografia, Recifes de coral, Scaridae, Algas marinhas

General abstract

The herbivory is one of the factors responsible for the control of algae biomass and cover, also shaping specific composition of their assemblages. Several organisms are herbivores, including parrotfishes, which by algae consumption open space for juvenile coral settlement and growth, performing a prime role in coral reef maintenance. Recent studies associate the decrease in live coral cover to the reduction on parrotfish abundance, triggered by severe fishing efforts targeting these species, and several of those are classified as endangered or near threatened species according to IUCN criteria. Several work have been addressing parrotfish function, however most of the theories encompassing herbivory by reef fishes was developed took place in the Indo-Pacific and Caribbean. Most of these studies generally address this matter as a species-specific trait, negleting distinct strategies a single species may have to choose their diet composition. In this context, this Thesis aimed to elucidate three main points, which resulted in the composing of three chapters, analyzing: (1) the influence of different social organizations in parrotfish feeding; (2) the influence of ontogenetic shifts and differential habitat use in parrotfish function; (3) the effect of herbivory by parrotfishes in Brazilian reef systems. For the first chapter, *Scarus iseri*, one of the most abundant parrotfish species of the Caribbean was selected, given most work addressing parrotfish social ecology was performed with this species. During the present study, two distinct social organizations were observed for this species, the stationary and territorial groups, both comprising few fish that use a limited area, but aggressively defended by its members only on the latter grouping. It was observed that individuals in different social groups occupied the reef habitats separately, having distinct size structures, where youngest individuals were more abundant in stationary groups habitats, due to aggressive exclusion of territorial fish. Intraspecific aggression, more frequent in territorial groups, were directed to protection of habitats with greater availability of preferred food. Individuals in territorial groups fed mostly of filamentous algae, a more edible and productive group of algae, while the diet of stationary groups individuals was mainly composed of detritus over the substrate and over sponges. It was possible to determine after this work that parrotfish can shift their feeding ecology depending on their social organization patterns thus changing their role in the reef environment. In the second chapter the study species was *Sparisoma axillare*, the most abundant parrotfish in most of the Brazilian reefs. This study focused its feeding ecology as juvenile in four distinct habitats of Tamandaré reefs: (1) macroalgae beds, (2) the back reef, (3) the reef flat, and (4) the fore reef. Individuals with less than 5 cm inhabited mostly the macroalgae beds and reef flat, while individuals over 5 cm had greatest densities on the back and fore reefs, a variation attibuted to distinct post-settlement habitat conditions. Aggressive interactions with the damselfish *Stegastes fuscus* were the main factor driving *S. axillare* distribution and feeding rates. Smallest individuals occurred in sites dominated by *S. fuscus* by presenting a cryptic behavior and feeding in low frequencies, as they grew larger, these individuals increased their feeding rates and went to a roving behavior. Juvenile feeding preferences were determined by food availability in each habitat, nevertheless, filamentous algae was the main food item among the smallest individuals, while individuals over 10 cm had a greater incidence of bites over sand. Through this study it was observed that a parrotfish species may alter its food habits accordingly to the food availability in its habitat, what can depend on fish size and its interaction with other species. In the third chapter, it was addressed the effect of herbivore fishes in Brazilian reef systems. For that, three experiments applying herbivore exclusion through caging were performed, taking into account: (1) effects on algae biomass; (2) effects on benthic cover; (3) effects on benthic succession. Herbivore exclusion did not result in algae biomass increases, as reported for other reef systems. Nevertheless, an increase in filamentous algae cover and species richness was observed in herbivore exclusion treatments, which grew both epilithically and as epiphytes. With the increment of filamentous algae cover, a decrease in the cover of sheet-like and jointed calcareous algae occurred, and the latter group presented a positive relationship with temperature throughout the experiment. Filamentous algae also presented such relationship with temperature and during periods of higher turbidity the increasing in their cover was halted. Regarding algal succession, herbivore exclusion rendered the higher permanence of pioneer species, the filamentous algae. However, regardless of herbivore removal, algae assemblages returned to a state of jointed calcareous dominance, a late-successional stage in algal succession. The findings attained herein resulted from the low densities of scrapping herbivores, mostly parrotfish, capable of removing great portions of calcareous algae while feeding, opening space on the reef for coral to settle. The present thesis emphasize the priority of management strategies focusing the conservation of this herbivore group, to assure the health of Brazilian reef environments.

Keywords: Oceanografia, Recifes de coral, Scaridae, Algas marinhas

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Capítulo 1

Fundamentação Teórica

1 - Composição, distribuição e crescimento dos recifes de coral brasileiros

A fauna de corais do Brasil possui três características que a difere de outros sistemas recifais do mundo: apresenta uma diversidade muito reduzida; suas principais espécies construtoras de recifes são endêmicas; e é composta de espécies com crescimento massivo (LEÃO *et al.*, 2003). Seis espécies de corais são endêmicas do Brasil, e entre estas algumas possuem afinidade com as espécies do Caribe, enquanto que outras são relativas a fauna coralina do Terciário, encontradas no Mediterrâneo e na Flórida apenas como fósseis (MAIDA; FERREIRA, 1997). Estas espécies menos derivadas são as formas mais comuns da fauna coralina brasileira, de crescimento massivo; sendo herança de fauna comum que existia durante o final do Mioceno e o início do Plioceno, quando ocorreu o isolamento da fauna caribenha quando o rio Amazonas passou a desaguar no oceano Atlântico (FROST, 1977). Além disso, os recifes brasileiros não possuem os acroporídeos ramificados, os principais corais da crista recifal e fore-reef caribenhos (LEÃO *et al.*, 2003).

Os recifes de coral brasileiros estão distribuídos desde a foz do rio Amazonas até o litoral catarinense; possuindo certos isolamentos geográficos resultantes da foz do rio São Francisco e da foz do rio Doce. A região Nordeste do Brasil é onde os recifes de coral se encontram mais abundantes, enquanto que as regiões Norte e Sudeste são consideradas regiões de "empobrecimento" em corais hermatípicos (LABOREL, 1969). Dentre as espécies de coral endêmicas brasileiras, *Mussimilia braziliensis* e *Favia leptophylla* são as de maior confinamento geográfico, ocorrendo apenas no litoral baiano; enquanto que *Mussismilia hispida*, *Mussismilia harttii*, *Siderastrea stellata* e *Favia gravida* possuem as maiores distribuições, ocorrendo desde ilhas oceânicas até a costa sudeste. *Porites astreoides*, *P. branneri*, *Agaricia agaricites*, *A. fragilis*, *Montastraea cavernosa* e *Madracis decactis* são cosmopolitas e comuns as faunas caribenha e brasileira, possuindo um papel secundário na construção dos recifes do nordeste brasileiro (LEÃO *et al.*, 2003) (Figura 1).

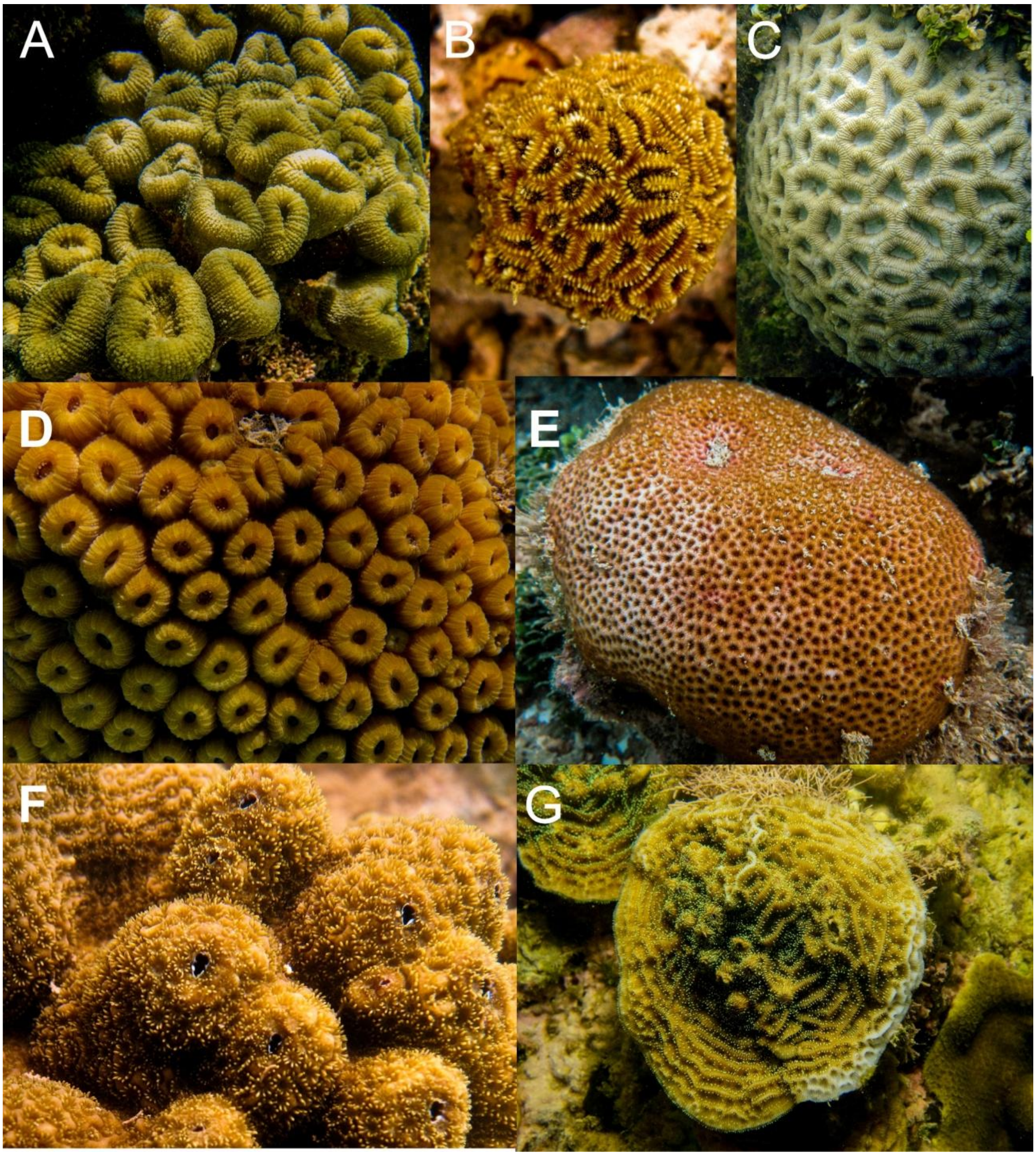

Figura 1 - Principais espécies de coral presentes na costa Nordeste do Brasil. A- *Mussismilia harttii*; B - *Favia gravida*; C - *Mussismilia hispida*; D - *Montrastrea cavernosa*; E - *Siderastrea stellata*; F - *Porites astreoides*; G - *Agaricia humilis*. Fotos do Autor.

O surgimento dos recifes de coral costeiros no Brasil acompanhou padrões de alterações no nível do mar pós-glaciação, e são caracterizados por quatro fases de crescimento (sensu LEÃO *et al.*, 2003): 1) iniciação e estabelecimento dos recifes 2) rápida crescimento vertical 3) crescimento lateral dos recifes e 4) degradação dos recifes. No período antecedente a 10.000 AP (anos antes do presente) o nível do mar no Brasil se encontrava abaixo da plataforma continental, devido ao último período glacial. Segundo estudos geológicos, entre 8.000 e 7.000 AP a plataforma continental brasileira começou a se tornar alagada (MARTIN, 1985), e os recifes brasileiros começaram sua formação sobre a plataforma (LEÃO *et al.*, 2006); os recifes mais antigos já datados possuem 6.600 AP. Entretanto, as formações recifais que se instalaram na borda da plataforma não conseguiram acompanhar a subida rápida do nível do mar, devido ao crescimento lento característico dos corais, e hoje a maioria destas formações se encontra recoberta por sedimentos e rodolitos de algas coralinas (KIKUCHI; LEÃO, 1998). Por outro lado, os recifes que surgiram mais próximos da costa apresentaram um rápido crescimento vertical com o aumento do nível do mar até os 5-4.000 AP, período no qual estes recifes puderam crescer mais de 10 m em altura em menos de 3000 anos. O crescimento vertical destas estruturas parou uma vez que alcançaram o nível do mar na época, que era aproximadamente quatro metros acima do nível atual (MARTIN, 1985), onde se iniciou um processo de crescimento horizontal. Estudos com datação demonstraram que os recifes de Alagoas e Pernambuco alcançaram seus topos entre 3.900 e 5.700 AP, provavelmente iniciando seu crescimento lateral neste período (BARBOSA *et al.*, 1986; DOMINGUEZ *et al.*, 1990). Como consequência da diminuição do nível do mar ao longo do tempo até os níveis atuais, todos os recifes próximos da costa se tornaram emersos, sofrendo a erosão das ondas, resultando no aplanamento das suas superfícies, dando aos recifes sua conformação atual.

Com a retração do nível do mar, os recifes também ficaram mais próximos da linha de costa, sendo submetidos aos impactos de altos níveis de sedimentação, turbidez e insolação. Tais impactos resultaram em uma mudança na comunidade coralina, incluindo das suas espécies dominantes, a diminuição dos tamanhos das colônias (de um tamanho médio de 60 cm para 12 cm) e um grande aumento da mortalidade de corais; resultando na diminuição na cobertura de corais. As condições ambientais extremas das águas brasileiras, que são opostas a maioria dos sistemas recifais descritos na literatura, excedem a tolerância da maioria das espécies de coral, limitando a presença de somente espécies mais resistentes e adaptadas (LEÃO *et al.*, 2003).

A costa brasileira não é afetada por eventos catastróficos, que possuem grande influência nos recifes do Indo-Pacífico e Caribe, sendo a maior ameaça aos recifes brasileiros o impacto humano. Dentre as atividades humanas que mais impactam os recifes encontram-se as más práticas de uso do solo, a poluição doméstica e industrial, a sobrexploração dos recursos recifais e o turismo descontrolado (MAIDA; FERREIRA, 1997). No nordeste do Brasil, o desmatamento para uso da madeira e a plantação de cana-de-açúcar deu origem a um aumento da sedimentação. Os recifes costeiros de Tamandaré, por exemplo, sofrem um alto impacto de sedimentação, podendo alcançar valores de até 99 $mg.cm^{-2}.dia^{-1}$ no inverno (MACEDO, 2009) (Figura 2), enquanto que em Abrolhos esses valores não ultrapassam os 20 $mg.cm^{-2}.dia^{-1}$ (LEÃO; KIKUCHI, 2005) e no Caribe não superam os 10 $mg.cm^{-2}.dia^{-1}$ (ROGERS, 1983).

Figura 2 - Imagem de satélite demonstrando a sedimentação sobre os recifes de Tamandaré, provocadas descargas fluviais da foz do rio Una (fonte: Macedo 2009)

No Brasil, devido a esses variados impactos de origem continental, as maiores coberturas coralinas são observadas em recifes mais distantes da costa, alcançando o máximo de ~30%, como observado em Abrolhos, na Bahia (PITOMBO *et al.*, 1988). Apesar da falta de estudos que quantificassem a perda de cobertura coralina no Brasil, existem relatos de uma redução na cobertura de coral nos recifes costeiros de aproximadamente 25% nos anos 60 (como observado por Jaques Laborel), para menos de 5% nos anos 2000 (FERREIRA; MAIDA, 2006). Estima-se que os recifes de coral em outras regiões do mundo encontram-se também em declínio em relação a cobertura coralina. Nos recifes da Grande Barreira de Corais, por exemplo, a cobertura média de corais mudou de mais de 30% para menos de 15% ocorreu nas últimas 3 décadas, associada a ciclones, eventos de branqueamento e explosões populacionais de predadores de coral (DE'ATH *et al.*, 2012). No Caribe, alguns sítios tiveram a cobertura de corais reduzida de ~40% para menos de 10% de 1970 a 1990 devido a sobrepesca, ciclones e doenças que afetaram os corais e os herbívoros controladores das algas (HUGHES, 1994). Em um cenário de mudanças climáticas, principalmente devido ao aumento da temperatura do mar, a incidência e a potência de eventos catastróficos, como cilones, vêm aumentando nas últimas décadas (EMANUEL, 2005; TRENBETH, 2005; WEBSTER *et al.*, 2005)

2 - As algas e suas funções ecológicas

COMPETIÇÃO ENTRE CORAIS E ALGAS

Todos os organismos bentônicos de recifes competem por espaço para viver nos substratos duros formados pelos corais e outros organismos construtores. Os corais e as algas são constantemente referenciados por tal competição por substrato, onde ambos a realizam através de diferentes estratégias de vida. Enquanto os corais apresentam crescimento lento e reproduzem em períodos específicos, muitas espécies de algas crescem rapidamente, reproduzem ao longo do ano e podem sobreviver a adversidades ambientais formando cistos. As algas são geralmente as primeiras espécies a colonizar os esqueletos de coral após sua morte, podendo levar ao equívoco de assumir que as estas são melhores competidoras que os corais (MCCOOK, 2001) (Figura 3).

Figura 3 - Ao ficarem fragilizados ou morrerem os corais são recobertos por macroalgas que impedem sua recuperação e o recrutamento de novos indivíduos. Foto do Autor.

Os corais são exímios competidores nos recifes, podendo inibir o crescimento de algas (de RUYTER VAN STEVENICK *et al.*, 1988, MCCOOK, 2001) ou sobrepor e mata-las (MEESTER; BAK, 1993; MEESTER *et al.*, 1994, 1997), tanto quando recrutas (LITTLER; LITTLER, 1997a), como quando adultos (BAK *et al.*, 1977). As algas também podem possuir efeitos positivos nos corais (JOMPA; MCCOOK, 1998; Heyward and Negri 1999) ou apresentar blooms que durem meses sem afetar os corais (COLES, 1988; MCCOOK, 2001). Poucas espécies de algas são capazes, de fato, de causar sozinhas a morte de um coral por sobrecrescimento, e os eventos registrados na literatura envolvem os gêneros *Lobophora*, *Dictyota*, *Halimeda*, *Dictyosphaeria*, e algumas espécies de algas vermelhas filamentosas e incrustantes (MCCOOK, 2001). Em geral, algas filamentosas ou grandes coriáceas raramente conseguiriam colonizar corais saudáveis (MCCOOK, 2001), e alguns tipos de corais são mais suscetíveis ao sufocamento causado pelo crescimento exacerbado das algas, e.g. corais em forma de placas em relação as formas massivas (HUGHES, 1989; SHULMAN; ROBERTSON, 1996).

A habilidade competitiva das algas é dependente de acúmulo de biomassa suficiente para sobrepor os corais (MILLER; HAY, 1996, 1998) e/ou de outros impactos provenientes de outras fontes, como o aumento da turbidez e da sedimentação (e.g. UMAR *et al.*, 1998). As perturbações externas e a competição com as algas são interativas, e corais estressados podem ser competidores menos bem sucedidos. A habilidade competitiva das algas também pode ser reforçada por certos impactos antropogênicos, como a eutrofização (MCCOOK, 2001).

ABORDAGENS ECOLÓGICAS SOBRE AS ALGAS: OS GRUPOS FUNCIONAIS

Uma vez que a maioria dos estudos com macroalgas envolve descrições taxonômicas, que podem não ser a melhor abordagem para detectar perturbações ecológicas, muitos estudos aplicam uma abordagem em grupos funcionais de algas, que permitem uma avaliação mais rápida de mudanças associadas a adaptação seletiva a perturbações (STENECK; DETHIER, 1994). Características ecológicas, fisiológicas e de desenvolvimento estão intimamente relacionadas com os aspectos morfológicos das macroalgas. Isso é devido ao fato que a estrutura das algas em um menor nível de organização permite, regula e limita cada uma de suas funções biológicas (LITTLER; LITTLER, 1984). Visto que os parâmetros morfológicos das algas podem ser mais facilmente e precisamente mensurados, estes podem prover uma base sólida para a análise de ecosistemas complexos (LITTLER; LITTLER, 1984).

Littler e Littler (1984) subdividiram as macroalgas em seis grupos funcionais: Filamentosas, Folhosas, Ramificadas ou Cilíndricas, Coriáceas, Calcárias articuladas e Calcárias incrustantes. Tal divisão ocorre baseada em características morfológicas externas e de sua anatomia interna, transcendendo afinidades filogenéticas entre as espécies e focando em suas habilidades e funções ecológicas. Ainda neste mesmo estudo, os autores comprovaram que estes grupos são consistentemente diferentes quanto a sua produtividade, resistência física a perturbações, susceptibilidade à herbivoria e conteúdo calórico. As algas filamentosas e as folhosas são em geral as mais produtivas, menos resistentes a perturbações físicas e a herbivoria e contém os maiores valores calóricos, enquanto as algas calcárias incrustantes possuem estas características de maneira antagônica. Os grupos restantes se encontram em um gradiente intermediário entre estes grupos extremos (LITTLER; LITTLER, 1984) (Figura 4). Esta classificação não só divide as espécies em grupos ecologicamente significantes, mas também permite que predições sejam feitas de acordo com os grupos funcionais predominantes.

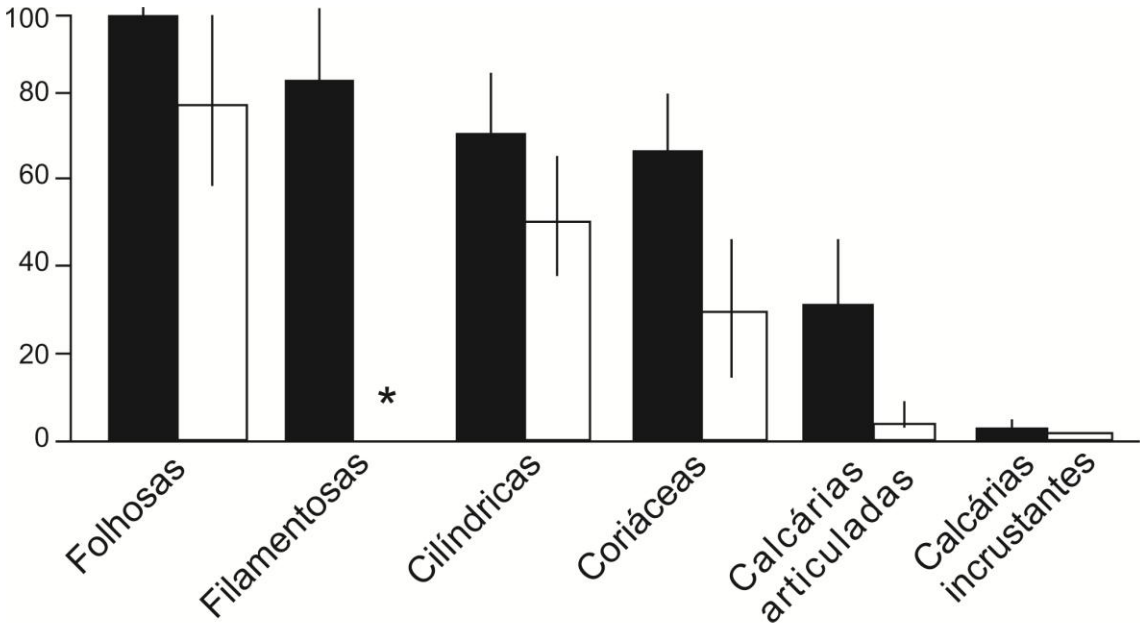

Figura 4 - Susceptibilidade dos grupos funcionais a herbivoria no Caribe. Barras pretas: perda gerada pela herbivoria por peixes; Barras brancas: perda gerada pela herbivoria por ouriços. Barras: 95% de intervalo de confiança.
*** por questões metodológicas os autores não foram capazes de estimar o consumo de algas filamentosas por ouriços (modificado de Littler and Littler 1983).**

Outra classificação, amplamente utilizada, considera a forma de crescimento e agrupamento das algas, as dividindo em dois grandes grupos, as algas eretas (ou simplesmente macroalgas) e as algas turf (do inglês, relva). Essa classificação ocorre porque muitas algas que ocorrem em habitats fisicamente estressantes ou sujeitos a herbivoria moderada crescem em agrupamentos coesos, chamados turfs, ao invés de ocorrerem como indivíduos separados (HAY, 1981). Esta forma de crescimento é energeticamente cara, sendo sua produtividade reduzida em até 60%, porém confere as algas menor dano fisiológico por dessecação durante marés baixas e menor perda de biomassa por herbivoria (HAY, 1981). As algas referidas como turf no Brasil podem ser dominadas pelas calcárias articuladas *Jania, Amphiroa* e *Haliptilon* (FIGUEIREDO *et al.*, 2008) ou conter apenas algas filamentosas não coralinas comuns, como *Anthithamnion, Ceramium, Digenea, Griffithsia, Gelidium, Sphacelaria, Enteromorpha, Cladophora* e *Bryopsis* (FIGUEIREDO, 1997, VILLAÇA; PITOMBO, 1997, COSTA *et al.*, 2002). A composição dos turfs brasileiros é similar a dos recifes caribenhos e da Grande Barreira de Corais (STENECK, 1988; ADEY, 1998; MCCOOK *et al.*, 2001). Por outro lado, avaliações taxonômicas em esse tipo de agrupamento são pouco frequentes, e sua riqueza específica é comumente subestimada (FIGUEIREDO *et al.*, 2008).

Apesar deste tipo de classificação ser frequentemente utilizada, algumas questões surgem quanto ao seu uso: (1) por se tratar de uma classificação que leva em conta a forma de crescimento das algas, espécies com características ecológicas distintas são reunidas em um mesmo grupo (e.g. espécies de crescimento lento e alta resistência a herbivoria, como as calcárias articuladas e as filamentosas, de crescimento rápido e muito susceptíveis); sendo negligenciados, portanto, muitos aspectos ecológicos da comunidade de algas, como por exemplo sua produtividade, crescimento e susceptibilidade a impactos físicos e herbivoria; (2) A maioria dos estudos que aplica este tipo de classificação, geralmente relacionados com a mensuração da herbivoria, não definem o que assumem por turf. Outros podem até divergir entre si em seu conceito: podem se referir apenas as algas filamentosas (e.g. ROBERTS, 1987; MCCLANAHAN, 1997), incluir outras vários tipos de algas (e.g. FERREIRA *et al.*, 1998a) ou até consistir de um agrupamento de algas, sedimentos e detritos (e.g. BONALDO; BELLWOOD, 2011). Outros autores utilizam a altura em relação ao substrato para separar o turf de outras formas de crescimento, onde o limite determinado para tal divisão varia entre os autores (e.g. HAY, 1981; RUITTON *et al.*, 2000; PADDACK; SPONAUGLE, 2008).

AS ALGAS DO BRASIL

As macroalgas estão entre os organismos mais comuns em recifes brasileiros. Ao norte do Brasil, as algas calcárias incrustantes, juntamente com os corais e moluscos vermetídeos, são os principais organismos construtores de recifes (KEMPF, 1968; MAIDA; FERREIRA, 1997; CASTRO; PIRES, 2001). A flora de macroalgas bentônicas brasileira incluem aproximadamente 700 taxa infragenéricos (HORTA, 2000; NUNES, 2005), o que corresponde a quase 80% das espécies encontradas nos trópicos (FIGUEIREDO *et al.*, 2008). Dentre estas, Rhodophyta é a divisão com maior riqueza de espécies, onde a ordem Ceramiales contém a maioria das espécies encontradas no Brasil (FIGUEIREDO *et al.*, 2008). Dentre Chlorophyta, a maior riqueza está nas ordens Bryopsidales e Cladophorales, enquanto que as algas da divisão Ochrophyta possuem mais representantes nas ordens Dictyotales e Ectocarpales (VILLAÇA *et al.*, 2006).

Algas eretas, calcificadas ou não, podem recobrir áreas extensas e prosperar com altas frondes sobre os recifes (FIGUEIREDO *et al.*, 2008). Nos recifes costeiros do Nordeste do Brasil, o maior número de espécies pertence à divisão Rhodophyta, a exemplo de Pitimbu, na Paraíba (LUCENA *et al.*, 2007) e Gaibu e Tamandaré, em Pernambuco (PEREIRA *et al.*, 2007; FEITOSA *et al.*, 2010) e Maracajaú, no Rio Grande do Norte (SILVA, 2006). Nesses trabalhos é possível enumerar várias espécies como importantes constituintes da flora recifal, como as vermelhas *Jania adhaerens*, *Gracilaria* sp, as verdes *Caulerpa racemosa*, *Halimeda opuntia* e as pardas *Dictyopteris*, *Dictyota*, *Padina* e *Lobophora*; que são consideradas espécies características de águas tropicais (PEREIRA, 2002) (Figura 5). *Halimeda* é um gênero especialmente importante no desenvolvimento dos recifes de coral, uma vez que contribuem com grandes quantidades de carbonato de cálcio para os depósitos de sedimento nos backreefs. Algumas espécies pantropicais de Dictyotales e Fucales, principalmente *Sargassum* são características de ambientes tropicais, se extendendo em distribuição também para floras de ambientes temperados (GARBARY, 2001).

De acordo com Horta (2001), a flora de macroalgas do Brasil está dividida em duas regiões biogeográficas: A região tropical, onde a flora está estabelecida dominantemente sobre recifes de corais, tendo como seu limite norte o oeste do Ceará e como limite sul, o sul do estado da Bahia; e a região temperada, onde as algas colonizam os espaços dos costões rochosos, apresentando seu limite norte o Rio de Janeiro e o limite sul na região de Rio Grande. Um empobrecimento da flora no sentido norte-sul é observado no Brasil, que pode estar relacionado à redução do substrato disponível, menor heterogeneidade de habitats e as maiores variações sazonais de temperatura ao Sul do país.

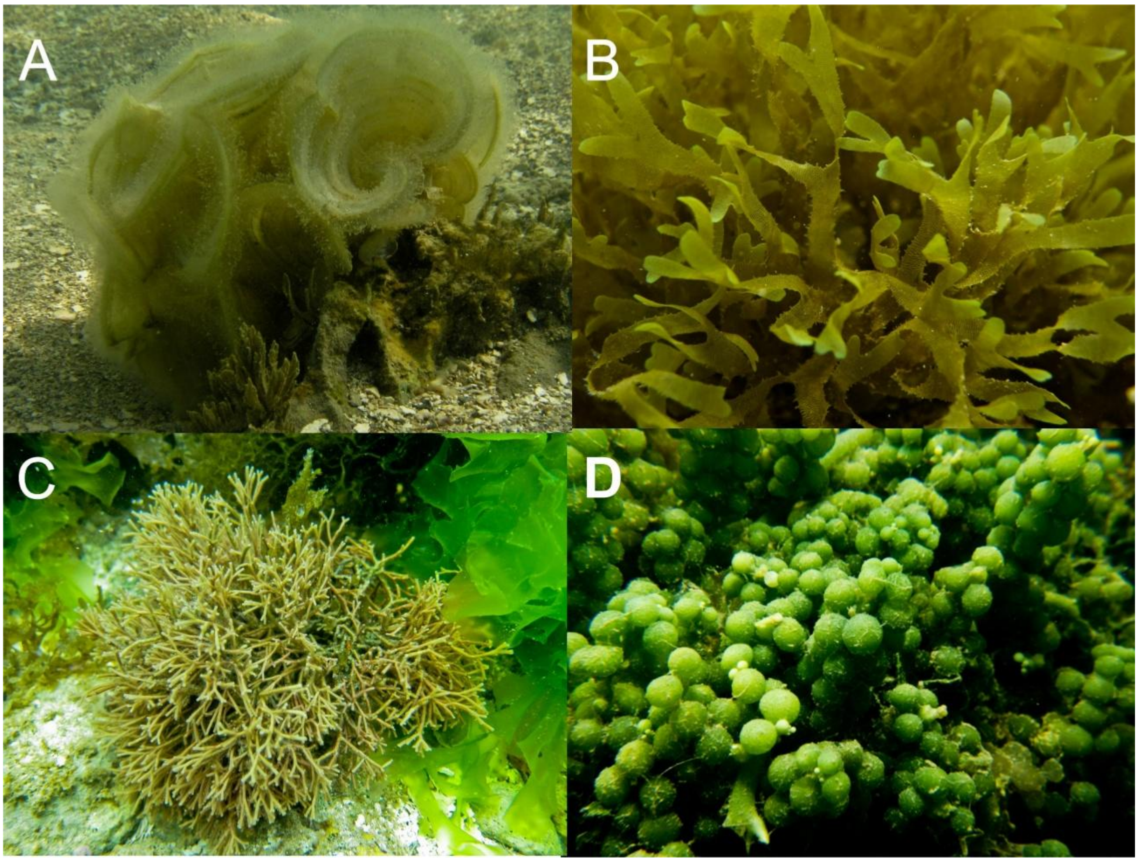

Figura 5 - Algumas das principais espécies da flora de macroalgas brasileira. A - *Padina antillarum*. B - *Dictyopteris delicatula*. C - *Jania* sp. D - *Caulerpa racemosa*. Fotos do Autor.

A flora do Atlântico Sul teve origem no Indo-Pacífico: as correntes que banhavam a costa brasileira provinham do Pacífico Sul, principalmente do Oceano Índico, trazendo os propágulos de várias espécies durante o Cretáceo, há 100 milhões de anos atrás (HOMRNERSAND, 1986; VAN DEN HOEK, 1987). Várias espécies possuem distribuições em ambos os lados do Atlântico e em trechos do Índico; por exemplo, 70% dos gêneros encontrados em Moçambique são também encontrados no Caribe (GARBARY, 2001). O Brasil possui reconhecidas afinidades com a flora caribenha, que podem ser devidas à sua origem comum Indo-Pacífica, mas alguns autores afirmam que a dispersão das espécies ocorreu em épocas e por rotas distintas, e não através de uma migração do Caribe ao Brasil, devido aos padrões de circulação global durante o Cretáceo, incluindo o surgimento da barreira do rio Amazonas (HORTA *et al.*, 2001).

3 - Herbivoria em ambientes recifais

A FUNÇÃO DA HERBIVORIA

Como mencionado anteriormente, muitos dos recifes contemporâneos estão perdendo sua capacidade de se regenerar dos impactos múltiplos que vem sofrendo ao longo das últimas décadas; tal degradação está levando estes recifes a uma rápida mudança para um estado alternativo (DONE *et al.*, 1992; HUGHES 1994; SCHEFFER, 2001; BELLWOOD *et al.*, 2004). A mais comum destas transições é a mudança da cobertura de uma dominância coralina para a dominância por algas, apesar de outros estados alternativos serem documentados (BELLWOOD *et al.*, 2004)

Por tal razão, os herbívoros de recifes de coral possuem um papel crucial na mediação da competição por substrato entre corais e macroalgas bentônicas. Esta função é determinante, pois ao consumirem as macroalgas os herbívoros impedem sua dominância sobre a cobertura coralina, estado no qual colonizam os esqueletos de corais adultos mortos e impedem o seu recrutamento (MUMBY *et al.*, 2006; HUGHES *et al.*, 2007; MUMBY, 2009). Além disso, os herbívoros conectam a produção primária de um ecossistema para todos outros membros da cadeia trófica (trofodinamismo), bem como atuam sobre a assembleia de plantas, tendo efeito tanto na distribuição e composição desta, como em sua produção e na própria composição dos vegetais (HAY, 1991).

Desde a década de 70, estudos relatavam o efeito dos herbívoros nos recifes. Foi observado, por exemplo, que altas densidades de donzelas poderiam afetar a produtividade, crescimento coralino, fixação do nitrogênio e cimentação do recife (VINE, 1974; BRAWLEY; ADEY, 1977; KAUFMAN, 1977). Tsuda e Bryan (1973) e Bryan (1975) também relatam que uma explosão populacional de siganídeos, que alcançou aproximadamente 13 milhões de indivíduos em Guam no Indo-Pacífico, ocasionou uma grande diminuição da cobertura algal (OGDEN; LOBEL, 1978).

Os primeiros trabalhos com manipulação experimental da herbivoria datam do início da década de 60, com os trabalhos de (RANDALL, 1961) no Hawaii e de (STEPHENSON; SEARLES, 1960) nos recifes de arenito da Heron Island, na Grande

Barreira de Corais. Os trabalhos conseguintes na década de 70 evidenciaram que os herbívoros poderiam ter um papel no assentamento e crescimento dos corais, onde o 'pastoreio' dos herbívoros abririam espaços no recife que favoreceria os corais (STEPHENSON; SEARLES, 1960; SAMMARCO *et al.*, 1974; BIRKELAND, 1977; KAUFMAN, 1977).

Dentre os principais herbívoros em ambientes recifais estão os peixes, os ouriços e a microfauna fital, que inclui crustáceos anfípodes, ostracodas e moluscos gastrópodes e quítons, podendo ainda serem citados as tartarugas, peixes-boi e outros invertebrados. Efeitos distintos nas algas são observados pela herbivoria realizada por cada um destes grupos. Por exemplo, se os ouriços dominam a comunidade de herbívoros a assembleia de algas resultante é composta em sua maioria por algas filamentosas de crescimento rápido, enquanto que uma maior diversidade de grupos funcionais de macroalgas e maior biomassa é observada quando os peixes são os principais consumidores (MCCLANAHAN, 1997).

INTERAÇÕES ALGAS-HERBÍVOROS

Herbivoria é a força determinante na distribuição e abundância de muitas algas, sendo sua morfologia, estrutura, química e habilidade competitiva comumente uma função direta da predação por peixes e grandes invertebrados (HAY 1997). Apesar de serem influenciadas pela competição com outros organismos bentônicos e perturbações físicas (LITTLER; LITTLER, 1984; STENECK; DETHIER, 1994), diversos experimentos demonstram que o controle dos herbívoros sobre a comunidade algal é determinante na maioria dos casos (RANDALL, 1965; HAY, 1985, 1991; LEWIS, 1986; CARPENTER, 1986; LESSIOS, 1988; MORRISON, 1988; HUGHES, 1994; HIXON; BROSTOFF, 1996). Para persistir nos recifes, as algas necessitam escapar, tolerar ou prevenir a herbivoria (LUBCHENCO; GAINES, 1981).

Apesar de poucas espécies de animais conseguir efetivamente se alimentar de algas em quantidades significativas, uma grande diversidade de histórias de vida, tamanhos, morfologias e fisiologias digestivas é apresentada pelos herbívoros, tornando quase impossível para suas presas prevenirem seu consumo por todos os herbívoros (HAY, 1997).

As algas podem alterar sua estrutura, afim de evitar a herbivoria: *Lithophyllum*, apresenta uma estrutura incrustante quando submetida a pressão da herbivoria, enquanto que quando essa influência é retirada, cresce com ramos eretos (STENECK; ADEY, 1976). Duas expressões fenotípicas também são encontradas em *Padina jamaicensis*, que pode alterar sua morfologia de uma forma prostática e altamente ramificada para uma forma ereta e folhosa em apenas quatro dias, se retirada a pressão da herbivoria (LEWIS *et al.*, 1987). Espécies de *Halimeda*, *Dityota* e *Laurencia* crescem como isoladas em condições de baixa herbivoria, mas quando com aumento da predação, reproduzem como clones densamente agregados (HAY, 1981).

A calcificação também é tida como uma tática para evitar a herbivoria, tornando as algas mais difícies de serem mordidas ou diminuindo seu valor nutricional pela adição de um material estrutural indigesto (LITTLER; LITTLER, 1980; STENECK, 1983, 1986; HAY, 1984b; DUFFY; HAY, 1990; DUFFY; PAUL, 1992; PITLIK; PAUL, 1997). Ensaios experimentais inserindo o $CaCO_3$ sem alterar a dureza ou valor nutritivo dos alimentos indicaram que o carbonato de cálcio pode alterar significantemente a preferência alimentar dos herbívoros, atuando também como um metabólito secundário (PENNINGS; PAUL, 1992; SCHUPP; PAUL, 1994).

A maioria das algas comuns em recifes (e.g. *Halimeda*, *Penicillus*, *Udotea*, *Caulerpa*, *Laurencia*, *Dictyota*, etc) produz defesas químicas que reduzem a alimentação dos herbívoros, os metabólitos secundários. Portanto, um grande número de diferentes compostos afeta o consumo por uma ou várias espécies de herbívoros (HAY; STEINBERG, 1992; SCHUPP; PAUL, 1994). Estas substâncias tem efeitos diferentes nos seus consumidores, por exemplo as taninas possuem um efeito redutor na digestibilidade, enquanto que alcalóides são realmente tóxicos (FEENY, 1976).

O efeito destas defesas dependem impreterivelmente da espécie de herbívoro que as consome. Ensaios demonstraram que os peixes papagaio são desencorajados pela presença de metabólitos secundários, mas não por CaCO3, enquanto que para os cirurgiões esse padrão é inverso (SCHUPP; PAUL, 1994; MEYER; PAUL, 1995; PENNINGS *et al.*, 1996; PAUL, 1997). Portanto, muitas espécies de algas empregam combinações de defesas estruturais, morfológicas ou químicas para evitarem sua predação (HAY, 1984; PAUL; HAY, 1986; HAY, 1996).

DISTRIBUIÇÃO E DIVERSIDADE DOS PEIXES HERBÍVOROS

Os peixes herbívoros são considerados, evolutivamente, os membros mais derivados de suas respectivas famílias e clados. Isso é devido a especialização necessária para utilizar as algas, de baixo conteúdo nutritivo e difícil digestão, como sua fonte de alimento principal. Entretanto, vários dos peixes herbívoros observados nas faunas recifais de hoje já possuiam ancestrais com forma e colorações semelhantes aos membros viventes há bastante tempo. Fósseis que datam 50 milhões de anos atrás encontrados no monte Bolca, na Itália, refletem uma ictiofauna recifal extremamente semelhante à observada nos dias de hoje (BELLWOOD; WAINWRIGHT, 2002). Apesar de existir uma fauna recifal comum no mar de Tethis, os mares tropicais sofreram diversos eventos de divisões, onde cada fragmento possui uma distinta história até o presente. Em algumas áreas, como o Mediterrâneo, seus ocupantes foram completamente eliminados, e em outras áreas eles prosperaram, sendo a ictiofauna atual derivada de uma série de fatores interativos, incluindo sua localização geográfica, conectividade regional, tamanho e batimetria (BELLWOOD; WAINWRIGHT, 2002).

A diversidade mais alta de vários grupos marinhos, de corais e equinóides até peixes recifais, é encontrada no Indo-Pacífico. Esse padrão se repete para os peixes herbívoros: mais de 100 espécies de pomacentrídeos e mais de 30 espécies de acanturídeos são encontrados na Grande Barreira de Corais (GBR). No Mar Vermelho são encontradas mais de 30 de pomacentrídeos e menos de 10 de acanturídeos e no Caribe menos de 10 espécies de pomacentrídeos e menos de 5 de acanturídeos. A quantidade de espécies de budiões na GBR quase dobra a quantidade observada no Mar Vermelho e no Caribe (> 20 versus >10) (BELLWOOD; WAINWRIGHT, 2002). Várias teorias foram formuladas para explicar a alta diversidade observada para a GBR, que pode ter atuado um centro de origem, refúgio ou centro de acumulação de biodiversidade. Esta região possui uma bacia relativamente rasa, o que pôde promover especiação de vários grupos por vicariância durante períodos onde o nível do mar era mais baixo (MCMANUS, 1985; SPRINGER; WILLIAMS, 1994), atuando, portanto, como um centro de origem. Esta bacia rasa também pode ter prevenido a perda de certos grupos durante estes baixos níveis do mar, servindo como um refúgio para a biodiversidade (ROSEN, 1984; WILSON; ROSEN, 1998). E por se tratar de uma região extensa e de grande conectividade, pode também ter acomodado espécies originadas em outras regiões, atuando como um centro de acumulação (PALUMBI, 1997; BELLWOOD; HUGHES, 2001).

As diferenças regionais entre as comunidades de herbívoros do globo são bastante marcadas não só em número de espécies: os siganídeos são somente observados no Indo-Pacífico, enquanto que os únicos peixes herbívoros do Mediterrâneo são *Sarpa salpa* (Sparidae) e *Sparisoma cretense* (Scaridae). Dentre a família Scaridae, *Sparisoma* é um gênero exclusivo do Atlântico, enquanto que

Leptoscarus, *Bolbometopon*, *Cetoscarus*, *Chlorurus* e *Hipposcarus* ocorrem somente no Indo-Pacífico. Nos recifes caribenhos os membros desta família são os peixes herbívoros mais abundantes, com uma dominância de indivíduos do gênero *Scarus* sobre *Sparisoma*. Exitem indicações que o gênero *Scarus* colonizou o Caribe através de ancestrais do Indo-Pacífico que atravessaram o Istmo do Panama, enquanto que o gênero *Sparisoma* tem origem no mar de Tethis (BELLWOOD, 1994). Aparentemente, os membros da família Scaridae que colonizaram o Brasil são provenientes da fauna caribenha, já que é possível observar que as espécies endêmicas brasileiras possuem espécies-irmãs no Caribe (MOURA *et al.*, 2001) (Figura 6) e *Sparisoma radians* ocorre em ambas as regiões. No Brasil, no entanto, o gênero *Sparisoma* domina sobre o gênero *Scarus* na maioria dos pontos da costa, e este último gênero é completamente ausente das ilhas oceânicas brasileiras (FERREIRA *et al.*, 2004). Uma possível explicação para tal distribuição é que o gênero *Scarus* no Indo-Pacífico é restrito a habitar recifes de coral (CHOAT, 1991), enquanto que os membros do gênero *Sparisoma* são possivelmente mais generalistas quanto ao seu habitat.

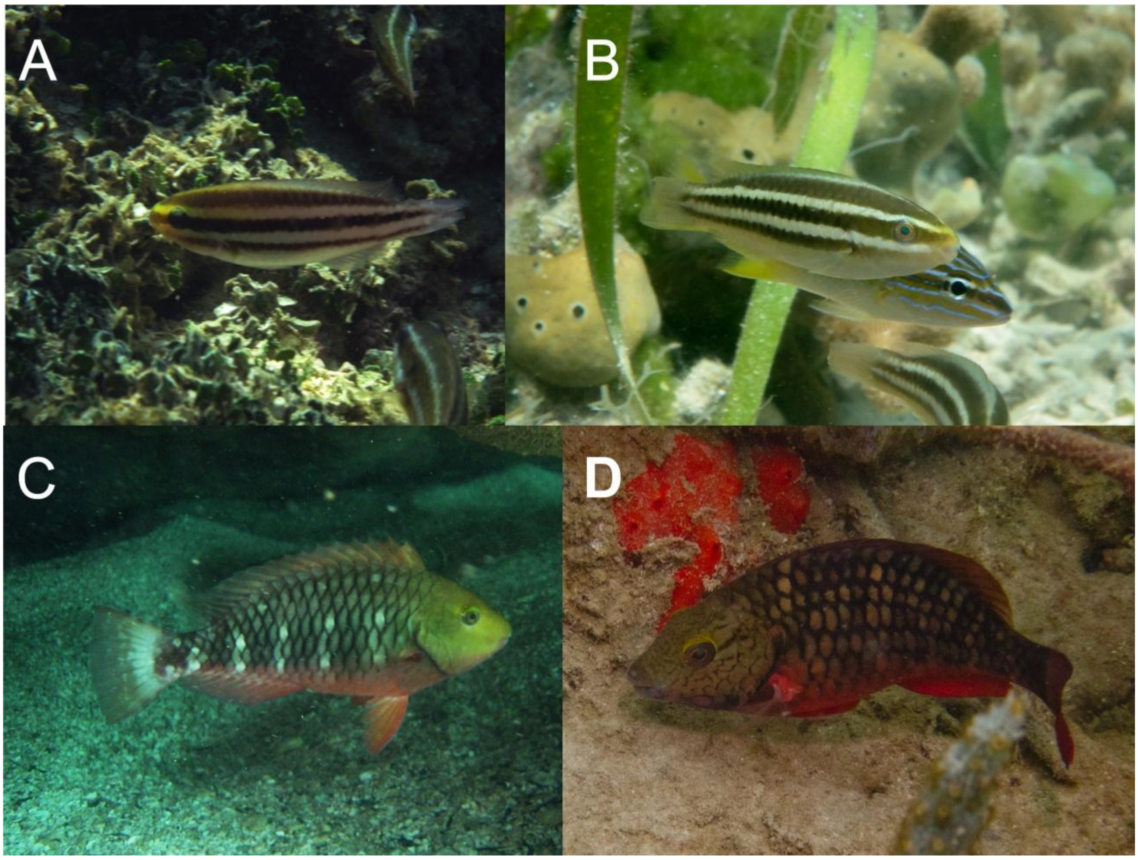

Figura 6 - Possíveis espécies-irmãs entre o Brasil (A, C) e Caribe (B, D). A - Juvenil *de Scarus zelindae*. B - Juvenil de *Scarus iseri*. C - Fase inicial de *Sparisoma amplum*. D - Fase inicial de *Sparisoma viride*. Fotos do Autor.

Além destas diferenças regionais na diversidade, a comunidade de herbívoros possui uma marcada diferença com o aumento de latitude, associada principalmente com mudanças na temperatura. Ao contrário dos ambientes tropicais, os recifes temperados são tipicamente dominados por algas, possuindo baixos níveis de herbivoria (MANN, 1973; GAINES; LUBCHENCO, 1982). É acreditado que tal diferença seja devida a uma mudança nos taxa que realizam a herbivoria nestes ambientes. Nos trópicos os principais herbívoros são os peixes, enquanto que em regiões temperadas são dominadas pelos ouriços (GAINES; LUBCHENCO, 1982; JONES; ANDREW, 1990). As táticas de forrageamento destes grupos diferem bastante: os peixes são altamente móveis, possuem uma grande variadade de aparatos alimentares e utlizam a visão para encontrar seu alimento, enquanto os ouriços se movem lentamente, possuem uma ação da mandíbula mais uniforme e encontram seu alimento por pistas químicas (GAINES; LUBCHENCO, 1982; JONES; ANDREW, 1990).

Aparentemente, os peixes herbívoros sofrem uma grande deficiência metabólica com a diminuição da temperatura. Por se tratarem de animais ectotérmicos, seu metabolismo depende da temperatura externa, e a distribuição de muitas espécies de peixes herbívoros segue padrões semelhantes aos de lagartos herbívoros terrestres, diminuindo sua presença com menor temperaturas, que difere de herbívoros endotérmicos, como os mamíferos (FLOETER *et al.,* 2005). Adicionalmente, por dependerem de um alimento com pouca qualidade nutricional, o limite crítico da temperatura necessário para um balanço energético positivo deve ser maior para os herbívoros do que para os carnívoros (FLOETER *et al.*, 2005).

Portanto, os grupos de herbívoros comuns ao ambiente tropical diminuem em número, biomassa e em diversidade com o aumento da latitude. Algumas espécies de peixes são mais adaptadas à herbivoria em condições de baixa temperatura e, por conseguinte, substituem a fauna tropical nesse papel funcional. Essas adaptações incluem uma redução das demandas metabólicas, como observado em Aplodactylidae e Stichaedae (FLOETER *et al.,* 2005). No Brasil, a fauna dominada por acanturídeos e escarídeos nos trópicos é substituída por indivíduos da família Kyphosidae em regiões frias (FERREIRA *et al.,* 2004). Estes herbívoros de regiões frias são, entretanto, reduzidos em número de espécies, o que é creditado a uma questão evolutiva, pois o uso de recursos menos energéticos (e.g. algas, esponjas e corais) ocorreu primariamente entre comunidades de peixes recifais tropicais, levando ao aumento de sua riqueza de espécies em águas quentes (HARMELIN-VIVIEN, 2002).

O PAPEL FUNCIONAL DOS PEIXES HERBÍVOROS

Os peixes herbívoros não são um grupo uniforme no que diz respeito a sua função nos recifes. Os peixes herbívoros são divididos em duas categorias principais de acordo com o uso de habitat. Aqueles ditos territorialistas, como as donzelas (família Pomacentridae), dominam porções do recife, chegando a modificar a flora e fauna instalada em seu domínio, através de comportamentos como o *weeding* e a seleção que ocorre devido ao seu hábito alimentar (LOWE-MCCONNELL, 1987; HATA; KATO, 2004) (Figura 7 A,B). Os herbívoros descritos como vagueadores, a exemplo dos peixes-papagaios e cirurgiões (famílias Scaridae e Acanthuridae, respectivamente), percorrem grandes áreas dos recifes em cardumes, se alimentando continuamente das macroalgas bentônicas (Figura 7 C-H). O grupo de herbívoros vagueadores é acreditado como chave que controlando a biomassa de macroalgas nos recifes de coral (HOEY; BELLWOOD, 2008).

As primeiras classificações dos peixes herbívoros foram realizadas na década de 60, sendo denominados como *browsers* ou *grazers* de acordo com a quantidade de substrato inorgânico ingerido (HIATT; STRASBURG, 1960; JONES, 1968). Os peixes *grazers* são aqueles que ingeriam grandes quantidades de substrato durante a alimentação, enquanto os *browsers* raramente ingeriam material inorgânico. Adaptações morfológicas como um estômago com paredes grossas ou adaptações na faringe para triturar o alimento são característicos dos *grazers*, enquanto os 'browsers' geralmente possuem estômagos com paredes finas.

Os membros da família Acanthuridae tendem a se alimentar retirando as porções superiores das macroalgas, deixando as porções basais intactas (CHOAT *et al.*, 2002). De maneira oposta, os peixes-papagaio (família Scaridae) apresentam uma morfologia oral única, com dentes fundidos, fortes músculos adutores, um aparelho faringeano para triturar o material abocanhado, permitindo que se alimentem das macroalgas retirando partes do substrato (BELLWOOD; CHOAT, 1990), consumindo não só a biomassa de algas, mas fornecendo áreas de substrato renovado para a colonização por organismos bentônicos, incluindo os corais construtores de recifes (BELLWOOD, 1995; BRUGGEMANN *et al.*, 1996; HOEY; BELLWOOD, 2008).

Nos recifes brasileiros, encontramos três espécies representantes da família Acanthuridae: *Acanthurus bahianus, A. chirurgus e A. coerulus*. As duas últimas espécies também ocorrem na ictiofauna caribenha. Dentre as categorias alimentares descritas para os herbívoros vagueadores, as espécies *A. bahianus* e *A. chirurgus* são considerados grazers, pois utilizam grande material detrital em sua alimentação, enquanto que *A. coerulus* possui uma maior seleção na alimentação, ingerindo algas mais seletivamente, sendo por tal considerado como browser (DIAS *et al.*, 2001; FERREIRA; GONÇALVES, 2006; FRANCINI-FILHO *et al.*, 2010). Adicionalmente, as duas primeiras espécies apresentam ainda adaptações morfológicas que os permitem alimentar dessas partículas em decomposição, como por exemplo um estômago com paredes mais grossas, não evidenciado para *A. coerulus* (DUARTE; ACERO, 1988). Mesmo com tais similaridades em sua dieta, foi observado que *A. bahianus* obtém os detritos de sua alimentação das macroalgas que o mesmo ingere, enquanto que *A. chirurgus* complementa sua dieta forrageando no próprio substrato (DIAS *et al.*, 2001). Pela ocupação de nichos alimentares diferenciados, é plausível de se supor que estas espécies apresentem diferentes impactos para o controle de macroalgas nos recifes brasileiros.

Os herbívoros vagueadores da família Scaridae do Atlântico Sul estão compreendidos em quatro gêneros: *Scarus*, *Sparisoma*, *Cryptotomus* e *Nicholsina*. Destes, os gêneros *Scarus* e *Sparisoma* são os mais representativos em recifes brasileiros, contando com oito espécies: *Scarus trispinosus*, *S. zelindae*, *Sparisoma amplum*, *Sp. axillare*, *Sp. frondosum*, *Sp. radians*, *Sp. rocha* e *Sp. tuiupiranga* sendo todas espécies endêmicas da costa brasileira, com a exceção de *Sparisoma radians*, que também ocorre no Caribe. Das espécies simpátricas *Scarus trispinosus*, *S. zelindae*, *Sparisoma amplum*, *Sp. axillare*, *Sp. frondosum*, *Sp. radians*, apenas a última é considerada como browser, principalmente por possuir um menor porte e conseguir selecionar mais facilmente o alimento ingerido, enquanto que as demais são consideradas grazers, ou excavators no caso de indivíduos adultos de maior porte, que conseguem retirar porções do substrato durante sua alimentação, deixando cicatrizes visíveis na matriz recifal (FRANCINI-FILHO *et al.*, 2008; FERREIRA; GONÇALVES, 2006)

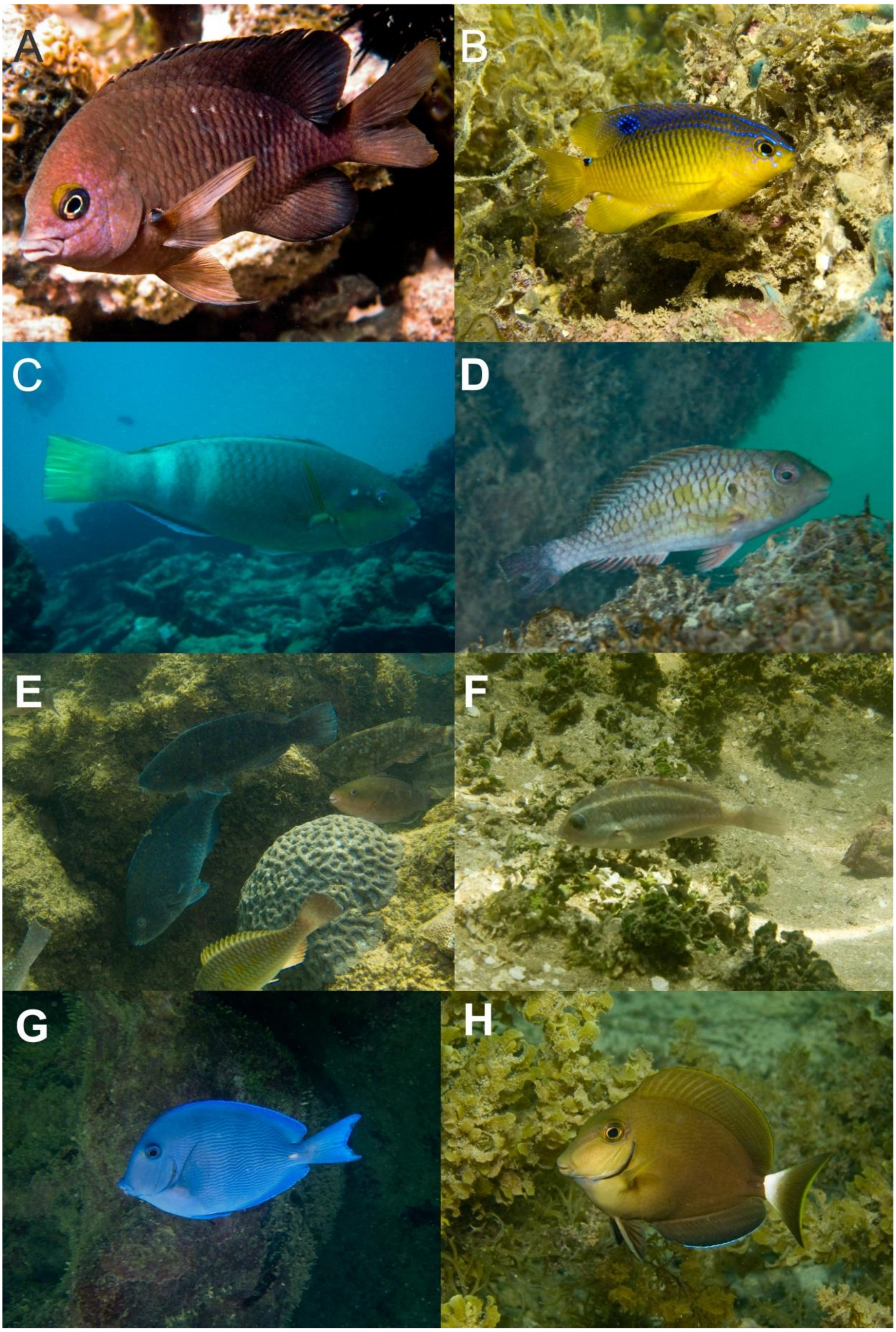

Figura 7 - Espécies de herbívoros dos recifes de coral do Brasil. A - *Stegastes fuscus* adulto. B - *Stegastes variabilis* juvenil. C - *Scarus zelindae* fase terminal. D - *Sparisoma axillare* fase inicial. E - *Scarus trispinosus* adulto. F - *Sparisoma frondosum* juvenil. G - *Acanthurus coeruleus* adulto. H - *Acanthurus bahianus* adulto. Fotos do Autor.

HERBIVORIA VERSUS CORALIVORIA

O impacto da coralivoria em recifes tropicais é controverso, já que poucas espécies são capazes de produzir grande dano ao consumir corais. De fato, apenas 18 de mais de 110 gêneros de corais foram registrados sendo consumidos, dos quais apenas 16% são consumidos ocasionalmente por peixes (ROTJAN; LEWIS, 2008). A coralivoria por peixes peixes-papagaio é realizada em dois comportamentos distintos (sensu BRUCKNER *et al.*, 2000): através de mordidas focadas, onde o indivíduo abocanha repetidamente uma única área, resultando numa extensa perda de tecido e deixando marcas no esqueleto do coral; ou através de mordidas rasas que são distribuídas ao longo da superfície de uma colônia, causando dano ao tecido dos corais, mas pouca perda à estrutura esquelética (Figura 8).

A espécie *Bolbometopon muricatum*, apesar de se alimentar de corais facultativamente, é o maior consumidor de tecido vivo de corais dentre os peixes coralívoros (ROTJAN; LEWIS, 2008). É estimado que uma população desta espécie pode consumir 13.5 kg de tecidos de corais por m² por ano (BELLWOOD *et al.*, 2003). Entretanto, esta espécie se alimenta preferencialmente de espécies de corais de crescimento rápido, como os acroporideos e pociloporídeos (BELLWOOD *et al.*, 2003) e pode, portanto, ser benéfico para as espécies de crescimento mais lento (ROTJAN; LEWIS, 2008).

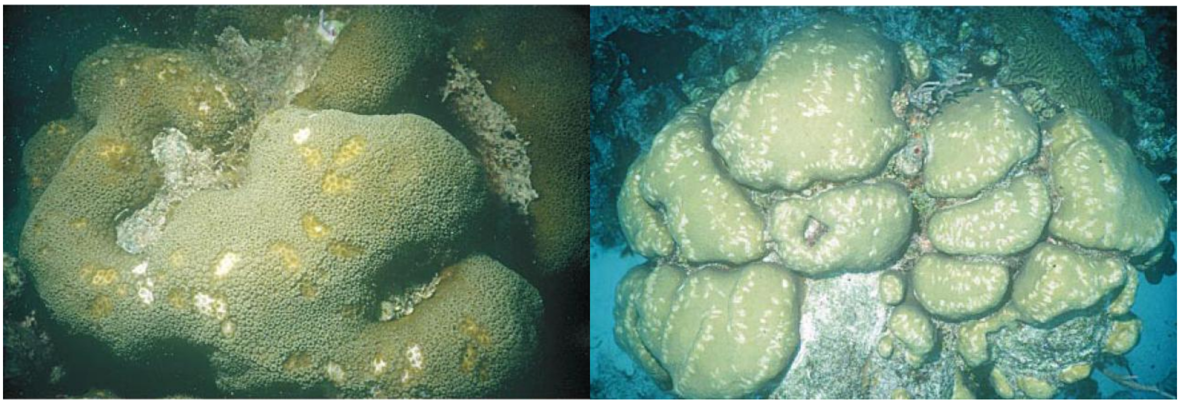

Figura 8 - Duas formas de impacto dos peixes-papagaio nos corais. Esquerda: através de mordidas focadas. Direita: ou através de mordidas rasas em vários pontos da colônia. (Retirado de Bruckner et al. 2000)

Em recifes saudáveis, a quantidade de coral vivo consumida por peixes-papagaio e ouriços aparenta ser improvável de ser prejudicial para o ecossistema recifal. No entanto, tendo em vista a tendência global para o declínio de cobertura coralina, o papel duplo destes herbívoros/coralívoros necessita ser reavaliado (ROTJAN; LEWIS, 2008). De toda maneira, apenas uma pequena parcela das espécies de peixes-papagaio é capaz de se alimentar efetivamente de tecido coralino: das mais de 80 espécies de escarídeos registradas (NELSON, 2006), apenas 21 são coralívoras, e todas elas o fazem de maneira facultativa (ROTJAN; LEWIS, 2008). Destas, seis espécies pertencem ao Caribe, duas ao Brasil e o restante ocorre no Indo-Pacífico, se alimentando dos geralmente dos gêneros *Pocillopora, Porites* e *Montrastrea,* e no Brasil dos gêneros *Favia, Mussismilia* e *Siderastrea* (RANDALL, 1967; RANDALL, 1974; BELLWOOD; CHOAT, 1990; CHOAT, 1991; BELLWOOD, 1995; BRUCKNER; BRUCKNER 1998,; MCCLANAHAN *et al.*, 2005; ROTJAN; LEWIS, 2005, 2006; FRANCINI-FILHO *et al.*, 2008).

DIETA E RITMO DA ALIMENTAÇÃO

Os primeiros estudos sobre a alimentação dos peixes recifais herbívoros foram conduzidos nos ambientes tropicais do Pacífico (HIATT; STRASBURG, 1960; HOBSON, 1974) e do Caribe (RANDALL, 1967; CARR; ADAMS, 1973). As análises de conteúdo estomacal não foram conclusivas, mas sugerem que a maioria dos herbívoros é generalista (OGDEN; LOBEL, 1978). Até então, poucos estudos haviam avaliado a disponibilidade e preferência alimentar, mas os que foram realizados indicavam uma preferência por espécies filamentosas (RANDALL, 1961; TSUDA; BRYAN, 1973; BRYAN, 1975; LOBEL; OGDEN, 1981; FRANCINI-FILHO *et al.*, 2010).

Em uma das primeiras revisões disponíveis acerca do assunto, Russ & John (1988) observaram que os estudos realizados entre 1960-1986, envolvendo quase 100 espécies de herbívoros do Indo-Pacífico e Caribe, indicavam uma grande dominância de algas filamentosas, detritos e material inorgânico na dieta das principais famílias de herbívoros recifais. Quase 100% das espécies de siganídeos e donzelas revisadas tinham algas filamentosas como principal alimento em seu conteúdo estomacal. Outras macroalgas foram observadas como principal item alimentar em apenas 7% das espécies destas famílias agrupadas (RUSS; JOHN, 1988).

Apesar de apresentarem uma preferência de se alimentar de algas com menor potencial defensivo, como as algas filamentosas, os peixes herbívoros de recifes de coral possuem grande plasticidade trófica. Por exemplo, as donzelas do gênero

Stegastes podem se alimentar de macroalgas, diatomáceas, detritos e pequenos animais e apresentam variações em sua dieta entre as espécies, fases de vida, entre diferentes estações do ano e entre diferentes localidades, sendo nestas duas últimas dependente da disponiblidade de alimento; (FEITOSA *et al.*, 2012; Tabela 1). Esta plasticidade trófica se extende para outros herbívoros: em Blenniidae (MENDES *et al.*, 2009), Odacidae (CLEMENTS; CHOAT, 1993), Kyphosidae (SILVANO; GUTH, 2006), Sparidae (HAVELANGE *et al.*, 1997), Scaridae (BELLWOOD, 1988) e Acanthuridae (DIAS *et al.*, 2001). Além de variar suas dietas, o ritmo da alimentação por peixes herbívoros varia em intensidade ao longo do tempo. Os peixes herbívoros são ativos durante o dia, e o pico da atividade alimentar dos acanturídeos e escarídeos é entre 12:00 e 13:00, enquanto que para as donzelas é entre 14:00 e 15:00 (FERREIRA *et al.*, 1998b). Diferenças sazonais na intensidade da alimentação também são observadas, e podem estar relacionadas com variações na temperatura, disponibilidade de alimento ou atividades reprodutivas das espécies (FERREIRA *et al.*, 1998a, b)

Tabela 1 - Sumário das dietas das espécies de *Stegastes* obtidas por estudos de conteúdo estomacal (modificado de Feitosa *et al.* 2012). * itens alimentares agrupados

Species	Macroalgae	Animals	Detritus	Diatoms	Cyanobacteria	Location	Reference
S. adustus	56.2*	43.8	*	*	*	West Indies	Randall (1967)
	15.8	0.0	-	68.8	15.4	Panama	Robertson (1984)
S. apicalis	40.0-89.0	2.5-30.0	-	-	2.5-16.0	Central GBR	Klumpp and Polunin (1989)
	75.0	>5.0	10.0	-	-	Central GBR	Ceccarelli (2007)
S. fuscus	~70.0	~30.0	-	-	-	South-Western Brazil	Ferreira *et al.* (1998a)
	42.2	11.3	5.8	17.7	7.3	North-Eastern Brazil	Feitosa *et al.* (2012)
S. leucostictus	22.6*	77.4	*	*	*	West Indies	Randall (1967)
S. lividus	97.0-99.0	1.0-3.0	-	-	-	Western Pacific	Lassuy (1984)
	30.0	-	70.0	>1.0*	*	Papua New Guinea	Ceccarelli (2007)
S. nigricans	26.0	0.0	74.0*	-	*	Central Pacific	Lobel (1980)
	45.0	0.0	55.0	-	-	Northern GBR	Wilson and Bellwood (1997)
	70.0	-	-	30.0	0.0	Papua New Guinea	Jones *et al.* (2006)
	69.4	13.9	16.7	-	-	SW Indian Ocean	Letourneur *et al.* (1997)
S. planifrons	24.4*	75.6	*	*	*	West Indies	Randall (1967)
	12.0	33.0	-	55.0*	*	Panama, West Indies	Lobel (1980)
	3.2	1.5	-	81.0	14.3	Panama	Robertson (1984)
S. rectifraenum	98.5	1.5	-	-	-	Gulf of California	Montgomery (1980)
	44.1	53.2	-	-	-	Gulf of California	Moreno-Sánchez *et al.* (2011)
S. variabilis	51.5*	48.5	*	-	-	West Indies	Randall (1967)
	41.3	11.9	5.3	20.4	8.3	North-Eastern Brazil	Feitosa *et al.* (2012)

5 - Ameaças aos herbívoros

Por possuírem um maior porte dentre os peixes herbívoros, os peixes-papagaio e os cirurgiões vêm sendo ameaçados pela pesca predatória, principalmente devido à sobrexplotação dos peixes carnívoros, como ocorre no estado de Pernambuco. De fato, a pressão exercida pela pesca tem diminuído o nível trófico médio das cadeias alimentares ao longo do mundo (PAULY *et al.*, 1998) e também no Brasil (FREIRE; PAULY, 2010) e a consequência é o aumento da pressão pesqueira sobre espécies pertencentes aos níveis tróficos mais baixos (FLOETER *et al.*, 2006 FRANCINI-FILHO, MOURA, 2008). Apesar das divergências regionais nas comunidades de peixes, os efeitos da pesca são consistentes em uma escala global, e últimos estudos indicam que a pesca reduziu a biomassa mundial de peixes herbívoros a menos da metade, quando comparados locais pescados e não-pescados (EDWARDS, 2014). Os grupos funcionais mais afetados pela pressão pesqueira são os mais importantes para o controle das macroalgas nos recifes. No Brasil, os peixes-papagaio tem sido alvo intenso de caça submarina durante as duas últimas décadas em muitos locais (FERREIRA; GONÇALVES, 1999). No cenário local, onde todas as grandes espécies de budiões são endêmicas (MOURA *et al.*, 2001), essa pressão de pesca pode resultar inclusive em uma perda para a biodiversidade global.

Uma das possíveis soluções de manejo para tal impacto é a criação de Áreas Marinhas Protegidas, considerada uma útil ferramenta de gestão disponível para superar problemas ecológicos incluindo a perda da biodiversidade (BOHNSACK; AULT, 1996, ALLISON *et al.*, 1998, DAYTON *et al.*, 2000, ROBERTS; HAWKINS, 2000, JACKSON *et al.*, 2001), alteração da estrutura trófica dos ecossistemas (PAULY *et al.*, 1998, 2002, JACKSON *et al.*, 2001), e crônica sobrepesca em todo o mundo (PAULY *et al.*, 1998, 2002, JACKSON *et al.*, 2001, GELL; ROBERTS, 2002). No entanto, a aceitação de reservas marinhas como ferramentas de gestão das pescas ainda permance controverso, devido a fatores sociais na proibição da pesca (NRC, 2001, HILBORN, 2002).

6 - O presente estudo

Os peixes herbívoros são contituintes principais da fauna recifal e desepenham uma função primordial na mediação da competição entre algas e corais. Vários estudos foram desenvolvidos neste aspecto, contudo a maioria das teorias que envolvem a herbivoria por peixes recifais foi desenvolvida no Indo-Pacífico. Ademais, tais estudos geralmente tratam desse tema como uma característica espécie-especifica, negligenciando diferentes estratégias que uma mesma espécie possa ter para escolher a composição de sua alimentação. Nesse âmbito, a presente Tese teve como objetivo elucidar três pontos principais, que resultaram na composição de três capítulos: (1) A influência de distintas organizações sociais na alimentação de peixes-papagaio; (2) A influência de mudanças ontogenéticas no uso de distintos habitats e na alimentação de peixes-papagaio; (3) O efeito da herbivoria por peixes-papagaio em ambientes recifais dominados por algas.

Para o primeiro capítulo, a espécie *Scarus iseri*, uma das espécies de peixe-papagaio mais abundantes do Caribe, foi selecionada, tendo em vista que a maioria dos estudos abordando a ecologia social deste peixes foi realizado com esta espécie. Para o segundo capítulo, a espécie estudada foi *Sparisoma axillare*, o peixe-papagaio mais abundante na maioria dos recifes de coral brasileiros. O estudo focou sua ecologia alimentar na fase jovem em quatro diferentes habitats dos recifes de Tamandaré. No terceiro capítulo foi abordado o efeito que espécies de peixes herbívoros possuem em um ambiente dominado por algas. Para tal, experimentos manipulativos de exclusão de herbivoria através de gaiolas foram realizados. Ao longo de 10 meses foram observados mudanças na biomassa e cobertura de algas, assim como o efeito da herbivoria na sucessão ecológica da cobertura bentônica.

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Capítulo 2

INFLUENCE OF SOCIAL ORGANIZATION ON *Scarus iseri* FEEDING PATTERNS

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ABSTRACT

Parrotfishes show a complex array of social organizations patterns, but few studies address the influence of social grouping on their feeding. *Scarus iseri*, one of the most studied species regarding this matter, presents three types of well-known social groups: Stationary, territorial and foraging groups. Herein, stationary and territorial groups were distributed differently in the reef environment and had different size structures, being the smaller individuals most abundant in stationary groups due to competitive exclusion by territorial individuals, and foraging groups were not found. Intraspecific aggression were more frequent in territorial groups, which protect habitats with higher abundance of preferred food. Individuals joining territorial groups fed mostly on filamentous algae, an algae type with higher palatability and nutritional value, while stationary group individuals had less availability of this food item and relied mostly on detrital matter over the substrate and over sponges. Through the present study, it was possible to determine that *Scarus* species may change their feeding ecology depending on their social organization and thus performing distinct roles in coral reefs trophic dynamics.

A influência da organização social nos padrões alimentares de *Scarus iseri*

RESUMO

Os peixes-papagaio possuem uma complexo padrão de organizações sociais, entretanto, poucos estudos analisam a influência dos agrupamentos sociais na sua alimentação. *Scarus iseri*, uma das espécies mais estudadas nesse aspecto, possui três tipos conhecidos de grupos sociais: os grupos estacionários, territoriais e de forrageamento. No presente estudo, os grupos estacionários e territoriais se distribuíram diferentemente no ambiente recifal, possuindo distintas estruturas de tamanho, onde os indivíduos de menor porte foram mais abundantes nos grupos estacionários, devido a exclusão competitiva por indivíduos territoriais, e os grupos territoriais não foram observados. Agressão intraespecífica foi mais frequente nos grupos territoriais, que protegem habitats com maior abundância de seu alimento preferido. Indivíduos em grupos territoriais se alimentaram principalmente de algas filamentosas, um tipo de algas que possui maior palatividade e valor nutricional, enquanto que indivíduos em grupos estacionários possuiram menor disponibilidade desse item alimentar e se alimentaram em maior parte de detritos sobre o substrato e sobre esponjas. Através do presente estudo foi possível determinar que espécies de *Scarus* podem alterar sua ecologia alimentar de acordo com sua organização social, realizando, portanto, distintos papéis na dinâmica trófica nos recifes de corais.

1 - Introduction

Parrotfishes are conspicuous members of the reef fauna worldwide and are found to play a primary role in the reef environment. Although primarily herbivores, some species have been found to consume sponges, controlling their distribution on the reefs (Wulff, 1997a,b, 2005; Dunlap & Pawlik, 1998). Some species are found to consume live coral, but with little effect to overall reef health (Bruckner & Bruckner, 2000; Francini-Filho *et al.*, 2008; Rotjan & Lewis, 2008; Mumby, 2009; Bonaldo *et al.*, 2011). Parrotfishes are classified according to feeding modes as browsers, scrapers or excavators species. Browsers crop portions of algae, preventing coral overgrowth and shading (Hughes, 1994; McCook, *et al.* 2001; Bellwood, *et al.* 2004). Scrapers remove algae and sediment by cropping algae thalli close to substrate, providing space for settlement of incrusting calcareous algae and corals (Hunte & Wittenberg, 1992; Bellwood, *et al.* 2004). Excavating fishes remove dead corals, exposing the reef matrix for settlement of coralline algae and corals (Bellwood & Choat, 1990; Bellwood *et al.*, 2003, 2004).

Despite this array of feeding modes, which is usually treated as a species-specific trait, parrotfish species seems to be generalists regarding to habitat use and feeding. They can inhabit several ecosystems, including seagrass beds, mangroves, coral reefs and rocky shores (Ogden & Buckman, 1975; Russ, 1984; Ferreira *et al.*, 2004; Paddack & Sponaugle, 2008). Within these environments, each parrotfish species hold particular feeding preferences (Wolf, 1985), which are largely affected by food availability (Feitosa & Ferreira, 2014).

Food availability, on the other hand, may be influenced by competition among herbivores, both inter- and- intraspecifically (Robertson *et al.*, 1976; Reinthal & Lewis, 1986). Interference competition play a major role in parrotfish feeding dynamics, reducing not only food availability, but also feeding rates (Feitosa & Ferreira, 2014). Damselfishes, for instance, are known to be especially aggressive when defending territories (Low 1971; Brawley & Adey, 1977; Itzkowitz, 1990; Hata & Kato, 2004), and several studies describe their influence on the feeding of parrotfishes (Robertson *et al.*, 1976; Robertson & Lassig, 1980; Bruggemann *et al.*, 1994; Feitosa & Ferreira, 2014).

Scarus iseri is one of the most studied species among parrotfishes regarding their ecology. Between the 60's and 80's several studies addressed this species reproductive patterns (Randall & Randall, 1963; Buckman & Ogden, 1973; Colin, 1975; Warner & Downs, 1977) and social organization (Buckman & Ogden, 1973; Ogden & Buckman, 1975; Warner & Downs, 1977; Clifton, 1989; Mumby & Wabnitz, 2002). It is know that *Scarus iseri* has a complex social organization, that involves three distinct social grouping (Buckman & Ogden, 1973; Ogden & Buckman, 1975; Warner & Downs, 1977): (1) Stationary groups comprise small groups of fish using a specific area without performing great migrations and have no intraspecific aggressiveness related to territory defense; (2) Territorial groups are small groups of adult fish, composed by one dominant male that defends a large spawning territory, encompassing several female feeding territories; (3) Foraging groups are large groups of schooling fish (>500), generally in multispecies schools, which perform great daily migrations.

Few studies had addressed *S.iseri* feeding behavior, and in special focusing on differences among social groups, and therefore the effects of social organization over feeding patterns of parrotfishes remains unclear. In order to clarify this matter, this study posed the following questions: (1) Are social groups equally distributed among reef habitats? (2)What is the role of interference competition within each social group? (3) Are feeding patterns affect by the social organization of *S. iseri*?

2 - Material and Methods

STUDY AREA

This study was conducted at Isla Colón, Bocas del Toro archipelago, Caribbean Panama (9º 22' N, 82º18' W). Panamanian tides show little amplitude, with a variation of less than 0.5 m (Glynn, 1972). The main coastal current affecting Panama comes from the neighboring Costa Rica and run east, exerting greater influence between June and August, when it flows closer to the coast (Guzmán, 2003). The highest temperatures occurs during the rainy season, (April to December), but little variation is recorded throughout the year (< 3°C) (Cubit *et al.*, 1989).

Panamanian coral reefs occur along the Caribbean coast, from the border with Colombia to ~25 km from the border with Costa Rica (Guzmán, 2003). In particular, one of the best reef growth and development is found in the Bocas del Toro archipelago, which comprises six large islands. These islands are surrounded by several shallow patch and fringing coral reefs occurring up to 20 m deep, being better developed on the leeward side of the islands (Guzmán, 2003). Panamanian coral fauna is diverse, and nearly doubles in species richness (> 65 species) compared to Costa Rica (Guzmán & Guevara, 1998, 2001).

Punta Caracol is located roughly in the middle of the leeward side of the Isla Colón (Figure 1A). Mangroves border the coast and an adjacent sandy bottom (~0.5 -2.0 m depth), extends for ~150 meters, where increase in slope is observed gradually. The intermediate zone is dominated by gorgonians and octocorals and at nearly 12 meters depth the inclination decreases, where it is observed a muddy flat with several heads of massive coral (Figure 1B).

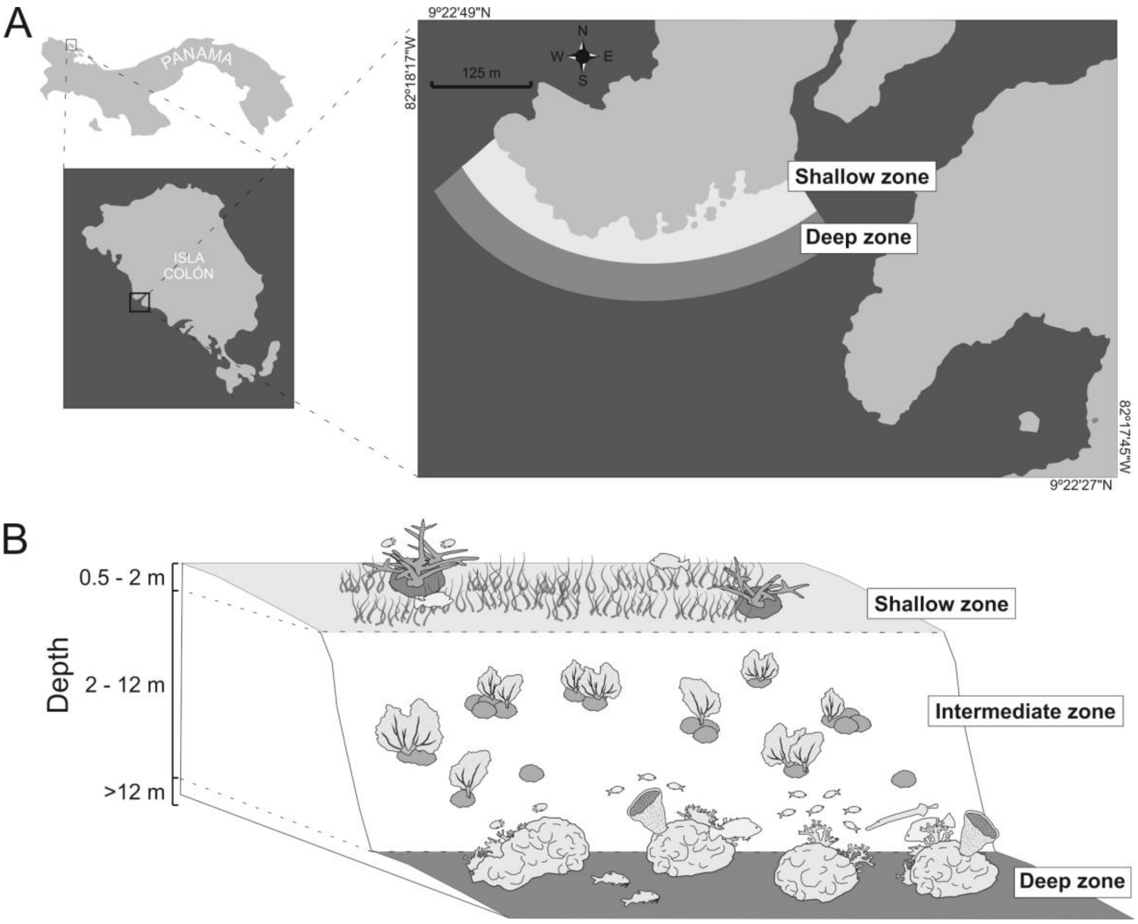


Figure 1 - Map of the study area (A). Profile showing distinct habitats present on the study area (B)

SAMPLING EFFORTS AND DATA ANALYSIS

Pilot dives were performed to identify the presence of distinct social groups of *Scarus iseri* in the study area, these groups were defined based on behavioral and grouping patterns described in previous studies (Buckman & Ogden, 1973; Ogden & Buckman, 1975; Warner & Downs, 1977). Two distinct social groups were identified, the stationary and the territorial groups (the foraging group was not observed in the study area). To determine the abundance and size structure of fish in each social group, 10 censuses were conducted within each social group's domain. To minimize the disturbance of laying transects, countings were based on 5 min timed swims along 100 meters, where every fish present between 2.5 m on either side of the diver was included, covering an area of 500 m^2 on each survey. Presumed competitors (other scarid species and acanthurids) observed were also included in the census, and size was estimated for *S. iseri* individuals, which were grouped in 5 cm size classes as: < 5 cm, 5 -10 cm, 10-15 cm, 15-20 cm, > 20 cm. Calibrations were made on each dive to maintain a proper swimming speed to cover the proposed area in 5 min. All surveys were parallel to the coast and haphazardly performed within the habitats used by the social groups. The censuses were conducted by the same diver to avoid diver associated bias (Williams *et al.*, 2006). *Scarus iseri* distribution was compared using a Permutational Multivariate Analysis of Variance (PERMANOVA) with one factor (Social grouping, Stationary x Territorial). Densities of competitor roving herbivores (surgeonfishes and parrotfishes besides *S. iseri*) between sites inhabited by distinct social groups were compared by unpaired t-tests for each roving herbivore species. For parrotfishes these tests were performed separately for life phase based on coloration differences as initial phase (IP) and terminal phase (TP) individuals.

To determine differences in substrate cover, i.e. food availability, between the habitats inhabited by the social groups, 180 photoquadrats (0.5 x 0.5 m) were taken and were distributed along nine 10-m transects (with 1 m distance between quadrats). Subsequently, 50 points per image were randomly selected at which the benthic organisms were identified, with 9000 points total for cover estimation using CPCe 3.6 (Kohler & Gill, 2006). To compare food availability a one factor PERMANOVA was performed using the same design aforementioned for *Scarus iseri* distribution within groups. To characterize those differences a Principal Components Analysis (PCA) was applied.

Attack and bite rates were determined by 3 minutes of direct observation of each individual (n = 80) using the focal animal methodology (Altmann, 1974). Attacks were agonistic encounters between two individuals, including chases, bites and aggressive displays which once performed, caused the attacked fish to swim away. Species and number of individuals that attacked *S. iseri* per minute were recorded and bite rates were estimated by counting bites on each substrate per minute. Attack and bite rates were classified according to the *S. iseri* life phases as aforementioned. Twenty individuals were observed for each phase within each social group. Attack and bite rates were compared using nested ANOVAs with two factors: Social grouping (Stationary and Territorial groups), and Life phase (IP x TP), nested within Social grouping, given the assumption that distinct social contexts can exert influence on life phases. Feeding items consumed were compared by a nested PERMANOVA with the same design described for bite rates. To examine how feeding preference changes within different social groups and life phases, the Chesson's electivity index (Chesson, 1983) was calculated for each individual:

$$\alpha_i = \frac{r_{ij} / p_j}{\sum r_{ij} / p_j}$$

α_i is the electivity for food item j by *S. iseri* life phase I; r_{ij} is the proportion of food item j used by *S. iseri* life phase i; p_j is the proportion of substratum j available in the microhabitat. The value of α_i ranges from 0 for food items never used by *S. iseri* life phase i to 1 for exclusive use of the food item j. This allowed testing of the hypothesis of different α's (electivities) among different social groups and life phases, using the same nested PERMANOVA design. PERMANOVA and PCA analyses were performed using Primer-e 6 PERMANOVA+ 1.0 software (Anderson *et al.*, 2008). T-tests and ANOVAs were performed using R 3.0.2 software. All tests were performed at 5% of significance (Zar, 1999).

3 - Results

Stationary and territorial groups of *S. iseri* presented significant differences on density and size structure (Pseudo-F = 3.85, p < 0.01; Table 1). In general, stationary groups had more individuals than territorial groups. Smaller individuals (< 15 cm) were particularly more abundant in stationary groups; more than twice the number of individuals in the first three size classes were observed in this group comparing to territorial groups (Figure 2).

Table 1 - Results of PERMANOVA analysis of *Scarus iseri* distribution between social groups

Source	DF	SS	MS	Pseudo-F	p	Unique perms
Social grouping	1	6018.2	6018.2	3.85	< 0.01	992
Residual	18	28111	1561.7			
Total	19	34130				

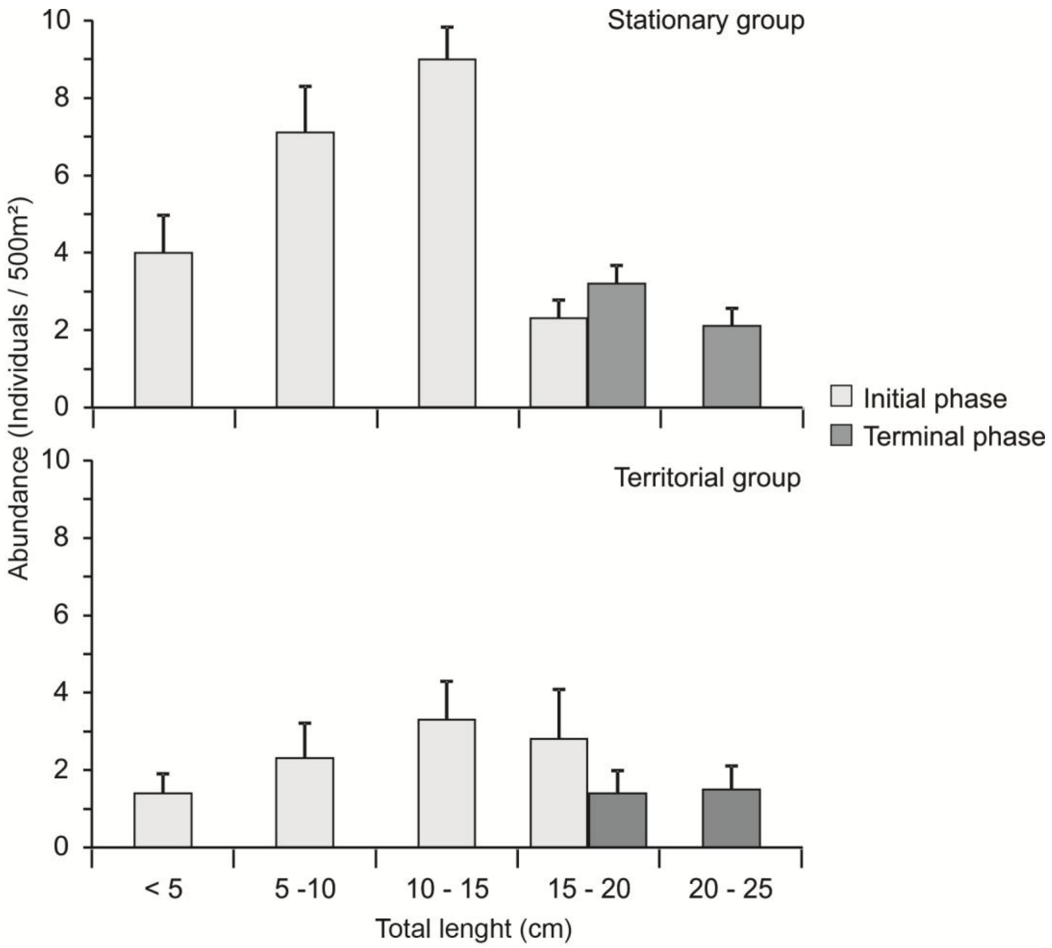


Figure 2 - ***Scarus iseri*** **population structure on the distinct social groups. Bars indicate standard error.**

Shallow habitats were inhabited by stationary groups, whereas territorial groups inhabit exclusively deeper coral reefs (> 12m depth). Intraspecific aggression was more frequent than interspecific attacks overall. IP *Scarus iseri* did not attack TP individuals and no significant differences were noted concerning social grouping ($F = 0.59$, $p =$ ns). Intraspecific attacks from TP *S. iseri* were directed to both life phases, but attack rates differed between these life phases ($F = 6.59$, $p < 0.01$). Individuals in territorial groups were significantly more aggressive ($F = 4.74$, $p < 0.05$), and higher attack rates were observed (Figure 3). Particularly, IP individuals underwent attacks from TP individuals over five times more than in territorial groups (1.10 ± 0.39 attacks min^{-1} vs.0.20 ± 0.12 attacks min^{-1} in stationary groups). TP *S. iseri* were less aggressive against other TP individuals, and very low attack rates were observed (0.05 ± 0.05 attacks min^{-1} in both social groups). (Figure 3).

Table 2 - Nested ANOVAs comparing attack rates towards *Scarus iseri*

	Interspecific Attacks		Intraspecific Attacks			
	Damselfishes		*Scarus iseri* IP		*Scarus iseri* TP	
Source	F	p	F	p	F	p
Social grouping	0.08	ns	0.59	ns	4.74	< 0.05
Life phase (Social)	3.96	ns	-	-	6.59	< 0.01

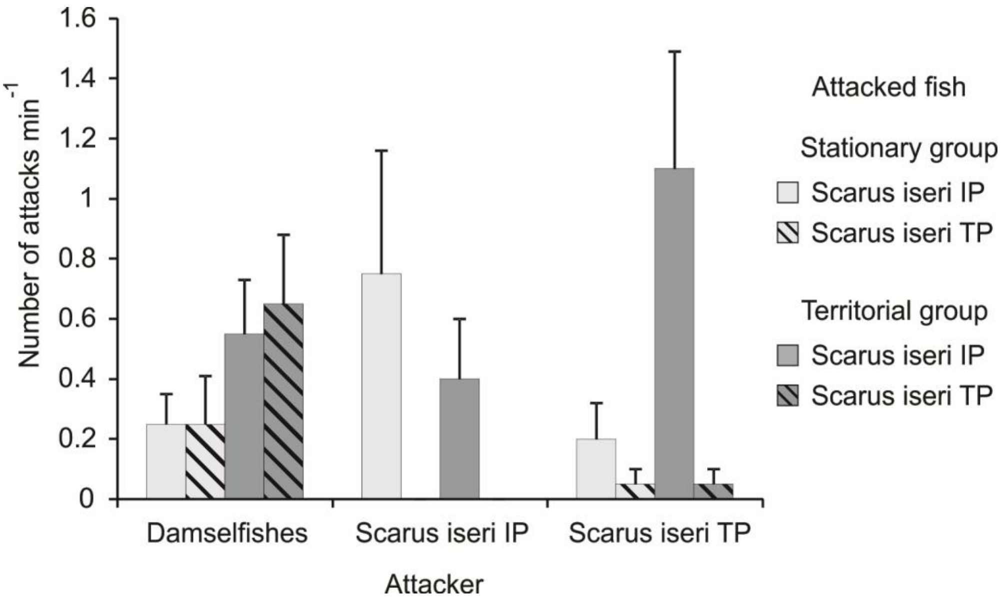


Figure 3- Mean attack rates (attacks min -1) towards *Scarus iseri* distinct social groups and life phases. Bars indicate standard error. IP = Initial phase; TP = Terminal phase.

Competitor roving herbivores (surgeonfishes and parrotfishes besides *S. iseri*) were found in low densities, with no differences among shallow and deep habitats (

Table 3). Interspecific aggression were performed solely by damselfishes towards *S. iseri*, and attacks between parrotfish species were not observed. Damselfishes attacked both *S. iseri* life phases in equal rates (F = 0.08, p = ns) regardless the social grouping (F = 3.96, p = ns) (Table 2, Figure 3). However, in stationary groups they were attacked exclusively by *Stegastes adustus*, the dominant damselfish species in shallow habitats, and only by *Stegastes planifrons* in deep habitats, inhabited by the territorial groups.

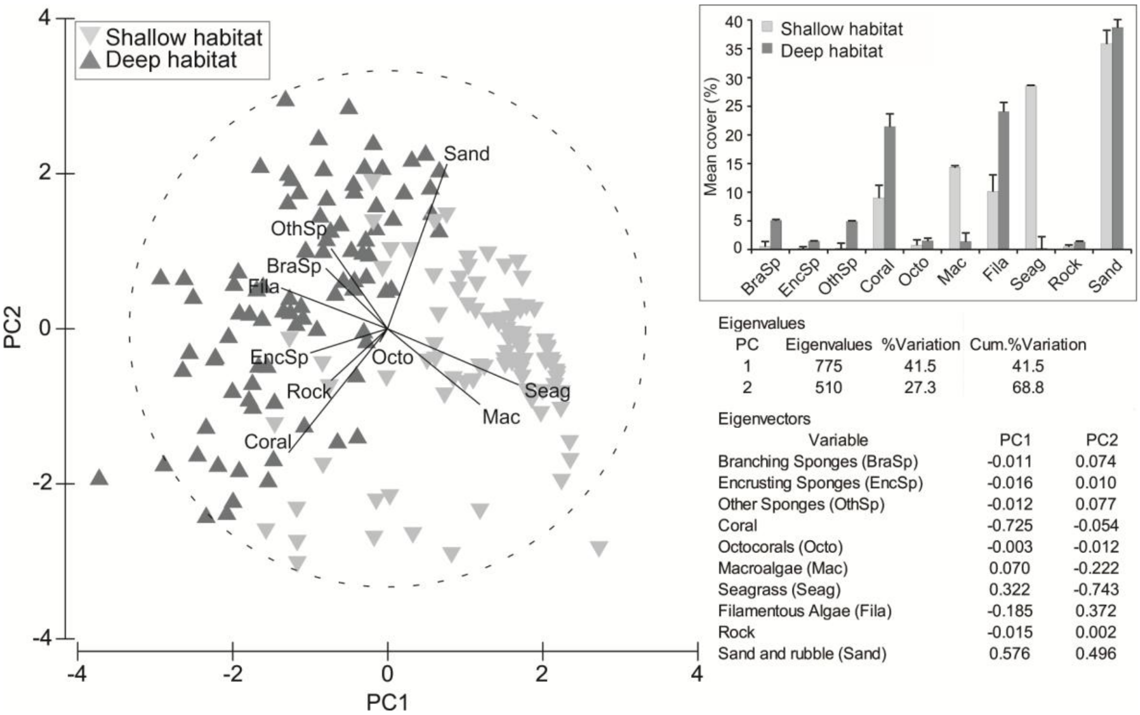
Table 3 - Density of roving herbivores (individuals 100m^{-2}) on shallow (< 12 meters) and deep (> 12 meters) habitats, with respective t-tests for each species observed on censuses. SE = standard error.

	Shallow		Deep			
	Mean	SE	Mean	SE	t	p
Sparisoma viride IP	1.90	0.84	0.30	0.15	-1.88	ns
Sparisoma viride TP	0.20	0.20	0.00	0.00	-1.00	ns
Sparisoma aurofrenatum IP	0.80	0.29	2.30	1.16	1.26	ns
Sparisoma aurofrenatum TP	1.30	0.42	0.80	0.42	-0.84	ns
Sparisoma rubripinne TP	0.70	0.52	1.00	1.00	0.29	ns
Acanthurus tractus	0.80	0.33	1.60	0.58	1.20	ns
Acanthurus coeruleus	1.30	0.67	0.10	0.10	-1.78	ns

Shallow and deep habitats were found to differ on substrate cover (Pseudo-F = 52.06, p < 0.01, Table 4). Shallow habitats were densely covered by the seagrass *Thalassia testudinea* and macroalgae, especially *Halimeda* and Dictyotaceae species (Mean ± Standard Error: 28.56 ± 2.94 and 14.29 ± 2.17, respectively). Heads of *Porites furcata* are also found (~ 9 % of the total cover) and, over the sand, the thin mats of filamentous algae covered the rubble formed with the broken coral branches comprised approximately 10% of the substrate cover (Figure 4). Deep habitats, inhabited by territorial groups, had a greater coral cover (21.43 ± 3.14), composed mainly by the brain coral species *Colpophyllia natans* and *Diploria strigosa*. Seagrass and macroalgae cover was significantly lower than at the shallower habitats inhabited by stationary groups (0.18 ± 0.12 and 1.38 ± 0.49, respectively). Conversely, in the areas inhabited by territorial groups sponge cover was more abundant (~11%) and diverse and filamentous macroalgae cover was significantly higher (24.06 ± 4.12) (Figure 4).

Table 4 - Results of PERMANOVA analysis of substrate cover between areas occupied by *S. iseri* social groups

Source	DF	SS	MS	Pseudo-F	P	Unique perms
Social grouping	1	76249	76249	60.041	0.001	999
Residual	178	2.26E+05	1269.9			
Total	179	3.02E+05				



Eigenvalues

PC	Eigenvalues	%Variation	Cum.%Variation
1	775	41.5	41.5
2	510	27.3	68.8

Eigenvectors

Variable	PC1	PC2
Branching Sponges (BraSp)	-0.011	0.074
Encrusting Sponges (EncSp)	-0.016	0.010
Other Sponges (OthSp)	-0.012	0.077
Coral	-0.725	-0.054
Octocorals (Octo)	-0.003	-0.012
Macroalgae (Mac)	0.070	-0.222
Seagrass (Seag)	0.322	-0.743
Filamentous Algae (Fila)	-0.185	0.372
Rock	-0.015	0.002
Sand and rubble (Sand)	0.576	0.496

Figure 4 - Principal Components Analysis of substrate cover and mean cover by each substrate category on areas occupied by *S. iseri* social groups

Bite rates changed between social groups (F = 19.61, p < 0.001), but not between life phases (F = 1.74. p = ns). *Scarus iseri* within stationary groups had higher mean bite rates than individuals of territorial groups. In particular, TP individuals in territorial groups presented half the bite rates of TP in stationary groups (Table 5).

Table 5 - Nested ANOVA comparing bite rates of S. iseri between habitats and life phases. Mean bite rates (bites min -1) by distinct social groups and life phases are also presented. SE = standard error .

Source	DF	SS	MS	F	p
Social grouping	1	13676	13676	19.61	< 0.001
Life phase (Social)	2	2426	1213	1.74	ns

Social grouping	Initial phase		Terminal phase	
	Mean	SE	Mean	SE
Stationary group	65.05	6.23	68.45	5.72
Territorial group	48.20	5.32	33.00	6.30

Table 6 - Results of nested PERMANOVA analysis of *Scarus iseri* feeding patterns between social groups and life phases

Source	DF	SS	MS	Pseudo-F	p	Unique perms
Social grouping	1	25438	25438	15.51	< 0.01	999
Life phase (Social)	2	13577	6788.5	4.14	< 0.01	999
Residual	76	1.25E+05	1639.8			
Total	79	1.64E+05				

Scarus iseri bites targeted mostly filamentous algae and substrata covered with sand and rubble; however, differences in food resource use were observed both for social grouping and life phases (Pseudo-F = 15.51, *P* < 0.01 and Pseudo-F = 4.14, *P* < 0.01, respectively, Table 6). *Scarus iseri* in stationary groups fed more on sand, especially TP individuals, whereas filamentous algae made the bulk of feeding of territorial groups fish. Considering life phases, IP *S. iseri* had higher bite rates on filamentous algae, while TP individuals bite mostly on sand, feeding occasionally over sponge surface (Figure 5).

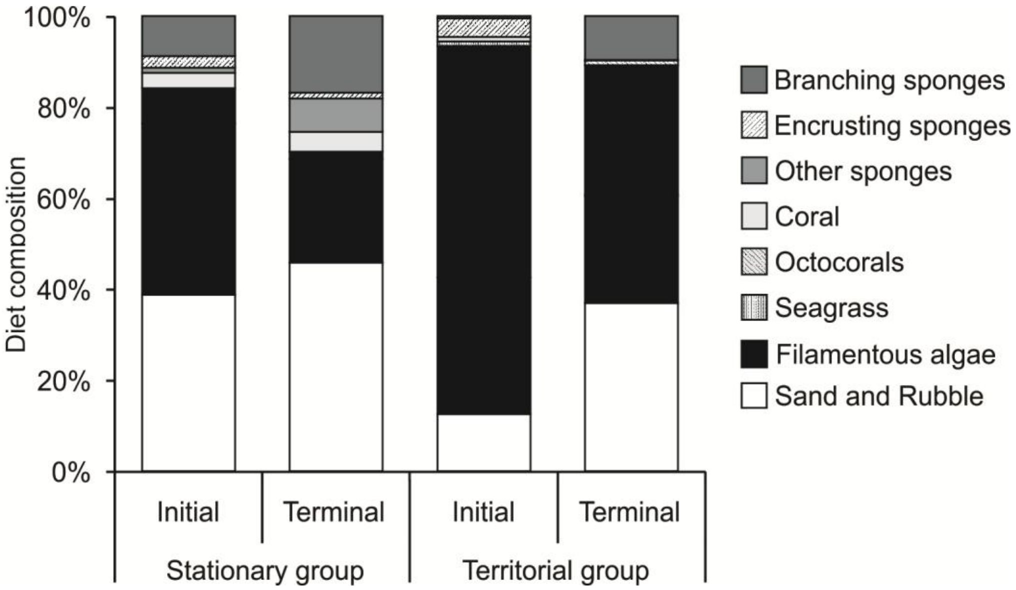


Figure 5 - *Scarus iseri* feeding patterns between social groups and life phases

Table 7- Nested PERMANOVA analysis of *Scarus iseri* feeding electivity between social groups and life phases

Source	DF	SS	MS	Pseudo-F	p	Unique perms
Social grouping	1	20889	20889	10.113	0.001	999
Life phase (Social)	2	9825.5	4912.8	2.3784	0.03	999
Residual	76	1.57E+05	2065.5			
Total	79	1.88E+05				

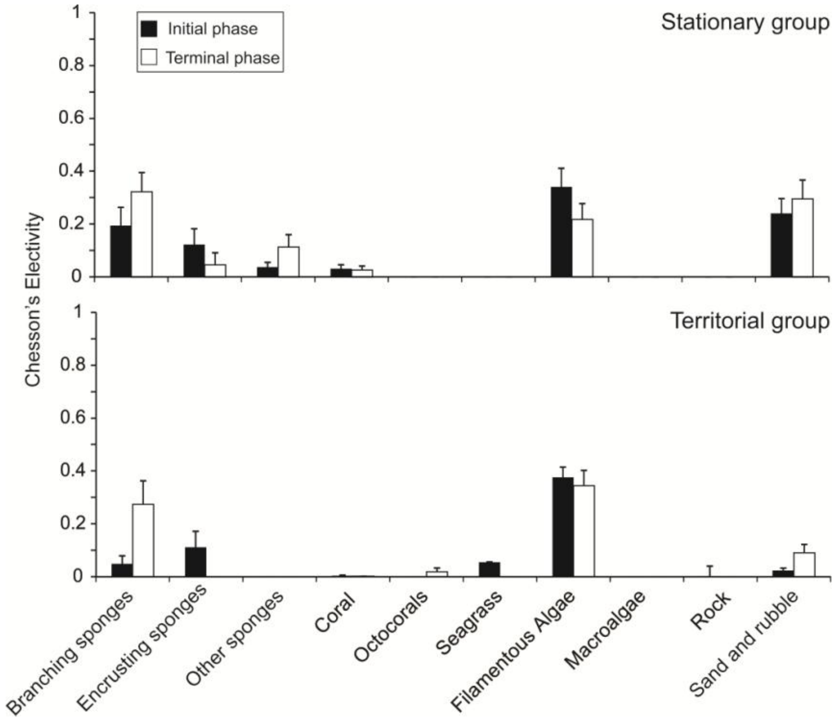


Figure 6 - Electivity of different life phases of *Scarus iseri* on the distinct social groups

Overall, *S. iseri* fed on highly abundant food items, such as filamentous algae and sand, which despite being quite plentiful, were highly preferred. Seagrass and coral had nearly negligible contribution to feeding, and erect macroalgae was not consumed at all. Electivity changed between social groups (Pseudo-F = 10.11, $p < 0.01$) and life phases (Pseudo-F = 2.38, $p < 0.05$) (Table 7), differences that closely reflected the feeding patterns described above. Filamentous algae were preferred for both social groups, but individuals in stationary groups supplemented nibbling over sand and sponges (Figure 6).

4 - Discussion

INTRA- AND INTERSPECIFIC COMPETITION

Scarus iseri has been considered one of the parrotfish species with higher levels of intraspecific competition (Mumby & Wabnitz, 2002). In the present study, it was observed that IP *S. iseri* suffered over five times more attacks from TP individuals within territorial groups. Aggression can be applied to confirm dominance of an individual fish over subordinates, and it may also limit their numbers inside a territorial group (Clifton, 1989; Mumby & Wabnitz, 2002). Indeed, higher densities of fish were found within stationary groups in the study area, composed especially of smaller individuals. In contrast, exclusion of small-sized individuals by competition with larger ones may explain their lower abundance within territorial groups. Clifton (1989) hypothesized that smaller individuals could be more persistent intruders by evading larger conspecifics, however dominant individuals showed no forbearance to smaller fish. Therefore, it is more likely that the greater abundance of fish with inferior competitive abilities, such as smaller individuals within non-territorial groups, is a result of intraspecific aggression.

Following this reasoning, such competition may occur differently along life phases of *S. iseri*. Attacks among IP individuals seem to be associated with competition for food, as these fish are known to defend feeding territories (Clifton, 1989). Although less frequently, TP individuals still perform intraspecific attacks when in stationary groups, where there is no competition for mating territories, suggesting that there is an aggression component also driven by food competition. Such competition may even be enhanced in habitats were preferred food is limited, such as feeding grounds held by stationary groups. While in territorial groups, TP individuals defend larger mating territories that encompass several females defending feeding territories (Clifton, 1989), thus evicting outsiders at both life phases from their territories.

Regardless of life phase and social group, *Scarus iseri* interspecific competition is mainly posed by damselfishes. *Stegastes adustus* and *S. planifrons* are the most abundant damselfishes in Caribbean reefs, but show little overlap in their distribution (Waldner & Robertson, 1980; Robertson, 1984; Gutierrez, 1998; Chaves *et al.*, 2013). In the studied area, *S. adustus* is a more habitat generalist in shallow depths, whereas *S. planifrons* seems to occur particularly over live massive coral colonies (Chaves *et al.*, 2013). Thus the habitat segregation between social groups allowed interactions to occur more often with *S. adustus* whenever *S. iseri* was inserted within stationary individuals or with *S. planifrons* while within territorial groups. In fact, *S. iseri* is the parrotfish species that suffers higher rates of aggressive interactions either by *S. adustus* or by *S. planifrons* (Robertson, 1984). These two damselfish species seem to be the ones with greater food overlap with *S. iseri*. They are known to feed on filamentous algae and microalgae instead of feeding on erect macroalgae, such as calcareous macroalgae and Dictyotaceae species that yield higher herbivore-deterring strategies (Lobel, 1980; Robertson, 1984). Despite the differences on damselfish species dominance on the habitats inhabited by stationary or territorial groups, both groups suffered equivalent attack rates. Once even highly territorial *S. iseri* did not show aggression towards damselfishes, we disbelieve that any advantages were provided by social context to parrotfish in regards to interspecific competition, i.e. overcoming damselfish territoriality.

FEEDING PATTERNS

It was observed that non-territorial *Scarus iseri* joining stationary groups had higher mean bite rates than individuals within territorial groups. Based on our findings and previous studies, two main hypotheses can be raised to explain this pattern: (1) territorial individuals spend more time defending territories than feeding, as dominance interactions limit the consumption of resources (as suggested by Clifton, 1989); or (2) they feed more frequently in order to achieve nutritional needs for relying on less-available or less nutritious food sources. Both hypotheses may be true, although it was observed herein that both groups fed in unequal proportions of sand and filamentous algae, supporting the latter hypothesis. Territorial fish ingested more filamentous algae, while stationary groups scavenged greater amounts of sand and accessory food items. Filamentous algae is a largely used food source, as this particular algal group is highly productive and palatable (Hay, 1991). Conversely, feeding on sand demands greater effort, as fish needs to either sort detritus, from inorganic sediment or to feed more frequently, which seems to be the strategy held by *S. iseri* while in stationary groups.

As previously mentioned, stationary groups inhabited sites that greatly differ on food availability, containing mostly *Thalassia testudinea* and macroalgae with herbivore deterrent strategies. The most preferred food, filamentous algae, had limited availability. Therefore, there is a great difference on food quality between sites on each social group occur, indicating a limited space suited for territories, as hypothesized by Buckman and Ogden (1973). Moreover, dominant fish in territorial groups have the advantage of using subordinates as food-finders, having priority of access to new patches once they are found (Clifton, 1991). That would balance the energy costs associated to territory defense and could explain low feeding rates by the lack of need for exploratory bites.

Until the present study, feeding preferences of *S. iseri* were unknown, and thus assessing general amounts of algae would have misleading outcomes as to food was equally available for *S. iseri* in both social groups. Despite being highly abundant, we found that macroalgae other than filamentous species are avoided by *S. iseri*. Most likely, *S. iseri* feeding is limited to algal functional groups with no deterrent strategies (e.g. secondary metabolites and calcification). Consequently, it seems reasonable that territorial groups defend territories where preferred food is highly abundant, although a previous study found no indication that groups defended certain areas such that more food was available (Clifton, 1989).

In addition, divergences were also found between life phases feeding and, generally, IP *S. iseri* fed mostly on filamentous algae, while TP individuals had higher bite rates on sand and in a lesser extent over sponges. *Scarus iseri* was found to be little attracted to feed upon sponges in previous study, especially more conspicuous species (Wulff, 1997a), which were the ones targeted by *S. iseri* herein. Separated experiments performed at our study site indicated that *S. iseri* does not feed on sponges (authors pers. obs.). Instead, the target bites over sponges were directed to accumulated detritus and/or overgrowing filamentous algae. The increase in bites over sponges in TP individuals happens concomitantly with the increase of bites over sand. So, it is feasible that a shift from algae as the bulk of feeding to a detritus-based diet occurs with growth in *S. iseri*. A similar pattern was already observed for other parrotfish species (Feitosa & Ferreira, 2014). If ontogenetic changes in diet are believed to lessen intraspecific competition, we hypothesize that aggression performed by TP individuals towards IP *S. iseri* seems to be more related to demonstrations of dominance, than competition for resources.

FURTHER REMARKS

This work is the first to consider how competition and feeding patterns may shift in distinct social contexts within a particular parrotfish species. Actually, most studies addressing parrotfish feeding ecology only describe general patterns, treating feeding as a species-specific trait. Such generalization has to be made with extreme caution, as one species feeding preferences is context-dependent, and shifts in feeding rates and food preferences may occur both socially and ontogenetically. *Scarus iseri*, by its wide preference for filamentous algae, may be considered a browser species; and as such, participate in coral reef dynamics by removing this fast-growing algae and opening space for coral to settle. Although it was not directly measured in the present study, the feeding habits of this species indicate it takes part in other processes on the reefs, such as nutrient recycling from detritus and preventing sedimentation over sponges.

Additionally, the current study presents novel findings on the motivations for *S. iseri* segregation into distinct social groups, what was the main subject of several previous works. Mostly, reproduction is thought to be the main factor driving territoriality, and there is an obvious reproductive component defining fish that join territorial groups. However, the superior food quality inside aggressively defended territories indicate there is competition for food resources, what is likely to be a more immediate force driving segregation into distinct social groups. Given the limited availability of space suited for territories, density-dependent processes are prone to take place, as intraspecific competition may subject inferior individuals to alternative social contexts.

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Capítulo 3

Distribution and feeding patterns of juvenile parrotfish on algal-dominated coral reefs

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ABSTRACT

By the consumption of algae, parrotfishes open space for young coral settlement and growth, thus playing a central role on the maintenance of coral reefs. However, juvenile parrotfish ecology is often overlooked due to the difficulty in discerning species during this phase. Herein, we present the first attempt to investigate changes in habitat use and diet that happen to juveniles of the Redeye parrotfish *Sparisoma axillare*, focusing on four zones within an algal-dominated reef: the macroalgal beds, back reef, reef flat, and fore reef. Smaller *S. axillare* juveniles (< 5 cm) preferred to inhabit the macroalgal beds and the reef flat, whereas juveniles larger than 5 cm were more abundant in the back and fore reefs due to distinct post-settlement habitat conditions. Aggressive interactions with the territorial damselfish *S. fuscus* were the primary driving factor of juvenile distribution and feeding rates. Attack rates increased with juvenile size and the lowest bite rates were observed in zones with higher densities of territorial damselfish. In previous studies, the persistence of parrotfish recruits in habitats dominated by damselfish was reduced, but herein newly settled parrotfish occurred more densely within the damselfish domain, by behaving as a cryptic reef fish. As these juveniles grew, their bite rates increased, a change associated with a shift from cryptic to roving behavior. Feeding preferences were determined by substrate cover, where juveniles fed on available food sources in each habitat. Juveniles relied on jointed calcareous algae in habitats dominated by these algae, a pattern not observed for thick-leathery algae. Filamentous algae were the preferred food for smaller fish, and for individuals greater than 10 cm, a higher ingestion of sand was observed. Most studies evaluating the functional role of parrotfish do not consider species feeding preferences. However, the potential for a species to turn an impacted reef back to a coral-dominated phase is influenced by their food selection, which is dependent on the algal species composition.

Distribuição e padrões alimentares de peixes-papagaio jovens em recifes dominados por algas

RESUMO

Através do consumo de algas, os peixes-papagaio abrem espaço para o assentamento e crescimento de corais juvenis, por conseguinte realizando um papel central na manutenção dos recifes de coral. Entretanto, a ecologia de peixes-papagaio jovens é comumente negligenciada devido a dificuldade existente em discernir espécies durante essa fase de vida. O presente estudo representa a primeira tentativa de elucidar as mudanças que ocorrem no uso de habitat e dieta de jovens do bobó *Sparisoma axillare*, focando em quatro zonas dentro de um recife dominado por algas: os bancos de macroalgas, o back reef, o topo recifal e o fore reef. Os menores jovens de S. axillare (< 5 cm) preferiram habitar os bancos de macroalgas e o topo recifal, enquanto que indivíduos maiores que 5 cm foram mais abundantes no back e no fore reef, devido a condicções ambientais distintas após o seu assentamento. Interações agressivas com o peixe-donzela *S. fuscus* foram os fatores determinantes da distribuição e taxas de alimentação dos jovens de *S. axillare*. As taxas de ataques aumentaram com o tamanho dos jovens e as menores taxas de alimentação foram observadas em zonas com maiores densidades de peixes-donzela. Em estudos anteriores, a persistência de recrutas de peixes-papagaio em habitats dominados por peixes-donzela foi reduzida, entretanto no

presente estudo foi observado que peixes-papagaio recém-assentados ocorreram em maiores densidades dentro dos territórios dos peixes-donzela, onde se comportaram como um peixe críptico. Na medida em que estes jovens cresceram, suas taxas de alimentação aumentou, uma alteração associada com a mudança de um comportamento críptico para um vagueador. Suas preferências alimentares foram determinadas pela cobertura do substrato, onde os jovens se alimentaram do alimento disponível em cada habitat. Os jovens se alimentaram mais de algas calcárias articuladas em habitats onde estas dominaram, porém esse padrão não foi observado para as algas coriáceas. Algas filamentosas foram o item preferido por peixes menores e para indivíduos maiores que 10 cm uma maior ingestão de areia foi observada. A maior parte dos estudos que avaliam o papel funcional dos peixes-papagaio não consideram as preferências alimentares de cada espécie. Entretanto, o potencial que uma espécie para transformar um recife impactado de volta a uma fase dominada por corais é determinada pelos alimentos que esta seleciona, que são dependentes da composição específica de algas.

1 - Introduction

Parrotfishes play a fundamental role on coral reefs: by feeding on algae, these fishes open space for coral settlement and also prevent algal dominance over coral (Mumby *et al.* 2006; Hughes *et al.* 2007; Mumby 2009). On southwestern Atlantic coral reefs, only five scarid species appear to actually perform this role (Ferreira & Gonçalves 2006; Francini-Filho *et al.* 2008), resulting in a low functional redundancy of scrapers and excavator species (Bellwood *et al.* 2004). Along the northeastern coast of Brazil, inshore coral reefs averaged a live coral cover of approximately 25% in 1960s (Jaques Laborel pers. comm.). Recently, these reefs suffered land-based impacts such as eutrophication (Flores-Montes *et al.* 2011; Paulo *et al.* 2011), tourism (Feitosa *et al.* 2012a) and high rates of herbivore fishing (Marques & Ferreira 2010). These kind of impacts may decrease coral cover, as observed in several studies (Belliveau & Paul 2002; McClanahan *et al.* 2002; Diaz-Pulido & McCook 2003; Bellwood *et al.* 2004; Hughes *et al.* 2007; Burkpile & Hay 2009; Hoey & Bellwood 2010a, 2010b). Indeed, despite the lack of quantitative records regarding the reduction of coral cover on southwestern Atlantic reefs, Ferreira & Maida (2006) found clear indications of a reduction in near-shore coral cover (< 5%) due to a shift towards algal domination. A decline in coral cover results in a loss of habitat complexity, greatly affecting fish community structure (Syms & Jones 2000). Hence, a phase shift to an algae-dominated state would be expected to greatly affect the density of reef fishes and/or their interactions with their environment. Nonetheless, most studies focus on the influence that parrotfish can exert on coral reefs (e.g., Bellwood 1995; Brunggemann *et al.* 1996; Mantyka & Bellwood 2007; Bennet & Bellwood 2011), while the effects of an already altered environment on parrotfish ecology are poorly understood.

Most parrotfish species are generalists in both habitat use and feeding. They can inhabit seagrasses, mangroves and coral and rocky reefs, including different habitats within each of these ecosystems (Ogden & Buckman 1973; Russ 1984a, 1984b; Paddack & Sponaugle 2008). Depending on the food availability within these environments, they feed differently, actively choosing their preferred food (Wolf 1985). Additionally, parrotfish can rely on food types other than algae, such as detritus, crustaceans, sponges, gorgonians and dead or live coral (Randall 1967; Bruggemann *et al.* 1994; McAffe & Morgan 1996; Bruckner & Bruckner 1998; Sánchez *et al.* 2004;

Ferreira & Gonçalves 2006; Roff *et al.* 2011). Interference competition may also structure habitat use in herbivores (Robertson & Gaines 1986). In particular, damselfishes aggressively defend territories (Low 1971; Brawley & Adey 1977; Itzkowitz 1990; Hata & Kato 2004), in which they may reduce feeding rates and food availability of competitors (Robertson *et al.* 1976; Reithal & Lewis 1986), or even abundance of juveniles (Sale 1976). Yet, these ecological aspects are rarely considered when measuring the impact of parrotfish on coral reefs. Generally, these approaches only consider the feeding of parrotfish on the epilithic algal matrix, regardless of which algal species compose this matrix, which may alter food selection. Additionally, most studies describe parrotfish feeding and distribution as a species-specific trait, primarily focusing on large adult fish (Bonaldo & Bellwood 2008) and commonly overlooking juveniles and the possible ontogenetic shifts in their ecology. Species identification of juvenile parrotfish is difficult as they lack features that are used for identifying adults, such as colored dental plates, humps and filamentous extensions of the caudal fins (Bellwood 1986). However, the low number of species in the Brazilian region and detailed observation allow the discernment of species in their juvenile phase. In light of the fact that reefs with low coral cover undergo habitat loss, the objective of the present study was to elucidate the following questions: (1) Do algal-dominated reefs have distinguishable habitats? (i.e. zones with discernible differences on organisms covering the substrate) (2) How do these distinct habitats influence herbivore distribution, bite rates and feeding preferences of juvenile parrotfish? (3) The interactions with other fish affect juvenile parrotfish distribution and feeding? (4) Do these influences change as the juveniles grow larger?

2 - Material and Methods

STUDY AREA

The present study was performed on the Tamandaré reef complex, situated off the northeastern coast of Brazil, where the only hermatypic coral formations in the South Atlantic are found. The study area is within the limits of the Costa dos Corais Marine Protection Area, which encompasses 135 km of coastline and has been protected by federal law since 1997. There are two distinct climatic periods during the year: a rainy season (from June to October) and a dry season (from November to May). The area has a coastal tropical climate with average temperatures near 30º C during the dry season and 24º C during the rainy season (Maida & Ferreira 1997). Sampling was conducted in two periods: between December 2010 and April 2011 and between February and May 2012, both during the dry season to minimize potential seasonal effects.

The coral reef formations in Tamandaré resemble fringing reefs, as they run parallel to the coast and present a shallow lagoon. These reefs have a distinctive growth form, developing as isolated columns that grow up to 5-6 m tall and then laterally expand at the top and are distributed along three lines. (Dominguez *et al.* 1990; Maida & Ferreira 1997). When these columns are densely aggregated, their tops coalesce and create large reef flats just below the surface (Ferreira *et al.* 1995; Maida & Ferreira 1997). Refer to Maida & Ferreira (1997) for a more detailed description**.**

Within this reef formation, four visually different habitats were selected for sampling: **(1)** macroalgal beds, primarily composed of dense mats of erect macroalgae occurring over coral rubble, characteristically a first line reef, as described by Maida & Ferreira (1997); **(2)** the rear portion of the second line reef, protected from wave action, generally called the back reef; **(3)** the top of the second line reef, which is subject to tidal changes and wave surges and highly dominated by territorial damselfish, generally called the reef flat; and **(4)** the front of the second line reef, also subjected to high wave action, called the fore reef (Fig. 1).

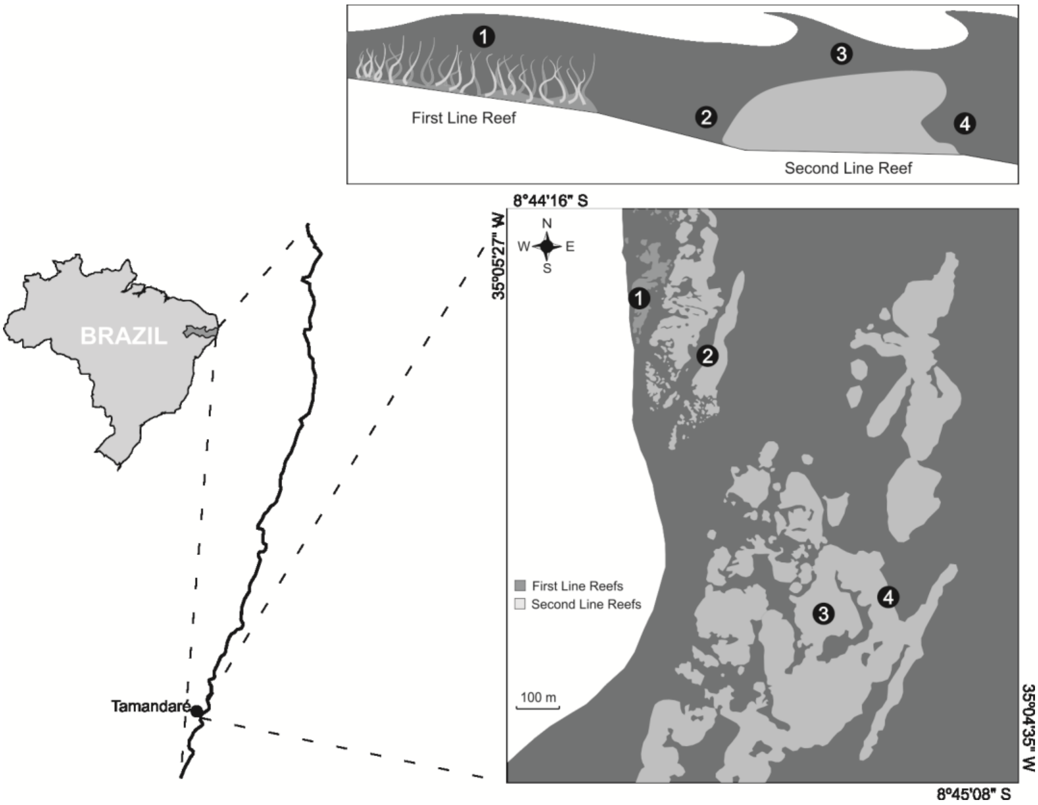


Fig. 1 - Map of study area, showing habitats analyzed; (1) macroalgal beds; (2) back reef; (3) reef flat; and (4) fore reef.

STUDY SPECIES

Southwestern Atlantic parrotfishes are generally represented by the genera *Scarus* and *Sparisoma*, with eight species total, all of which are endemic to the Brazilian area, with the exception of the Bucktooth parrotfish *Sparisoma radians*, which is also found in the Caribbean. *Sparisoma* individuals are consistently more abundant along the coast, but both genera decrease in abundance to the south (Ferreira *et al.* 2004). On Brazilian reefs, scarids compose as much as 20% of the relative abundance of the ichthyofauna and, in the study area, scarids represent up to 14% (Ferreira *et al.* 2004).

The most abundant parrotfish species on coastal reefs are the Greenlip parrotfish *Scarus trispinosus*, the Fourspot parrotfish *Scarus zelindae*, the Redeye parrotfish *Sparisoma axillare*, the Brazilian parrotfish *Sparisoma amplum*, the Saddled parrotfish *Sparisoma frondosum* and the Bucktooth parrotfish *Sparisoma radians* (Ferreira and Gonçalves 2006; Francini-Filho *et al.* 2010). *Scarus trispinosus* is an endangered species (IUCN) and was heavily fished in the study area; thus, it occurs now in very low abundances outside of no-take areas. In the present study, juvenile identification was based on coloration (Fig. 2): *S. zelindae*, *S. axillare* and *S. frondosum* have white stripes occurring from their snout to the caudal peduncle and a white belly. *Sparisoma amplum* lacks these features and presents sparse white dots on a darker flank. *Scarus zelindae* is easily recognizable as it presents a yellowish snout and a third white stripe at the base of the dorsal fin. *Sparisoma axillare* and *S. frondosum* juveniles are more similar, differing by a whitish saddle marking at the top of the caudal peduncle that is present on the latter species (which also remains through their adult initial phase). Although occasionally less visible, the white saddle is always displayed after a few seconds of observation. *Sparisoma radians* differs from other species by a presence of greenish or bluish marks around the eye that persist throughout its life.

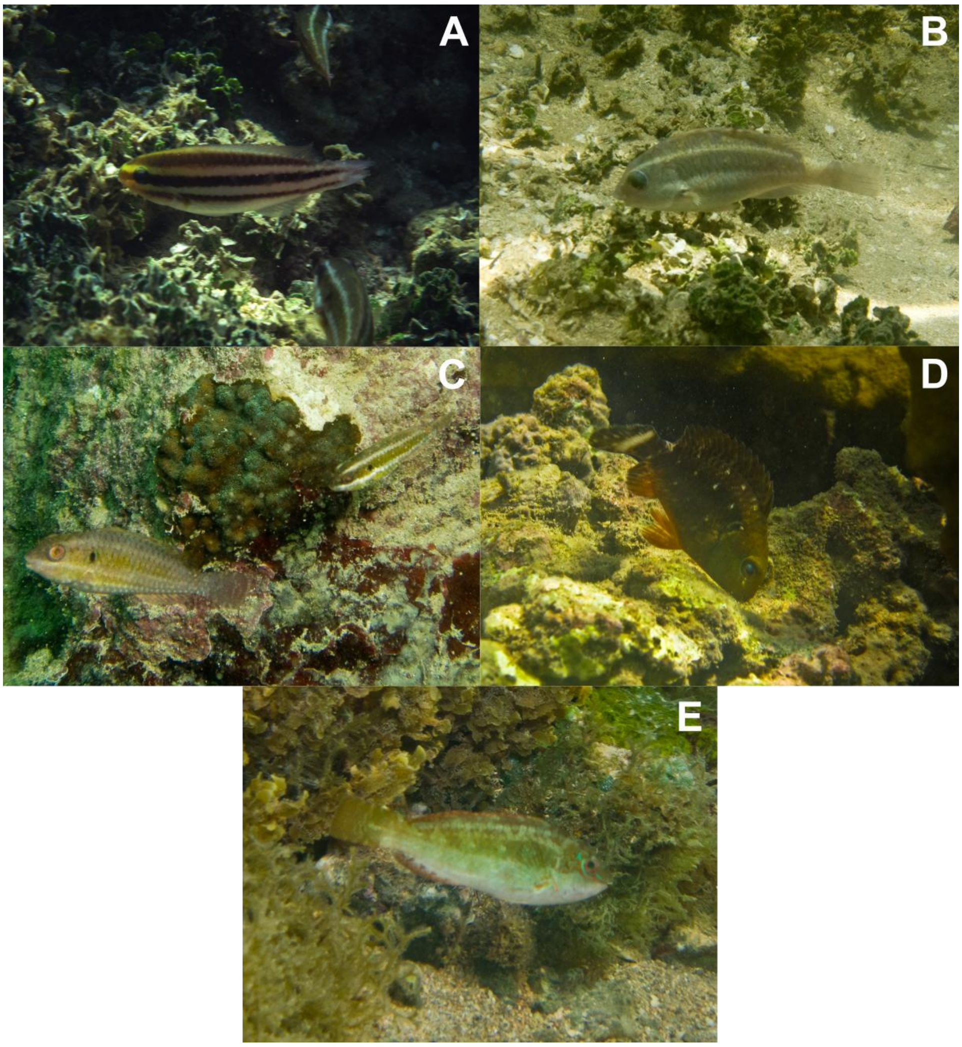


Fig. 2 - Commonly observed juvenile parrotfish in the study area; (A) *Scarus zelindae*; (B) *Sparisoma frondosum*; (C) *Sparisoma axillare*; (D) *Sparisoma amplum*; (E) *Sparisoma radians*.

Sparisoma axillare is a conspicuous species in the southwestern Atlantic, common from the Manoel Luis Reefs in northern Brazil to the Santa Catarina coast in southern Brazil, occurring also off the Brazilian oceanic islands (Moura *et al.* 2001). This species is found in coral reefs, algal reefs, seagrass beds and rocky reefs, at depths ranging from 1 to at least 54 m (Feitoza *et al.* 2005). Given its high abundance and widespread distribution along the southwestern Atlantic coral reefs, including the studied reefs, *Sparisoma axillare* was chosen as a model species for the evaluation of size-dependent distribution and feeding patterns along the four habitats studied.

Despite its high abundance in these environments, the larger terminal males are relatively rare in shallower areas (< 10 m), likely due to fishing pressure (Ferreira *et al.* 2009). In the shallow areas, the initial phase individuals are caught by hook and line and spear fishing, representing 29% of the artisanal fisheries landings (Ferreira *et al.* 2001). Terminal phase individuals are captured by spear fishing and are common in the catches of trap fisheries operating in deeper areas (Marques and Ferreira 2010).

SAMPLING AND DATA ANALYSIS

To determine differences in substrate cover among the four habitats analyzed, 300 40 x 40 cm photoquadrats (75 quadrats in each habitat) were taken, distributed along five 15-m transects (with 5 m of spacing between quadrats). Subsequently, using CPCe 3.6 (Kohler & Gill 2006), 50 points per image were randomly selected at which the benthic organisms were identified, totaling 15000 points for cover estimation. The macroalgae observed were assigned to ecological groups according to their morphological and functional-forms as filamentous, sheet-like, coarsely branched, thick leathery, jointed-calcareous or encrusting calcareous (Littler & Littler 1984) (Table 1). The functional-form group 'fleshy' was included because *Colpomenia* and *Dictyosphaeria* species could not be classified into any other group proposed by these authors. For comparisons of substrate compositions among the analyzed habitats, a Permutational Multivariate Analysis of Variance (PERMANOVA) with one factor (habitat, with each of the four habitats as a level) was applied, and for characterizing the differences, a Principal Components Analysis (PCA) was performed.

To estimate the abundance of the herbivore species along the habitats, 60 20 x 2 m belt-transects (15 censuses in each habitat) were performed (modified from Brock 1954). Each census registered the abundance of roving herbivores in a first swim over the transect, and in a second swim, territorial damselfish and sea urchins were counted. All transects were parallel to the coast, haphazardly arranged, laid at least 3 meters apart, without choosing for any specific substrata but ensuring it to be placed inside habitats shown on Figure 1. To avoid bias associated with the experience level of the diver (Williams *et al.* 2006) and fluctuations in abundance related to daily migration (Willis *et al.* 2006) or tides (McClanahan *et al.* 2007), all censuses were conducted by one diver, in the afternoon and during low tides.

Table 1 - Observed genera of macroalgae assigned to functional-form groups (sensu Littler and Littler 1984)

Filamentous	Sheet-like	Coarsely branched	Thick-leathery	Jointed calcareous	Fleshy
Bryopsis *Gelidium*	*Anadyomene* *Canistrocarpus* *Dictyopteris* *Ulva*	*Acanthophora* *Acetabularia* *Caulerpa* *Hypnea* *Laurencia* *Palisada*	*Gracilaria* *Lobophora* *Padina* *Sargassum*	*Jania* *Halimeda*	*Colpomenia* *Dictyosphaeria*

Within the same censuses described above, *Sparisoma axillare* juvenile abundance was categorized into five size classes, from their smallest size on the reefs (1.0 cm total length, Gaspar 2006), until early adulthood (according to their total length - TL): size class 1 (< 2.5 cm TL), size class 2 (2.5-4.9 cm TL), size class 3 (5.0-7.4 cm TL), size class 4 (7.5-10.0 cm TL) and size class 5 (10.0 - 15.0 cm TL). According to Véras (2008), the length at first maturity (L_{50}) for *S. axillare* is around 20 cm. A PERMANOVA with the same one-factor design aforementioned for substrate cover was applied to examine differences in habitat occupation by size.

Attack rates towards *S. axillare* and feeding by this species were evaluated through 3 minutes of direct observation of each individual (n = 225), using the focal animal methodology (Altmann 1974). Attacks were agonistic encounters between two individuals, including chases, bites and aggressive displays which once performed, caused the attacked fish to swim away. Bite rates over each substrate, species and number of individuals who showed agonistic encounters towards the studied species were recorded underwater on PVC sheets and classified according to the aforementioned size classes. There were made 15 replicates for each size class on each habitat, totaling more than 11 hours of direct observation. All observations were made during the late morning and early afternoon, when tropical herbivorous fish are known to have greater bite rates (Ferreira *et al.* 1998) and to avoid bias associated to daily variation on bite rates. Attacks towards different sized juvenile *S. axillare* and their bite rates were tested using two PERMANOVAs with two factors - habitat and size classes - in which the latter was nested into habitat, considering the assumption that the habitat can influence the behavioral patterns of each size class.

To observe how feeding preference changes for different-sized *S. axillare* juveniles in the studied habitats, Chesson's electivity index (Chesson 1983) was applied:

$$\alpha_i = \frac{r_{ij} / p_j}{\sum r_{ij} / p_j}$$

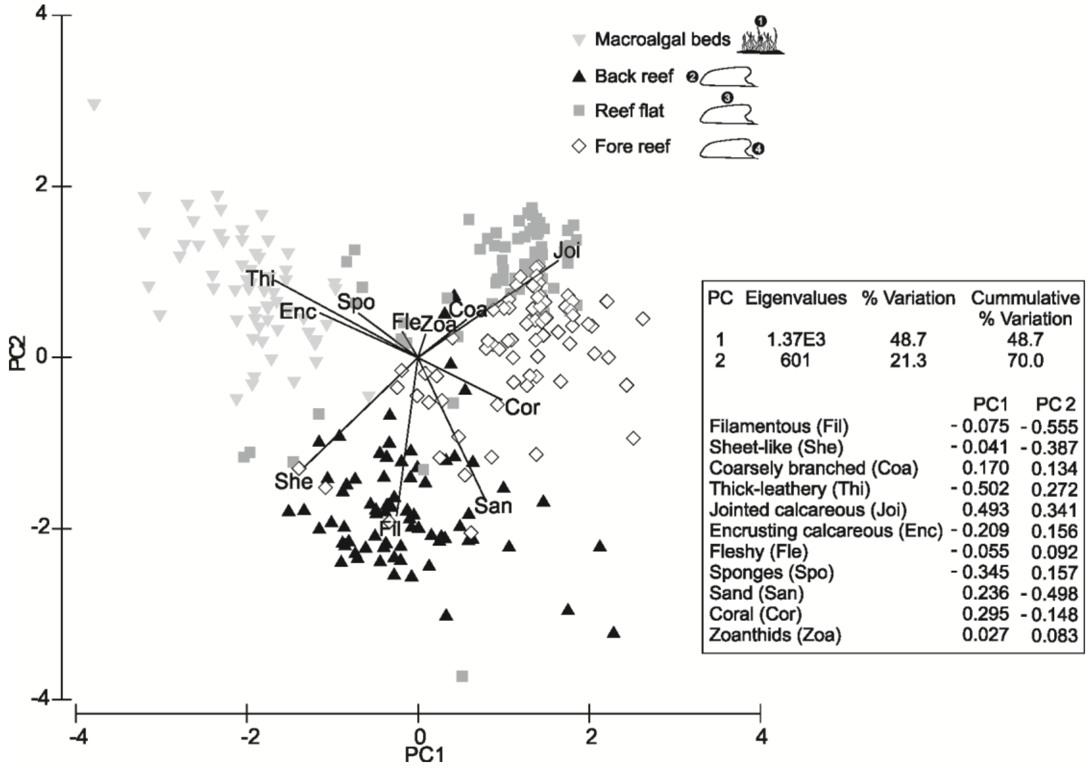
where α_i is the electivity for food item j by *S. axillare* of size class i, r_{ij} is the proportion of food item j used by *S. axillare* of size class i, and p_j is the proportion of substratum j available in the habitat. The value of α_i ranges from 0 for food items never used by *S. axillare* of size class i to 1 for exclusive use of food item j. This index was calculated for each individual, as suggested by Chesson (1983). This allowed the test of the hypothesis of different values of α (electivities) among different habitats and size classes, using the same two-factor nested PERMANOVA design as for attack and bite rates. PERMANOVA and PCA analyses were performed using Primer-e 6 PERMANOVA+ 1.0 (Anderson *et al.* 2008). All tests were performed at a 5% level of significance (Zar 1999).

3 - Results

HABITAT COMPARISONS

The selected habitats were shown to be significantly different in their substrate cover (Pseudo-F = 96.34, $p < 0.01$, all pair-wise t tests with $p < 0.01$). The principal component analysis explained 70.0% of the data variation for the first two PC axes (Fig. 3). In this analysis, the macroalgal bed samples were mostly distinguished by thick-leathery (54.16%) and sheet-like macroalgae high cover (25.84%), to which the species *Sargassum polyceratium* and *Dictyopteris delicatula* were the main contributors. This habitat also had less presence of jointed calcareous species (5.48%). The back reef was dominated by sheet-like and filamentous forms (33.95 and 20.43%, respectively), also with a great presence of sand (27.51%). On both the reef flat and the fore reef, the jointed calcareous algae were the most abundant group (55.49 and 45.76%, respectively), primarily composed of *Halimeda opuntia* and *Jania* spp. These two habitats were separated primarily by the greater presence of sand on the fore reef (26.67 versus 8.11% on the reef flat). Sponges were observed solely on the macroalgal beds, and zoanthids, primarily *Palythoa caribaeorum*, were only on the reef flat, both in minor proportions (2.21 and 2.35%, respectively). Coral cover was very low (< 1.5%) (e.g., *Siderastrea stellata*, *Millepora alcicornis* and *Agaricia agaricites*), but present in all analyzed habitats.

Herbivore densities varied between the analyzed habitats (Pseudo-F = 49.97, $p < 0.001$, all pair-wise t tests with $p < 0.001$). The Ocean surgeonfish *Acanthurus bahianus* inhabited only the fore reef (Mean individuals/40 m^2 = 1.66, Standard Error ± 0.89). The Blue tang *Acanthurus coeruleus* and the Doctorfish *Acanthurus chirurgus* occurred in low densities (< 1 ind/40 m^2), with the former found in all habitats but the fore reef, and the latter found only on the macroalgal beds and the fore reef. *Sparisoma axillare* were observed exclusively as juveniles, and it was the parrotfish species found in the highest densities (5 - 8 ind/40 m^2) in all analyzed habitats. *Sparisoma radians* inhabited the macroalgal beds and back reef (2.33 ± 0.63 and 0.20 ± 0.14 ind/40 m^2, respectively). *Scarus trispinosus* was only observed on the fore reef (0.80 ± 0.22 ind/40 m^2).



PC	Eigenvalues	% Variation	Cummulative % Variation
1	1.37E3	48.7	48.7
2	601	21.3	70.0

	PC1	PC 2
Filamentous (Fil)	- 0.075	- 0.555
Sheet-like (She)	- 0.041	- 0.387
Coarsely branched (Coa)	0.170	0.134
Thick-leathery (Thi)	- 0.502	0.272
Jointed calcareous (Joi)	0.493	0.341
Encrusting calcareous (Enc)	- 0.209	0.156
Fleshy (Fle)	- 0.055	0.092
Sponges (Spo)	- 0.345	0.157
Sand (San)	0.236	- 0.498
Coral (Cor)	0.295	- 0.148
Zoanthids (Zoa)	0.027	0.083

Fig. 3 - Principal components analysis of substrate cover between the different habitats. Fil - Filamentous algae; She - Sheet-like algae; Coa - Coarsely branched algae; Thi - Thick-leathery algae; Joi - Jointed calcareous algae; Enc - Encrusting calcareous

Although *Sparisoma frondosum*, *Sparisoma amplum*, and *Scarus zelindae* are present in the study area, they were not registered in the censuses. Adults of the Bluespotted damselfish *Stegastes fuscus* were observed in all habitats but the macroalgal beds, reaching its highest densities on the reef flat and fore reef (19.67 ± 1.24 and 14.45 ± 1.53 ind/40 m^2, respectively). Juveniles from this species inhabited all habitats but were found more densely on the reef flat (6.33 ± 0.75 ind/40 m^2). The Cocoa damselfish *Stegastes variabilis* adults were only observed on the fore reef (1.47 ± 0.67 ind/40 m^2), and its juveniles reached their highest density on the macroalgal beds (7.80 ± 0.51 ind/40 m^2). Sea urchins were more numerous on the reef flat (21.00 ± 1.34 ind/40 m^2) and the fore reef (19.33 ± 1.65 ind/40 m^2) (Fig. 4).

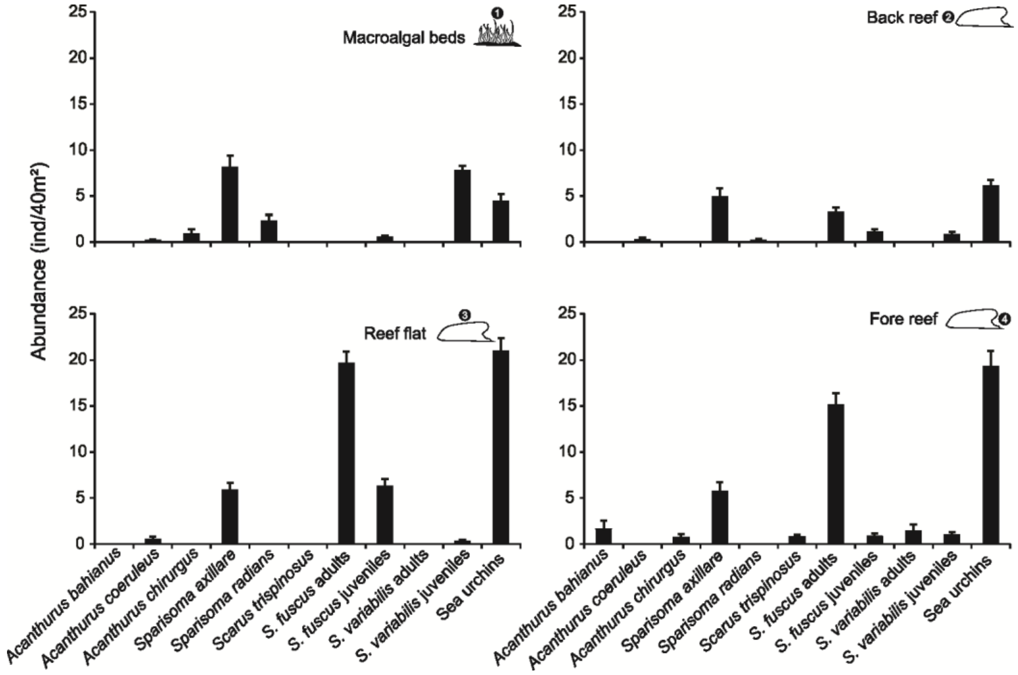


Fig. 4 - Distribution of competitors between the different habitats. Bars indicate standard error.

DISTRIBUTION OF SPARISOMA AXILLARE

Juvenile *S. axillare* had distinct habitat occupation according to their sizes (Pseudo-F = 29.31, $p < 0.01$, all pair-wise t tests with $p < 0.01$). Smaller individuals were primarily found on the macroalgal beds and reef flat, whereas individuals greater than 5.0 cm in total length reached higher density on the back and fore reefs. Individuals from size class 2 had higher densities on the macroalgal beds (2.87 ± 0.35 ind/40 m^2), but all size classes occurred within this habitat. *Sparisoma axillare* from size class 1 were not found on the back reef, where individuals in size class 3 had higher density (1.83 ± 0.27 ind/40 m^2). Only the smallest individuals were found on the reef flat, with greatest densities in size class 1 (2.67 ± 0.23 ind/40 m^2). Only larger juveniles were observed on the fore reef, with size class 4 being the densest (2.87 ± 0.40 ind/40 m^2) (Figure 5).

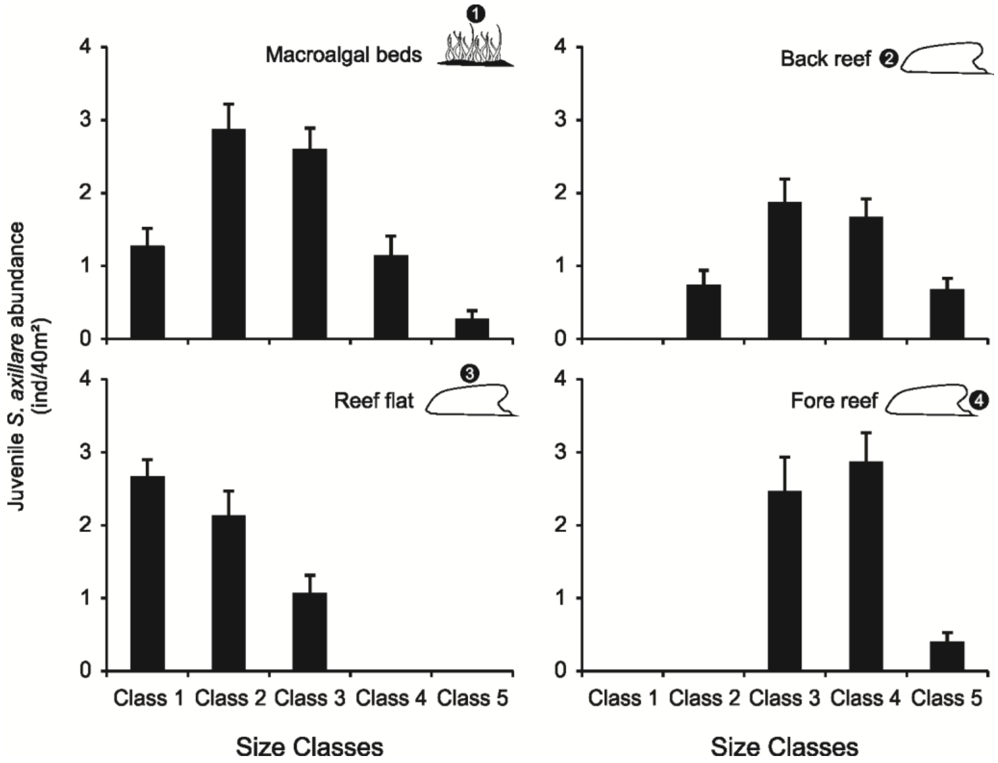


Fig. 5 - Size distribution of juvenile Sparisoma axillare between the different habitats. Bars indicate standard error.

INTERSPECIFIC INTERACTIONS AND FEEDING PATTERNS

Due to the differential occupation of other herbivores among the habitats, the attack rates towards *S. axillare* varied (Pseudo-F = 10.40, $p < 0.001$). The attacks were mostly performed by adult *Stegastes fuscus* (> 87%) and interactions with any other species did not exceed 6%. The lowest attack rates were observed on the macroalgal beds (0.00 ± 0.02 attacks min^{-1}) and intermediate values were found on the back reef (0.38 ± 0.01 attacks min^{-1}). The greater attack rates were observed on the reef flat and the fore reef (1.20 ± 0.02 and 0.98 ± 0.02 attacks min^{-1}, respectively), where adults of the Bluespotted damselfish *S. fuscus* occurs in higher densities. There were also distinct attack rates towards the different size classes of the Redeye parrotfish *S. axillare* (Pseudo-F = 5.86, $p < 0.001$), and the smaller *S. axillare* size classes generally suffered significantly lower rates (Table 2). On macroalgal beds, there were no significant differences for attack rates among size classes, all of which occurred at very low rates. *Sparisoma axillare* individuals from Size 1 were never targeted (Table 2).

Table 2 - PERMANOVA comparing the agonistic encounters towards different-sized juvenile *Sparisoma axillare* (attacks min-1); asterisks - significantly different groups in pair-wise tests; ns - non-significant.

Main test					
Source		Pseudo-F		p	
Habitat		10.40		< 0.001	
Size Class (Habitat)		5.86		< 0.001	
Habitats					
Habitats		Mean		SE	
Macroalgal beds		0.00*		0.01	
Back reef		0.38**		0.02	
Reef flat		1.20***		0.01	
Fore reef		0.98***		0.03	
Size Classes within Habitats					
Macroalgal beds			Back reef		
Size Class	Mean	SE	Size Class	Mean	SE
1	0.00^{ns}	0.01	2	0.00**	0.00
2	0.00^{ns}	0.01	3	0.00**	0.00
3	0.00^{ns}	0.02	4	0.73*	0.02
4	0.00^{ns}	0.02	5	0.80*	0.02
5	0.00^{ns}	0.01			
Reef flat			Fore reef		
Size Class	Mean	SE	Size Class	Mean	SE
1	0.00*	0.00	3	0.60*	0.03
2	1.27**	0.01	4	1.13**	0.04
3	2.33**	0.05	5	1.20**	0.02

Bite rates were negatively influenced by the distinct occupation pattern of adults of the Bluespotted damsefishl *S. fuscus* among the habitats (Pseudo-F = 21.75, $p < 0.001$) (Table 3). On the reef flat, where individuals had the highest attack rates, the lowest bite rates were observed (9.31 ± 0.19 bites min^{-1}). Juvenile *S. axillare* on the fore reef had intermediate bite rates (12.32 ± 0.35 bites min^{-1}). Juveniles on the macroalgal beds and the back reef had the highest bite rates and were considered to have similar average bite rates in pair-wise PERMANOVA tests (13.69 ± 0.32 and 15.85 ± 0.35 bites min^{-1}, respectively). Bite rates were also distinct between *S. axillare* size classes (Pseudo-F = 3.76, $p < 0.001$). However, the most attacked size classes had the highest bite rates, with the exception of individuals on the macroalgal beds, which did not show ontogenetic differences (Table 3). The highest bite rates were attained by size classes 4 and 5 on the back reef (18.18 ± 0.31 and 16.58 ± 0.31 bites min^{-1}, respectively), whereas the lowest values were observed for size class 1 on the reef flat (7.84 ± 0.28 bites min^{-1}).

Table 3 - PERMANOVA comparing the bite rates of different-sized juvenile Sparisoma axillare (bites min-1); SE - standard error; asterisks - significantly different groups in pair-wise tests; ns - non-significant

Main test					
Source		Pseudo-F		p	
Habitat		21.75		< 0.001	
Size Class (Habitat)		3.76		< 0.001	
Habitats					
Habitats		Mean		SE	
Macroalgal beds		13.69*		0.32	
Back reef		15.85*		0.35	
Reef flat		9.31**		0.19	
Fore reef		12.32***		0.35	
Size Classes within Habitats					
Macroalgal beds			Back reef		
Size Class	Mean	SE	Size Class	Mean	SE
1	13.11^{ns}	0.28	2	13.91*	0.40
2	13.95^{ns}	0.28	3	14.73*	0.36
3	14.00^{ns}	0.40	4	18.18**	0.31
4	13.84^{ns}	0.43	5	16.58**	0.31
5	13.56^{ns}	0.23			

Reef flat			Fore reef		
Size Class	Mean	SE	Size Class	Mean	SE
1	7.84*	0.28	3	9.91*	0.35
2	9.38**	0.12	4	13.16**	0.25
3	10.71**	0.17	5	13.89**	0.45

Bites were taken over various substrata, and electivity changed throughout habitats (Pseudo-F = 37.902, $p < 0.001$; all pair-wise t tests with $p < 0.001$) and among all size classes (Pseudo-F = 3.3337, $p < 0.001$). A high selectivity for filamentous algae was observed for smaller juveniles. On the reef flat, for instance, filamentous algae represented less than 3% of the total bottom coverage, but it represented up to ~ 40% of the feeding of *S. axillare* in size class 1. This high selectivity for filamentous algae tended to decrease and to be replaced by higher feeding rates on sand as juveniles attained larger sizes. Filamentous algae were especially selected by individuals of size class 5, which differed significantly in feeding preferences from the other size classes. On the fore reef, individuals from all size classes showed a marked preference for jointed calcareous macroalgae. Sheet-like (on the macroalgal beds and back reef) and thick-leathery (on the back reef) algal forms were ingested occasionally as accessory food items. Although encrusting calcareous and fleshy macroalgae occurred in minor proportions in all habitats, these forms were completely avoided by *S. axillare* (Fig. 6).

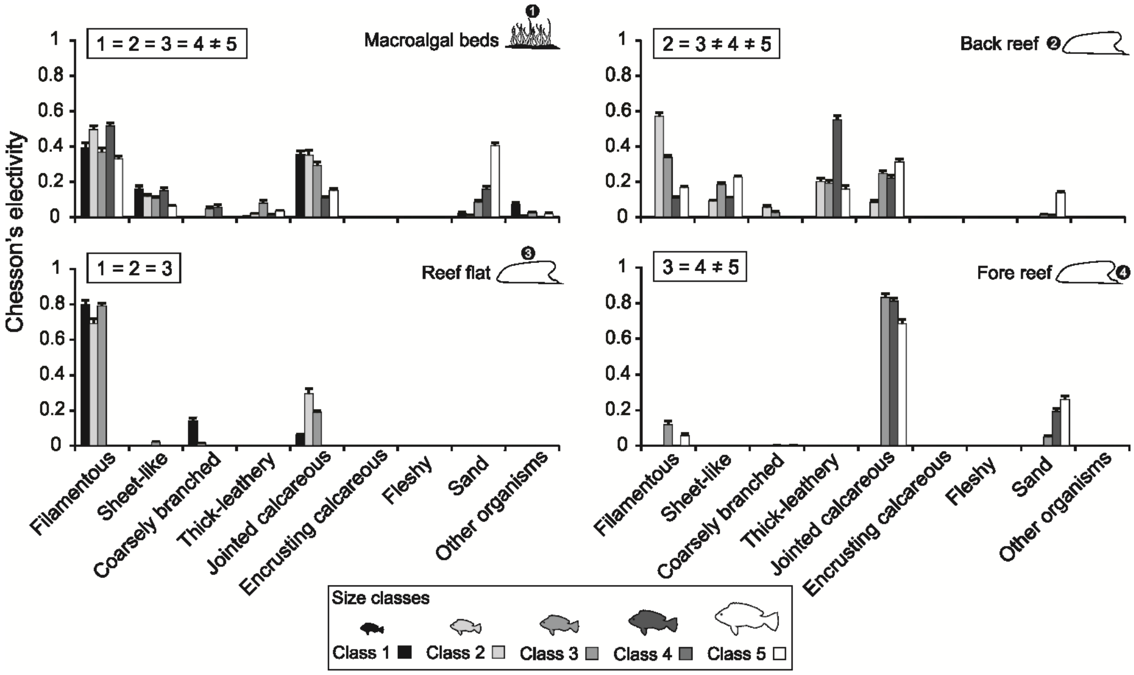


Fig. 6 - Feeding electivity in different size classes of juvenile *Sparisoma axillare* between the habitats. Bars indicate standard error. Upper-left boxes indicate significant differences between size classes found on pair-wise comparisons.

4 - Discussion

The studied algal-dominated coral reefs provided different habitats in terms of substrate composition, which significantly influenced the associated herbivore guild. In particular, juvenile *Sparisoma axillare* showed differences in their habitat use by size, showing habitat segregation and differences in behavior through its early life on reefs.

Smaller *S. axillare* juveniles (< 5 cm) preferred to inhabit macroalgal beds and the reef flat, whereas juveniles larger than 5 cm were more abundant on the back and fore reefs, showing that habitat use greatly changes during the early developmental stages of this species. The absence of individuals smaller than 2.5 cm on the back and fore reefs is most likely due to differential mortality and/or migration as parrotfish seem to lack habitat selection during settlement, as noted in previous study (Tolimieri 1998). Spatial variation on herbivore distribution as observed herein can still take place due to effects other than habitat differences, such as historical processes and chance events, and in this case the clarification of such patterns would require a different sampling design, including several sites for each habitat. This brings a caveat to the conclusions we draw here on abundance patterns. Nevertheless, it was observed on previous study that *S. axillare* recruitment rates, damselfish populations and algal cover are maintained spatially and over time (Ferreira *et al*. 1995; Gaspar 2006; Feitosa *et al*. 2012b), being very likely that juvenile *S. axillare* distribution patterns observed here are due to these habitat differences. In addition, larval availability is expected not to differ among the habitats addressed herein, considering their proximity to each other and the local circulation patterns. Thus, post-settlement events most likely determine the observed patterns of juvenile zonation, by altering fitness and survivorship after settlement. Interspecific interactions, e.g. attacks by damselfish, may enhance the predation risk of juveniles while they are focused on avoiding territorial herbivores (Sweatman & Robertson 1994). It was observed herein that attacks towards *S. axillare* increased as juveniles grew larger, suggesting that the occurrence of juvenile *S. axillare* within habitats dominated by adult *S. fuscus* is reduced with growth.

Damselfish territoriality had a negative effect on the patterns established during the settlement of the Stoplight parrotfish *Sparisoma viride* in the Caribbean, and the persistence of new recruits in habitats dominated by these fish was reduced (Tolimieri 1998). Conversely, in the present study, *S. axillare* recruits (> 2.5 cm) were more abundant in the environment with the greatest abundance of damselfish, primarily due to cryptic coexistence within their territories. Individuals in this size class were observed to differ from other juveniles in their overall foraging and behavioral patterns, closely resembling a cryptic reef fish. They stand static in a curved position over the substrate, blending in color to the predominant algae covering it, occasionally moving to forage, which occurs in sparse bouts. Cryptic reef fishes are extremely benthic-attached and generally present inconspicuous colors (Deloach and Humann 1999), remaining motionless inside holes, crevices and caves or besides coral and algae (Depczynski and Bellwood 2004). Generally, larger sizes or groupings have been thought to be advantageous for overcoming territorial defense by damselfish (Robertson 1976; Bruggemann *et al.* 1994; Pereira *et al*. 2012). However, in this study *Stegastes fuscus* seems to ignore the presence of the Redeye parrotfish *S. axillare* recruits and early juveniles. This cryptic coexistence seems to be very advantageous for newly settled *S. axillare* as damselfish may exclude larger grazers, greatly reducing intra- and interspecific competition for smaller individuals.

There is little evidence that scarids have strict habitat requirements. Instead, they appear to be habitat generalists and their biomass is weakly related to the cover of particular reef feeding substrata (Gust 2002). However, this study demonstrates that the cover may influence protection to juvenile parrotfish. For instance, the high canopy of *Sargassum* can provide more shelter than the densely packed jointed calcareous macroalgae cover (similarly to other Fucales species *sensu* Bulleri *et al.* 2002). Higher densities of juvenile may be attributed to a combination of shelter availability (lower post-settlement mortality), low wave energy (Williams 1982; Russ 1984a) and lower damselfish aggression (Tolimieri 1998). For *S. axillare*, food availability seems to have less influence on juvenile distribution, as individuals of the same size were capable of relying on existing food sources in each habitat. Similarly, *Sparisoma viride* prefers to inhabit habitats dominated by *Dictyota* spp. in previous study, regardless of its occasional use as food (Paddack & Sponaugle 2008).

Competition with territorial damselfishes may reduce the bite rates of parrotfishes (Robertson *et al.* 1976) or limit access to food resources (Robertson *et al.* 1979; Bruggemann *et al.* 1994). Consistently, it was observed herein that individuals who inhabited sites with higher densities of territorial damselfishes, especially the highly aggressive adults of the Bluespotted damselfish *S. fuscus*, presented the lowest overall bite rates. In circumstances of reduced competition thus less exposure to predators, individuals can direct energy to growth and reproduction instead of predator avoidance (Lima 1986). Additionally individuals may forage more regularly and beyond territory boundaries (Madin *et al*. 2010; Jones & Dornhaus, 2011). Body mass loss and decreased feeding rates have also been linked to the cost of anti-predatory defense (Perez-Tris *et al.* 2004). This work recorded that as juvenile *S. axillare* grew, their bite rates also shifted, with larger juveniles attaining higher feeding rates. This change from cryptic to roving behavior may also be due to variations in feeding preferences. Parrotfishes undergo a shift from omnivorous feeding to feeding on plant materials, which occurs during growth from 1.0 to 3.0 cm TL (Bellwood 1986), a transition associated with changes in their morphology (Bellwood 1988; Bruggemann *et al.* 1994; Chen 2002). Thus, most likely growth triggers the movement out of damselfish dominated areas, with cryptic behavior being replaced by the roving habit.

Given it is necessary for parrotfish certain time to be able to feed on algae, recruits are likely to be more selective browsers, with lower feeding rates focused on more nutritious food (Bellwood 1986). In adulthood, however, *Sparisoma axillare* have few differences in their resource use and feeding preferences (Bonaldo *et al.* 2006). In the present study, a marked shift in the feeding preferences of juveniles was detected, both among differently sized individuals and among habitats with distinct cover (i.e., distinct food availability). This trophic plasticity may be an essential feature to inhabit an altered environment such as these algal-dominated reefs, as the resulting algae community may alter access to preferred food. For instance, the sympatric parrotfishes *Sparisoma amplum* and *Scarus trispinosus,* are known to feed on live coral (Francini-Filho *et al.* 2010), a scarce food resource in the studied habitats (< 1.5%), which may have influenced their very low densities in censuses performed herein.

In all the analyzed habitats, *S. axillare* was observed to selectively browse for filamentous algae, an algal resource known to be highly productive and palatable (Hay 1991). However, this preference for filamentous algae tends to diminish as *S. axillare* grows, when they begin to ingest more sand, which occurs more obviously at sizes greater than 10 cm TL. Adults from this species (> 20 cm) rely primarily on detritus (Ferreira & Gonçalves 2006), which is the most likely reason for feeding on sand. Ontogenetic shifts in feeding greatly reduce intraspecific competition, which can be quite advantageous because this species also suffers from high rates of interference competition with territorial damselfish.

It was recorded herein that on the reef flat and on the fore-reef habitats juvenile *Sparisoma axillare* bites were mostly directed to the highly abundant jointed calcareous forms. Jointed-calcareous macroalgae have a complex branching morphology and a high degree of calcification, and some species, such as *Halimeda* spp., also produce secondary terpenoid compounds (Paul & Fenical 1983; Hay & Fenical 1988), causing them to be one of the functional groups most resistant to herbivory (Steneck & Watling 1982; Littler & Littler 1984; Hay 1991; Hay 1997). In addition, this macroalgae is a poor source of nutrition (Littler & Littler 1984). These algae were also extensively grazed by adult *S. axillare* in previous studies (Bonaldo *et al.* 2006; Francini-Filho *et al.* 2010). This type of compound does not appear to strongly deter herbivory by *S. axillare* (as suggested by Bonaldo *et al.* 2006); less-palatable algae may also be an indispensable resource, considering the abundance of these algae across the analyzed habitats. Jointed-calcareous algae have the potential to accumulate detritus and epiphytic palatable algae, which are also known to be key food items for sympatric *Stegastes* damselfishes (Feitosa *et al.* 2012b). Thus, the nutritional quality of these macroalgae may be underestimated on a first look, also making them an essential food source given their high abundance on algal-dominated reefs.

Previous studies focusing on the impact of parrotfish on algae through consumption usually group together algal communities in an epilithic algal matrix. However, as shown here, the feeding preferences of these fish are greatly dependent of the species composition. Once a given reef becomes algal dominated, parrotfish can alter food selection and interspecific interactions depending on the resulting algal community. The potential for a parrotfish species to turn an environment back to a previous coral-dominated phase seems to be influenced by their food selection, which is, from the results of the present study, highly dependent on the algal species composition.

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Capítulo 4

Herbivory in Brazilian coral reefs: effects on algae biomass, cover and succession

João Lucas Leão Feitosa & Beatrice Padovani Ferreira

Artigo a ser submetido a Coral Reefs

Abstract

The herbivory is a indispensable component of coral reef systems, accounting for the control of algae biomass and cover, also shaping specific composition of algae assemblages. However, the role of herbivory in performing this proccesses in Brazilian coastal reefs, a distinctive reef system, is still unkown. Aiming to evaluate herbivory in Brazilian reef systems, three experiments applying herbivore exclusion through caging were performed, taking into account: (1) effects on algae biomass in six months; (2) effects on benthic cover in ten months; (3) effects on benthic succession in four months. Herbivore exclusion did not result in algae biomass increases, as reported for other reef systems. Nevertheless, an increase in filamentous algae cover and species richness was observed in herbivore exclusion treatments, which grew both epilithically and as epiphytes. With the increment of filamentous algae cover, a decrease in the cover of sheet-like and jointed calcareous algae occurred, and the latter group presented a positive relationship with temperature throughout the experiment. Filamentous algae also presented such relationship with temperature and during periods of higher turbidity the increasing in their cover was halted. Regarding algal succession, herbivore exclusion rendered the higher permanence of pioneer species, the filamentous algae. However, regardless of herbivore removal, algae assemblages returned to a state of jointed calcareous dominance, a late-successional stage in algal succession. The findings attained herein resulted from the low densities of scrapping herbivores, mostly parrotfish, capable of removing great portions of calcareous algae while feeding, opening space on the reef for coral to settle. This results emphasize the priority of management strategies focusing the coservation of this herbivore group, to assure the health of Brazilian reef environments.

Resumo

A herbivoria é um componente indispensável nos recifes de coral, sendo responsável pelo controle da biomassa e cobertura de algas, bem como molda a composição específica de suas assembleias. Entretanto, a função da herbivoria em realizar tais processos ainda é desconhecida para os recifes costeiros do Brasil, um sistema recifal distinto dos mais estudados pela literatura. Com o objetivo de avaliar a função da herbivoria nos recifes costeiros brasileiros, três experimentos utilizando a exclusão da herbivoria com gaiolas foram realizados, observando: (1) a influência da herbivoria na biomassa de algas em seis meses; (2) a influência da herbivoria na percentual de cobertura bentônica ao longo de 10 meses; (3) a influência da herbivoria na sucessão ecológica da cobertura bentônica ao longo de quatro meses. Foi observado que a exclusão da herbivoria não resultou em um aumento da biomassa de algas, como observado na literatura. Entretanto, foi registrado um aumento na cobertura e riqueza das algas filamentosas nos tratamentos de exclusão da herbivoria, que ocorreram de forma elítica e epifítica. Com o aumento da cobertura de algas filamentosas, foi observado uma diminuição na cobertura de algas folhosas e calcárias articuladas, onde o último grupo apresentou uma relação positiva com a temperatura ao longo do experimento. As algas filamentosas também apresentaram uma relação positiva com a temperatura e em períodos de maior turbidez o crescimento de sua cobertura foi interrompido. No experimento de sucessão, a exclusão da herbivoria resultou em uma maior continuidade das espécies pioneiras na sucessão ecológica, as algas filamentosas.

Entretanto, a independentemente da remoção da herbivoria a asesembleia de algas retornou a um estado de dominância de algas calcárias articuladas, um estado sucessional avançado. Os achados obtidos no presente estudo resultaram da baixa densidade de herbívoros raspadores (i.e. peixes-papagaio), capazes de retirar grandes porções de algas calcárias articuladas com sua alimentação, abrindo espaços no substrato para o assentamento de corais. Tais resultados salientam a prioridade da criação de estratégias de manejo voltadas para a preservação de tal grupo, para que a saúde dos ambientes recifais brasileiros seja garantida.

1 - Introduction

Coral reef herbivores affect the distribution and species composition of the macroalgae community, individual algae productivity, morphology, chemical composition and connect primary production to higher level consumers (Hay 1991). By algae consumption, herbivores mediate coral/algal competition for substratum, enhancing coral recruitment and survival (Mumby et al. 2006; Hughes et al. 2007a; Mumby 2009). Besides being restricted by top-down control through herbivory, algal growth in reef systems worldwide is recognized to be influenced by bottom-up control, mainly by nutrients availability as well. Nevertheless, as a general pattern, herbivory is the primary factor driving macroalgal abundance, yet, nutrient enrichment can interact with herbivory to magnify its effects on algae communities (Burkepile and Hay 2006).

Despite these overall patterns of macroalgal control, distinct effects of herbivory are found when taking into account which groups compose the herbivore community. For instance, sea urchins dominance results in a filamentous algae community while a greater diversity of algal functional groups and higher standing crop are found when fish are the major algae consumers (McClanahan 1997). Studies revealed that even within a particular herbivore community, each species' feeding preferences have a prime role in shaping the macroalgae community, and that various species act in synergy to control the overall algae growth (Burkepile and Hay 2008, 2010, 2011).

Herbivore fishes are classified into three functional groups according to their feeding modes: excavators, scrapers and grazers; that act complementarily in macroalgal control (Bellwood et al. 2004). Excavator species have powerful jaws that gouge the substratum, exposing the reef matrix for settlement of corals and incrusting calcareous algae (Bellwood and Choat 1990; Bellwood et al. 2003, 2004). Only large parrotfish are morphologically adapted to perform this role, generally leaving profound scars while feeding (Bellwood and Choat 1990; Bonaldo et al. 2011). Smaller parrotfish act generally as scrappers, having a weaker bite and feed removing algae and sediment, facilitating the survival and growth of coral (Steneck 1988; Hunte and Wittenberg 1992; Bellwood et al. 2004). Grazers or browsers remove portions of erect macroalgae when feeding, controlling their overgrowth and shading effects on coral (Hughes 1994; McCook et al. 2001), a role performed widely by surgeonfishes.

Despite this vast array of feeding modes, few species rely on algae as their sole food source (Hay 1991). Moreover, striking regional differences in species richness and composition are found in coral reefs. Caribbean reefs, for example, hold only a fraction of the species found on the Great Barrier Reef: approximately 28% for fish species (Bellwood and Wainwright 2002). This reduction results in less functional redundancy, i.e. fewer species in a functional role, to this reef system (Bellwood et al. 2004; Cvitanovic et al. 2007). Fewer herbivore species may render an assemblage more vulnerable to catastrophic phase shifts as from coral-dominated to a macroalgal-dominated environment, particularly when subject to human exploitation and impacts (Bellwood et al. 2004; Cvitanovic et al. 2007). In Brazil, the reef ichthyofauna is similar to the Caribbean basin, composed of the same main families, however with even fewer species (Maida and Ferreira 1997). For instance, only two parrotfish species are recognized as excavators, effectively opening space for coral to settle, a role performed only by large adult fish (Francini-Filho et al. 2008).

Besides being a peculiarly low-diversity system, Brazilian reefs are characterized as being built by endemic coral species, composed mainly by massive forms (Maida and Ferreira 1997; Leão et al. 2003). Most reefs in Brazil are distributed only a few kilometers or less from the coastline, as a result of geological conditions at the time of their formation (see Leão et al. 2003 for a thorough explanation). The reefs from the northeastern coast are particularly subjected to harsh conditions of sedimentation, that can reach up to 99 mg.cm^{-2}.day^{-1} (Macedo 2009), whereas in the Caribbean this values seldom exceeds 10 mg.cm^{-2}day^{-1} (Rogers 1983). Additionaly, these reefs are also heavily affected by fisheries, given their proximity to the shore and historical subsistence of coastal communities on fishing. Parrotfishes have been increasingly targeted by spear fishing in coastal reefs in the last decades (Ferreira and Gonçalves 1999).

This particular fishery targets large adult fish, i.e. excavator parrotfishes, being also more difficult to monitor and manage. Locally, parrotfishes are also main targets of trap fishing, yielding catches that reach more than 250 tons per year at the Brazilian monitored fishing sites; most of which is intended to foreign markets (Marques and Ferreira 2010; MPA 2011). Aiming to attenuate the fishing impacts, marine protected areas have been designed along these coastal reefs. The Costa dos Corais Marine Protection Area, is the largest conservation unit in the Southwestern Atlantic encompassing 135 km of coastline and has been protected by federal law since 1997. In

1999, fishing and tourism activities were prohibited in approximately 3 km² of this area. A significant increase in lutjanids populations was observed within this area (Ferreira et al. 2000), proving the potential of this measure in the recuperation of stocks (Ferreira and Maida 2006). Nevertheless, large parrotfish densities remain very low, and individuals with more than 20 cm occurs in densities of less than 2 individuals per 100 m² (Ferreira and Maida 2006). Surgeonfishes, on the other hand, are historically of little interest for fishing in this area (Ferreira and Maida 2006), and occur in reasonably stable populations (Lino and Ferreira unpub. data).

In this scenario surgeonfish and damselfish dominate the herbivore community in terms of biomass, while parrotfishes persist with depleted populations. Given the rising threats imposed by parrotfish fishing worldwide, which are particularly menacing to low redundancy systems, we aimed to address the role of a herbivore community that lacks key functional groups. Three distinct aspects of herbivore function on algal community were then experimentaly examined: (1) influence on algal biomass; (2) influence on algal cover; (3) influence on algal succession.

2- Material and Methods

STUDY AREA

The present study was performed on the Tamandaré reef complex, situated off the northeastern coast of Brazil, the region where the only hermatypic coral formations in the Southwestern Atlantic are found. The area has a coastal tropical climate with average temperatures near 30º C during the dry season (from November to May) and 24º C during the rainy season (from June to October) (Maida & Ferreira 1997). Given a distinctive coral fauna, these reefs grow as isolated columns that can reach 5-6 m and then laterally expand just below the surface, creating large reef flats (Dominguez *et al.* 1990; Ferreira *et al.* 1995; Maida & Ferreira 1997). Despite the lack of long-term quantitative records, there are clear indications that a reduction on live coral cover took place in these reefs. Coral cover diminished from a approximately 25% in 1960s (as indicatede by Jaques Laborel) to less than 5% in the 2000s (Ferreira & Maida 2006). Currently, algae predominate among organisms covering the reef flats, where jointed calcareous are the most abundant group, primarily composed of *Halimeda opuntia* and *Jania* spp (~40-70%). Sessile animals are only found in minor proportions; zoanthids and corals occur sparsely and comprise ~2% each (Feitosa and Ferreira 2014).

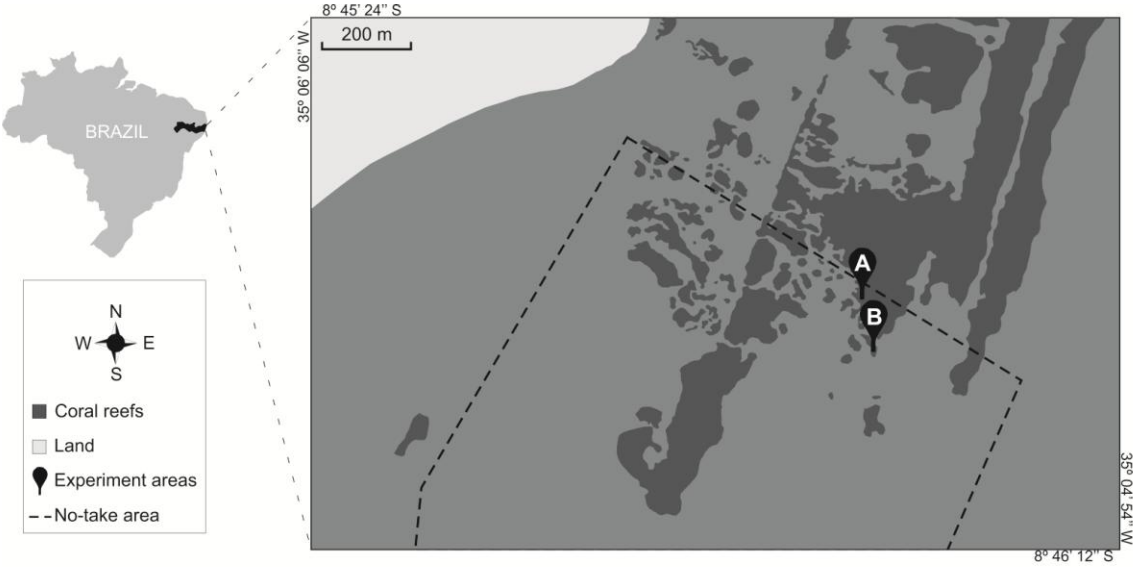

Fig 1 - Map of the study are showing the sites for experiments installation

The study area is within the limits of the Costa dos Corais Marine Protection Area, in which, fishing and tourism activities were prohibited in approximately 3 km^2 of its area, including five large reefs and several reef patches. Within this no-take area, two reef patches about 100 meters apart were selected for experimental procedures, based on lower turbidity and wave surge and greater abundance of roving herbivores (Fig 1). These reefs are typical coastal reefs of the Southwestern Atlantic Region, where reefs occur very close to the coastline (less than few kilometers apart) and are found in shallow waters (less than 7 meters deep). In the study area, higher abundances of parrotfish are found with higher wave surge. Additionally, fishing play a major role that enhances this trend, as parrotfishes are more strongly fished inside protected lagoonal areas. Inside Costa dos Corais no-take area, after 10 years of fishing prohibition, sites protected from wave surge parrotfish density reaches up to ~0.07 individuals/m², while nearly twice these densities can be found in exposed sites and channels (Ferreira et al. unpublished data). In contrast, in highly fished sites parrotfishes are found in densities as low as 0.019; in the particular area where experimental procedures were conducted, parrotfish densities are of 0.076 individuals/m² (Ferreira et al. unpublished data).

EXPERIMENTAL DESIGN AND DATA COLLECTION

The herbivore exclusion experiments were designed with three treatments: (1) full cages excluded both fishes and sea urchins thus simulating a herbivore-depleted environment; (2) partial cages had the same dimensions however were covered with nets only on the sides - excluding sea urchins, but the open roof enabled feeding by herbivorous fishes; (3) Open plots were utilized as controls for herbivory in the algal community. Full and partial cages consisted of 40 x 40 x 25 cm stainless steel frames, which were fixed to substrate by 15 cm stainless steel stakes. This frame was covered with 3 cm screen mesh, mounted with cable ties (SupFig 1). The net extended over the surrounding substrata (~10 cm), to prevent herbivores penetration underneath the cages. Open plots were marked on the reef by placing nails at four opposite corners of a 40 x 40 cm square. All plots were cleared of fouling organisms with plastic brushes every two weeks. Open-sided control cages were not included, as previous studies indicated that these plots attracted predators that sheltered inside the plots, thus creating artifacts on herbivores behavior or density (Burkepile and Hay 2009, authors' pers. observ.). Nevertheless, artifacts on algal development, water flow and sedimentations from cages built of mesh size of 3 cm are found to be minimal (Miller and Hay 1998; Miller et al. 1999; Smith and Smith 2001; Mcclanahan et al. 2003). Moreover, this mesh size permits small fishes, such as small damselfishes, parrotfishes and wrasses, to feed inside the plots. This feature was observed in previous work and thought to imply minimal effect in algal development (McClanahan et al. 2002; Mcclanahan et al. 2003; Sotka and Hay 2009; Bennett et al. 2010) or even found to balance potential artifacts caused by mesograzers (e.g. crustaceans and gastropods) that could use cages as refuges (Lewis 1986).

With this experimental design, three experiments were carried out: (1) six months of exclusion (April to September 2013), for evaluating herbivory effects on algae biomass and changes in epiphytic algae at the end of the period; (2) ten months of exclusion (April 2013 to February 2014), to assess herbivory effects on benthic cover throughout the period; (3) 4 months of exclusion (October to February 2014) after full removal of all organisms within plots, to evaluate herbivory effects on algal succession throughout the period. Number of sets was determined as four for biomass analysis (after Feitosa et al. 2012) and for cover estimation a pilot survey was carried out, in which the minimal replicates was determined as six, after stabilization of the main algae groups mean and variance on cumulative number of samples (SupFig 2).

Algal samples scrapped from the experiment 1 were frozen and taken to the laboratory where both epilithic and epiphytic macroalgae species were identified to the lowest possible taxonomic levels. Epilithic algae samples were then dried at 60 °C for 24 h and weighed (0.01 g precision). Dry weights were used to estimate algal biomasses in this samples. The other two experiments were monitored every two weeks with photoquadrats using CPCe 4.1 (Kohler & Gill 2006). In this software 100 points per cage were randomly selected at which the benthic organisms were identified. Macroalgae were assigned to ecological groups according to their morphological and functional-forms as: filamentous, sheet-like, coarsely branched, thick leathery, jointed-calcareous or incrusting calcareous (Littler and Littler, 1984). Genera included in each functional-form category are listed in Table. 1.

DATA ANALYSES

In order to compare algae biomass an one-way ANOVAS was applyed for each functional form, utilizing data on experiment 1, collected after six months of caging. The second experiment was analyzed through linear mixed-effects modeling (LME). This approach permitted the inclusion of both categorical and continuous variables in a repeated measures design, most appropriate for monitoring the algal community using non-independent samples over time. The categorical predictors were the three treatments applied (full cages, partial cages and open plots). Continuous variables selected for inclusion in models were environmental parameters acquired through remote sensing and which may influence and/or reflect seasonal shifts in the algal community. Images derived from Moderate Resolution Imaging Spectroradiometer (MODIS) on NASA's Aqua satellite were utilized for estimating Sea Surface Temperature (SST), Chlorophyll a concentration (Chla), Photosynthetically Available Radiation (PAR), Particulate Organic Carbon (POC) and Particulate Inorganic Carbon (PIC). This radiometer is present in both Terra and Aqua satellite and provides a complete global coverage in 1 to 2 days intervals. Mapped images with a 4.63 km resolution (Level 3) containing monthly averages for the selected parameters were processed through the software SeaDas 7.0.2. By utilizing monthly averages, instances of missing or red flag data could be avoided. Prior to model fitting, these parameters were tested for collinearity using Pearson's correlation coefficient. On this analysis, Chla, PAC, POC and PIC showed significant correlation between each other (SupTable 1, SupFig 3) and therefore only Particulate Organic Carbon (POC) was chosen to be included in the model. Time of closure was also considered as a continuous variable in the models and referred to experiment time in days from installation. The LME was fitted using the package *nlme* in R software, where interactions between treatment and the continuous variables were considered in the full model. The backward stepward removal of non-significant terms from the full model, based on log-likelihood ratio tests, was applied for model selection (Zuur et al. 2009). A repeated measures PERMANOVA was applied in the third experiment data, for comparing changes in the whole algae community using two factors: treatments (same levels described above) and time (between months), using Bray-Curtis similarities. Data derived from percentage cover estimation (second and third experiments) were arcsine-transformed.

3 - Results

First experiment: Effects on algal biomass and epiphytes

Macroalgae dominated all plots and a total of 36 taxa of algae were found on samples. The most dominant algal taxa were the jointed calcareous *Amphiroa*, *Halimeda opuntia* and *Jania*; the sheet-like *Dictyopteris delicatula*; the filamentous: *Gelidium crinale*; and the coarsely branched: *Hypnea spinella*, *Laurencia*, *Caulerpa racemosa* and *Gelidiella acerosa* (Table. 1). Other organisms composed a nearly negligible part of substrate cover; corals, for instance, generally covered < 5% of the plots. No other sessile organisms competed for substrate except for zoanthids, which never exceeded 2% of the total cover.

Biomass did not show significant differences between treatments (Filamentous: F = 4.20, p = ns; Coarsely branched: F = 0.66, p = ns; Jointed-calcareous: F = 2.07, p = ns). Sheet-like algae were found with a biomass greater than 0.01g only inside fully caged treatments (Table. 1). Despite these little differences in biomass, a higher number of epiphytic algae species were found inside full cages (26 genera, against 18 and 13 inside partial and open plots, respectively). These epiphytes were mainly filamentous forms, and the red algae *Griffthisia*, *Polysiphonia*, *Wrangelia* and *Antithamnion* were most common inside herbivore exclusion treatments. Jointed-calcareous and coarsely branched macroalgae hosted from 1.7 to 3 times more epiphytes inside full cages than other treatments (Table. 1).

Table. 1 - Algae species found inside biomass experiments. Biomass for each functional group are given in bold (Mean per plot ± Standard error). Number of epiphytic species harbored by epilithic algae in each functional form are in bold and italicized. D = dominant, F = frequent, C = common and R = rare species. NI = non-identified species.

	Epiphytic algae			Epilithic algae		
Functional Group/Species	Cage	Partial	Open	Cage	Partial	Open
Coarsely-branched				**1.83±1.02**	**0.75±0.16**	**3.48±2.72**
				12	***4***	***4***
Acanthophora spicifera				R	R	R
Botriocladia occidentalis				R		
Caulerpa racemosa	R			F		F
Gelidiella acerosa	R			F	F	C
Gracillaria				R		
Hypnea musciformis					F	
Hypnea spinella	C	F		C	F	D

Laurencia	R	R		D	R	
Palisada perforata		R	R			R
Filamentous				**0.90 ±0.18** ***8***	**2.33 ±0.55** ***9***	**0.73 ±0.47** ***9***
Acrochaetaceae NI	C	R				
Aglaothamnion	F					
Antithamnion	C	R				
Antithamnionella	R		R			
Bryopsis plumosa	R		R			R
Calithamnion	R					
Ceramium	D	D	D			
Champia			R	R		
Cladophora	C	R				
Dipterosiphonia	F	R	R			
Ectocarpaceae NI	F					
Gelidium crinale	F	F	R	C	D	D
Griffthisia	D	F	F			
Gymnothamnion	R					
Herposiphonia	D	C	D			
Heterosiphonia	R					
Neosiphonia	D	C	F			
Polysiphonia	D	R				
Pterocladiella						R
Spyridia						R
Wrangelia	D	F	R			
Jointed-calcareous				**48.35±19.84** ***24***	**26.18±12.73** ***8***	**9.03±2.70** ***14***
Amphiroa		R		D		F
Halimeda opuntia				D	F	F
Jania	R	F		C	F	C
Incrusting calcareous						
Incrusting calcareous NI	D	F	F			
Sheet-like				**5.00 ± 1.84** ***9***	**< 0.1** ***6***	**< 0.1** ***7***
Dictyopteris delicatula	C	F	C	F	F	F
Dictyota	R					

SECOND EXPERIMENT: EFFECTS ON ALGAL COVER

Selected LME models indicated that most groups changed significantly along the second experiment. Most algae functional-forms showed significant interaction between the variables treatment and time, i.e. herbivore-manipulated plots differed on cover throughout the time. This interaction was not significant on log-likelihood ratio tests only for coral and coarsely branched algae (Table. 2) and for the latter, time showed to hold no relationship to this group's cover at all (F= 0.74, p = ns, Table. 3). Particulate organic carbon (POC) exerted influence only on algae and no interaction between POC and treatments for herbivory was found for any group (Table. 2). Despite being selected for composing the models, POC only had significant relationships with filamentous and coarsely branched algae cover (F= 28.6, $p < 0.001$ and F = 4.47, $p < 0.05$, respectively, Table. 3). Sea surface temperature (SST), was only found to have effect in jointed-calcareous (F = 6.9, $p < 0.01$) and filamentous algae, where in the latter this effect differed between treatments (F = 7.59, $p < 0.001$, Table. 3).

Filamentous algae was influenced by POC with no interaction between the treatment factor. SST and time, conversely, interacted with the distinct treatments variable, being significant on post-hoc tests on cage plots (Table. 4). At the beginning of the experiment, filamentous algae covered ~10% of the substrate in all plots and fluctuated between this value and 20% in all plots for the following five months. These months correspond to the rainy season, which presented the highest levels of organic carbon and a drop of nearly 3ºC in SST. From October onwards temperature increased, and filamentous algae greatly thrived inside full cages, a pattern not observed on partial and open plots. By the end of the experiment, filamentous algae in full cages reached more than three times the cover observed in other treatments (Fig 2).

Jointed calcareous algae presented, in general, a positive relationship with temperature, decreasing in cover until September, but increasing readily with higher temperatures. Nevertheless, such response was delayed and less pronounced inside full cages, where these algae had 10% less cover than other plots by the end of the experiment. Sheet-like algae changes were only related to time, and appeared to decrease in cover with time as an overall pattern, proved to be significant for all plots (Table. 4). Yet, this reduction was more pronounced inside full cages (Fig 2). Coral and incrusting calcareous algae, both found to cover low percentages of the substrate (< 5%) were found to significantly change over time, however without any particular trend.

Table. 2 - LME model selection for each functional group. Factors: treat = Treatment; time = Time of enclosure; sst = Sea Surface Temperature; poc = Particulate Organic Carbon. Interaction terms between variables and are listed as "categorical variable: continuous variable".

Group	Term	Log-Likelihood	AIC	p
Filamentous	**Interactions**			
	Full	-1037.048	2102.096	
	treat:time	-1058.029	2140.059	< 0.0001
	treat:sst	-1047.568	2119.136	< 0.0001
	treat:poc	-1037.317	2098.633	ns
	Single Factors			
	treat + poc + treat:time + treat:sst	-1037.317	2098.633	
Jointed calcareous	**Interactions**			
	Full	-1144.31	2316.62	
	treat:time	-1148.083	2320.165	< 0.05
	treat:sst	-1147.062	2318.125	ns
	treat:poc	-1144.572	2313.144	ns
	Single Factors			
	treat + sst + poc + treat:time	-1147.463	2314.927	
	treat + sst + treat:time	-1156.835	2331.669	<.0001
Sheet-like	**Interactions**			
	Full	-1115.993	2259.986	
	treat:time	-1119.025	2262.05	< 0.05
	treat:temp	-1117.806	2259.613	ns
	treat:poc	-1116.11	2256.22	ns
	Single Factors			
	treat + sst + poc + treat:time	-1118.003	2256.006	
	treat + poc + treat:time	-1118.371	2254.742	ns
	poc + treat:time	-1118.978	2251.956	ns
	treat:time	-1124.354	2260.707	< 0.001
Coral	**Interactions**			
	Full	-326.5273	681.0547	
	treat:time	-326.6174	677.234	ns
	treat:temp	-327.5722	679.1445	ns
	treat:poc	-327.3305	678.6611	ns
	Single Factors			
	treat + time + sst + poc	-329.4414	674.8828	
	treat + time + poc	-329.5081	673.0162	ns
	time + poc	-330.6042	671.2083	ns
	time	-331.2082	670.4164	ns
Incrusting calcareous	**Interactions**			
	Full	-628.1986	1284.397	
	treat:time	-633.1889	1290.378	< 0.001
	treat:sst	-631.0531	1286.10	ns
	treat:poc	-629.2910	1282.58	ns
	Single Factors			
	treat + poc + sst + treat:time			
	poc + sst + treat:time	-636.3466	1288.693	< 0.05
Coarsely branched	**Interactions**			
	Full	-714.1538	1456.308	
	treat:time	-714.3477	1452.695	ns

treat:sst	-714.5415	1453.083	ns
treat:poc	-714.3138	1452.628	ns
Single Factors			
treat + time + sst + poc	-715.0140	1446.028	
treat + time + poc	-715.1635	1444.327	ns
treat + poc	-717.3677	1446.735	< 0.05

Table. 3 - Significance of the variables for the LME models selected. Abbreviations are listed in Table 2.

	Filamentous		Jointed calcareous		Sheet-like		Coral		Incrusting calcareous		Coarsely branched	
Source	F	p	F	p	F	p	F	p	F	p	F	p
treat	28.68	< 0.001	4.54	< 0.05					2.52	ns	1.47	ns
time							12.62	< 0.001			0.74	ns
sst			6.9	< 0.01					2.98	ns		
poc	28.6	< 0.001	0.8	ns	3.68	ns			3.61	ns	4.47	< 0.05
treat:time	32.7	< 0.001	14.6	< 0.001	20.58	< 0.001			5.63	< 0.001		
treat:sst	7.59	< 0.001										

Table. 4 - Significance of the interactions for each treatment level.

	Filamentous		Jointed calcareous		Sheet like		Incrusting calcareous	
Source	t	p	t	p	t	p	t	p
Cage:time	9.57	< 0.001	1.15	ns	7.80	< 0.001	-0.90	ns
Partial:time	-1.44	ns	4.63	< 0.001	3.83	< 0.001	-4.01	< 0.001
Open:time	-0.43	ns	5.67	< 0.001	4.48	< 0.001	-1.89	ns
Cage:SST	2.73	< 0.01						
Partial:SST	-3.85	< 0.001						
Open:SST	-0.65	ns						

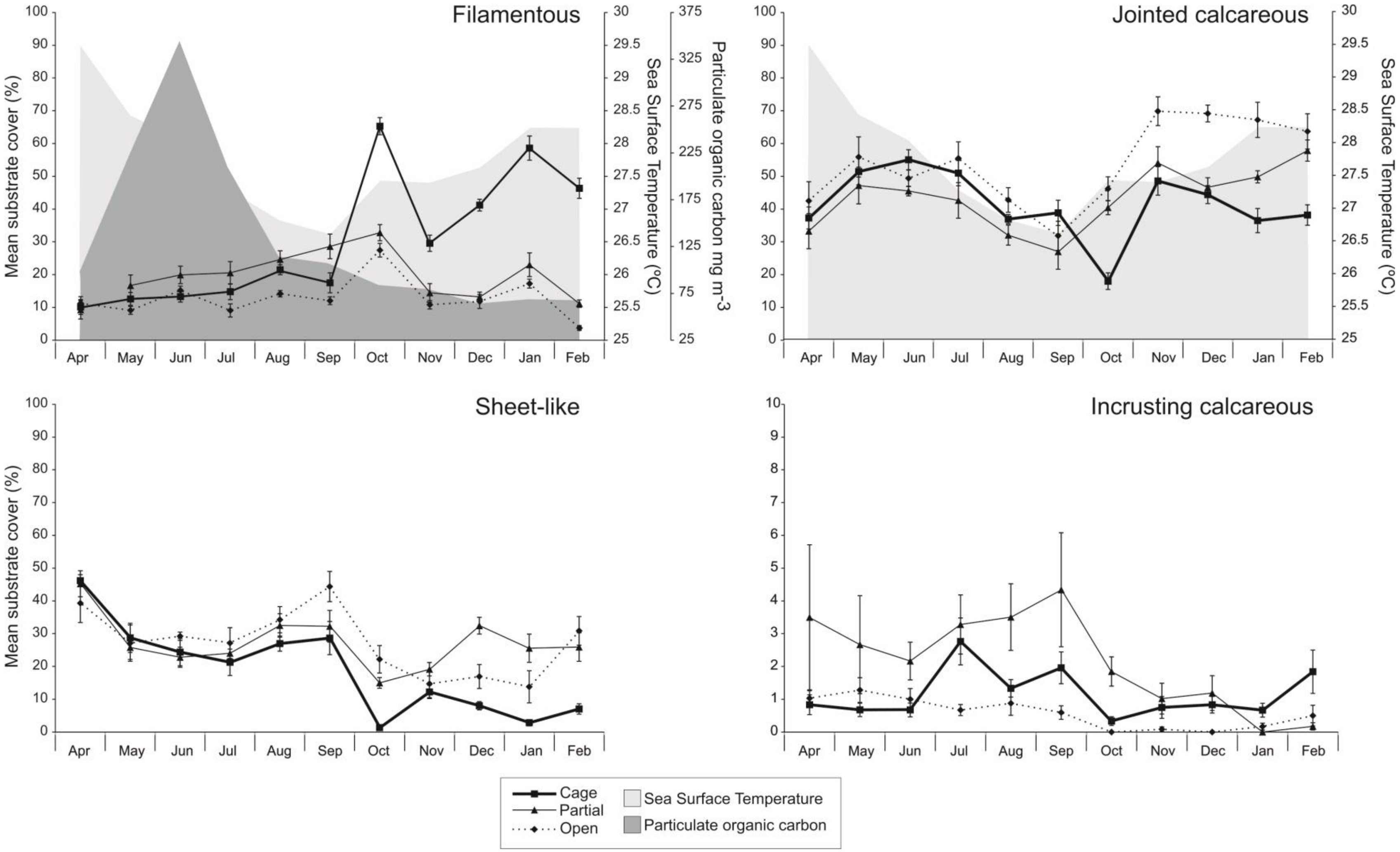

Fig 2 - Mean substrate cover for the most abundant functional groups of algae inside each treatment. SST and POC fluctuations are showed only for those groups which they were found to have significant influence on LME. Bars indicate standard error.

THIRD EXPERIMENT: EFFECTS ON ALGAL SUCCESSION

On the third experiment, there were significantly distinct patterns of ecological succession both between treatments and time, as well as in their interaction (Table. 5). In general, at early successional stage algae community was composed primarily of filamentous forms. In November, sheet-like macroalgae dominated plots, however full cages community was already significantly distinct from open plots (Table. 5, pair-wise tests). Starting from November, partial and open plots presented a tendency of decreasing in filamentous and sheet-like cover, while fully caged plots increased in filamentous cover until January. Jointed calcareous settled and grew to dominate all plots at the end of the experiment in about four months. At this point the three treatments differed in cover, and full cages held over 10% more coverage of filamentous algae than other plots (Fig 3).

Table. 5 - Repeated measures PERMANOVA on the algae succession experiment

Main test

Source	Pseudo-F	P(perm)
Treatment	23.49	0.001
Time	96.39	0.001
Treatment:Time	2.72	0.001

Pairwise comparisons

	October		November		December		January		February	
	t	p	t	p	t	p	t	p	t	p
cage x open	0.56	0.697	2.76	0.018	2.39	0.009	4.46	0.004	3.44	0.007
cage x partial	0.51	0.657	1.07	0.295	1.40	0.179	3.13	0.009	3.63	0.004
open x partial	0.45	0.773	1.19	0.32	1.28	0.202	2.25	0.042	2.11	0.032

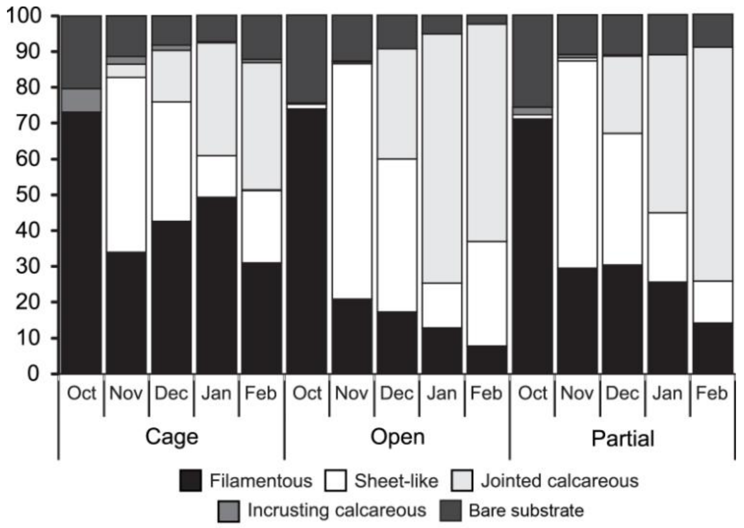

Fig 3 - Algae succession after complete removal of organisms inside plots

4 - Discussion

HERBIVORE CONTROL OVER ALGAL BIOMASS

In the present study we observed no changes in algal biomass between treatments. This finding is particularly unique, as in most studies excluding herbivores resulted in a tremendous increase in algae biomass (e.g. 2 x increase after 5 weeks in Belliveau and Paul 2002; 9-20x increase after 3 years in Hughes et al. 2007b; 4-6 x increase in 10 months in Burkepile and Hay 2009; 17 x increase in 4 months in Jessen and Wild 2013). Despite owning 40-60% of their dry weight to $CaCO_3$ accumulation (Borowitzka et al 1990; Bandeira 1997), jointed calcareous algae was consistently the group with higher biomass inside all plots. These algae are among the less-preferred species for fish to feed on, due to the aggressive herbivore-deterrent strategies they possess (Hay 1991). It also seems reasonable that herbivore feeding preferences may take part in the prevalence of this group, where the lack of the specific few fishes that are capable of control this particular group's biomass is accountable for the findings obtained. Supporting this assumption, experiments performed previously evidenced that the control of jointed calcareous algae, mainly *Halimeda tuna*, was solely performed by parrotfishes, while surgeonfishes have a negligible rate of consumption of these algae (Burkepile and Hay 2008). Conversely, surgeonfishes had an important role in the control of turf algae, especially *Kallymenia westii*, leading to the conclusion that complementary feeding by herbivorous fishes is necessary for controlling algae with distinct herbivore-deterrent strategies (Burkepile and Hay 2008).

HERBIVORE CONTROL OVER EPIPHYTES

The effect reduced herbivory resulted in a greater richness of epiphyte inside herbivore exclusion treatments, a pattern apparently driven by fish, as fully caged plots significantly differed from partial and open plots. Epiphytes occurred mostly over jointed-calcareous and coarsely branched macroalgae, which hosted from 1.7 to 3 times more epiphytes in full cages than other treatments, most of which were red filamentous forms. Similarly, in seagrass ecosystems fish were observed to prefer red epiphytes, whereas browns epiphytes are mainly consumed by amphipods (Duffy and Hay 2000).

Epiphytes presence typically implies losses of production, biomass and reproductive output to their host (D'Antonio 1985; Worm and Sommer 2000). Epiphyte loads increase host's weight, resulting in dislodgement and breakage (Buschmann Gomez 1993). They also compete with their hosts for resources, especially for inorganic carbon (Sand-Jensen 1977) and light (Dixon 1999). On the other hand, epiphytes can act as a protective coating, preventing host consumption by being rejected by herbivores as food (Karez et al. 2000). In previous study, significant reduction on the cover of certain algae species was only attained with the presence of a mixed-species herbivore community, where species acted synergistically on algal control (Burkepile and Hay 2008). By the results attained herein, it is uncertain if the epiphytic forms that thrived in exclusion plots were detrimental to their hosts or if they held secondary metabolites that could have impaired their consumption by other herbivores, e.g. larger parrotfishes, which occur in low densities in the study area.

THE ROLE OF ENVIRONMENTAL CONDITIONS ON ALGAL COVER

Given the great demand of effort in the field, most of the classical work comprising herbivory exclusion were relatively brief, lasting in general 4 months or less (e.g. Sala and Boudouresque 1997; Thacker et al. 2001; Belliveau and Paul 2002; Mcclanahan et al. 2003; Lapointe et al. 2004). Therefore, the effect and interaction of seasonal changes in environmental quality with herbivory to control the growth macroalgae remain relatively understudied.

Actually, some algae species suffer greatest influence of shifting environmental conditions than of reduced herbivory, while for others species these factors interact (Ferrari et al. 2012). During the present study, filamentous algae cover was greatly enhanced in the absence of fish top-down control, reaching more than three times the cover of partial cages and open plots. Yet, this increase only took place with favorable conditions of temperature and turbidity, thus suggesting growth is particularly limited by the environmental conditions in this group. Similarly, filamentous epiphyte biomass are found to respond positively with light and temperature (Alcoverro et al. 1997; Lepoint et al. 1999; Toyohara et al. 1999) and to nutrient input. The latter is prone to have a quicker response on filamentous algae, given their fast-growing traits (Worm and Sommer 2000). Additionally, both nutrient and grazing effects in epiphytes seems to only take place during summer in some seagrass systems (Neckles 1993; Hauxwell et al. 2003).

Jointed calcareous algae cover also responded positively to temperature increases. Similarly, *Halimeda opuntia* abundance was positively correlated with temperature on the reefs of the Caribbean (Ferrari et al. 2012) and the greatest herbivore abundance favored the predominance of this genus in Kenya (McClanahan 1997). Nevertheless, reducing herbivory exerted a negative effect on these algae cover, mostly because filamentous forms grew as epiphytes. A similar response was observed for sheet-like macroalgae. In previous study which encompassed the interaction of herbivory and environmental conditions, herbivory did not seem to control some sheet-like forms directly: this algae abundance significantly changed with water temperature and light instead (Ferrari et al. 2012).

HERBIVORE CONTROL OVER ALGAL SUCCESSION

Herbivory is an important mechanism affecting algal succession, particularly on coral reefs where the relationship between algae and corals is largely controlled by herbivores (Ceccarelli et al. 2011). In the present study, it was observed that herbivores influenced the presence of filamentous algae, but did not prevented the dominance of jointed calcareous algae. In fact, the cover of this algae was enhanced inside grazed plots. In the literature, the effects of both damselfish and roving herbivores are much more intense. Damselfishes are commonly reported to decelerate succession, favoring the presence of edible algae and preventing settlement of jointed calcareous algae (Hixon and Brostoff 1996; Ceccarelli et al. 2011). The foraging by roving herbivores also constrained succession, resulting in a diverse mid-successional community, which includes the predominance of corticated algae (Ceccarelli et al. 2011) or filamentous and encrusting calcareous algae (Hixon and Brostoff 1996; Burkepile and Hay 2010). The dominance of jointed calcareous algae is considered a late-successional stage of macroalgae asssemblages, generally observed in non-grazed environment (Ceccarelli et al. 2011).

Essentially, different functional groups of herbivores may have contrasting effects on succession, which may explain different trajectories of coral reef recovery after disturbance (Burkepile and Hay 2010; Ceccarelli et al. 2011). Additionally, the impact of consumer richness on communities often varies with the diversity of the prey community (Hillebrand and Cardinale 2004; Bruno et al. 2008). We believe the results attained herein were largely affected by the actual herbivore community and algae succession was an expected outcome of their feeding preferences. In the study area, damselfish largely feed over epiphytes and detritus accumulated over jointed calcareous algae, which comprise nearly 90% of their diet (Feitosa et al. 2012). The most abundant roving herbivores, the surgeonfishes, also feed mainly on filamentous species (Ferreira and Gonçalves 2006). Conversely, large parrotfishes, which are capable of scrapping considerable amounts of jointed calcareous algae from substrate while feeding (author's personal observation) and that are less deterred by algae calcification (Schupp and Paul 1994; Meyer and Paul 1995; Pennings et al. 1996; Paul 1997), have reduced populations.

OVERVIEW AND IMPLICATIONS

The findings of the present study, both concerning local herbivore community effects on algae biomass, algal cover, epiphytes and algae assemblages successions point out to the role mixed-species herbivore communities have on coral reefs. In Brazilian coastal reefs corals suffer with accentuated human impacts, such as high levels of parrotfish fishing, high sedimentation rates and nutrient input. Parrotfish within the study area reach at maximum ~0.150 individuals/m², while in other Brazilian reefs, in particular Abrolhos reefs, they can reach as much as ~0.4 individuals/m²; relatedly, coral cover in these reefs greatly differ, as in the present study coral cover never exceeded 5%, while in Abrolhos coral cover is of ~15% in average (Fracini-Filho et al. 2010; Ferreira et al. unpublished data). Regardless the fact the succession experiment initiated during September/October, at the occasion of some coral species spawning, not a single recruit was observed to settle on the bare substrate inside plots. Similarly, trials with settlement plates performed in the study area also lacked the presence of coral recruits (Mauro Maida, pers. comm.). It is feasible that the amount of recruits was also reduced by the low coral cover observed in the study area. The high biomass of algae is also detrimental, as they promptly colonized bare surfaces, restoring the jointed calcareous dominance as seeing outside plots within few months. In addition, algae also seems to lack other benthic competitors, such as sponges and bryozoans within the study area, which could assist reducing algal biomass on theses reefs. Therefore, conservation measures for Brazilian reefs must be immediate and mandatory, especially concerning the restoration of parrotfish and corals populations.

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Capítulo 5

Conclusões gerais
e Anexos

Conclusões gerais

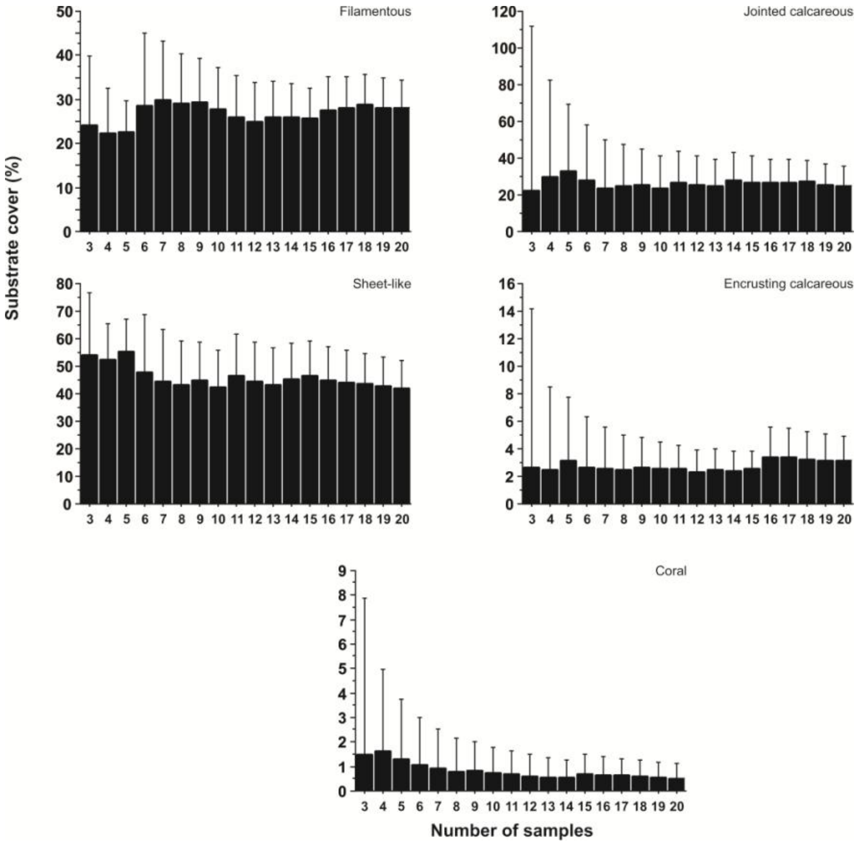
Apesar da maioria dos trabalhos avaliando o papel dos peixes-papagaio no ambiente recifal tratar a alimentação como uma característica específica das espécies, o presente trabalho demonstra que esta pode ser variada e se adaptar para diferentes condições ambientais ou comportamentais. Para *Scarus iseri*, a espécie mais abundante dos recifes caribenhos, a estrutura social foi determinante para sua alimentação. Indivíduos participando de agrupamentos sociais territorialistas se beneficiaram de uma maior abundância de seu alimento preferido, as algas filamentosas, enquanto que os peixes que não participavam deste tipo de associação complementaram suas dietas com detritos. Esta diferença é determinante para o papel que estes peixes possuem no ambiente recifal, as algas filamentosas possuem estratégias de vida de crescimento rápido e são as primeiras a colonizar substratos novos. Os peixes-papagaio que se alimentam destas algas estão atuando no controle de sua biomassa nos recifes, podendo facilitar o assentamento dos corais. Enquanto que os peixes que se alimentam dos detritos participam de fluxos de energia e de nutrientes distintos, que reciclam nutrientes provenientes de fontes, tornando-os disponíveis para os outros consumidores na teia trófica. A dieta dos peixes-papagaio também pode variar de acordo com seu tamanho e a disponibilidade de alimento. Demonstrou-se que *Sparisoma axillare*, a espécie mais abundante na maioria dos recifes brasilieiros, pode ser bastante generalista; através da variação da sua dieta, os jovens desta espécie puderam habitar os diversos ambientes presentes nos recifes costeiros do Brasil, se adaptando aos alimentos presentes em cada um deles. Esta estratégia generalista os permite ocorrer em vários ambientes e provavelmente é um fator importante para o sucesso desta espécie em locais impactados, como a maioria dos recifes costeiros do Brasil.

O presente trabalho demonstrou que nestes recifes, que divergem dos recifes "clássicos" reportados na literatura mundial por sua formação e condições ambientais peculiares, os peixes-papagaio possuem uma função primordial no controle das macroalgas. Nos recifes onde sua densidade é reduzida, devido principalmente a pesca, o restante da comunidade de herbívoros não consegue controlar a biomassa de algas como um todo, se restringindo esse controle a cobertura de apenas algumas espécies. Sem a função "raspadora" dos peixes-papagaio é muito possível que os corais sejam prejudicados, em especial o assentamento de suas larvas e crescimento dos seus recrutas.

De fato, a retirada do papel funcional atribuído aos peixes-papagaio é bastante preocupante, principalmente porque este grupo possui estratégias de vida muito complexas e ainda pouco estudadas. Por exemplo, a facilidade da pesca em locais mais rasos pode afetar um certo grupo social que desempenha um papel funcional específico neste ambiente. Em outras palavras, a presente Tese demonstra que o impacto relacionado a pesca destes peixes pode ser maior do que o esperado apenas pela retirada de um recurso do ambiente recifal, e vem a salientar e embasar a necessidade da criação de estratégias de manejo da pesca voltada para este grupo de peixes recifais.

Anexos

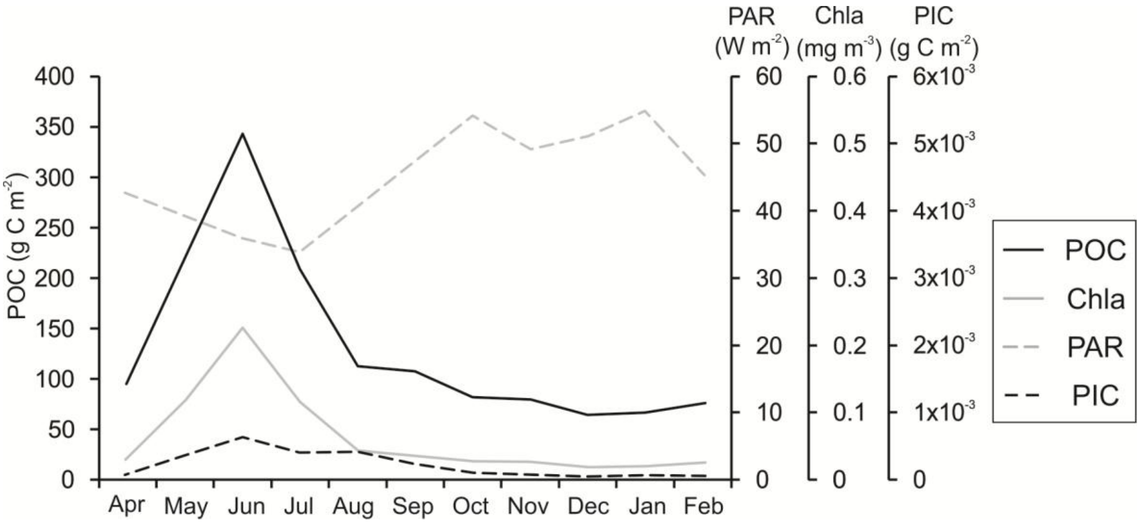
SupFig 1 - Example of the cages installed on the experiments



SupFig 2 - Mean and variance stabilization with increasing number of samples taken. Bars indicate 95% of confidence intervals.

SupTable 1 - Pearson's correlation index between continuous variables. Chla - Chlorophyll a; SST - Sea Surface Temperature; PAR - Photossynthetically available radiation; PIC - Particulate inorganic carbon; POC - Particulate organic carbon

Variables compared	R^2	p
Chla x SST	-0.27	ns
Chla x PAR	-0.99	< 0.01
Chla x PIC	0.98	< 0.01
Chla x POC	0.99	< 0.01
SST x PAR	0.17	ns
SST x PIC	-0.42	ns
SST x POC	-0.27	ns
PAR x PIC	-0.96	< 0.01
PAR x POC	-0.99	< 0.01
PIC x POC	0.99	< 0.01



SupFig 3 - Relationship between continuous variables. Abbreviations are listed on SupTable 1.