UNIVERSIDADE FEDERAL DE PERNAMBUCO
CENTRO DE TECNOLOGIA E GEOCIÊNCIAS
DEPARTAMENTO DE OCEANOGRAFIA

Padrões de distribuição, idade e crescimento de peixes-donzela (Pomacentridae): uma abordagem de variações espaciais e temporais.

Laís de Carvalho Teixeira Chaves

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Tese submetida ao curso de Doutorado do Programa de Pós Graduação em Oceanografia da Universidade Federal de Pernambuco, como requisito para obtenção do título de Doutor em Oceanografia.

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”Daqui a alguns anos estará mais arrependido pelas coisas que não fez do que pelas que fez. Solte as amarras! Afaste-se do porto seguro! Agarre o vento em suas velas! Explore! Sonhe! Descubra!” Mark Twain

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RESUMO GERAL

Esta tese, dividida em cinco capítulos, aborda os padrões de distribuição de peixes-donzela em diferentes sistemas recifais brasileiros e na costa caribenha do Panamá, bem como o estudo sobre os parâmetros da história de vida da espécie *Stegastes fuscus* amplamente distribuída na costa brasileira. Em relação à sua distribuição na costa brasileira, o objetivo específico é determinar quais os fatores ambientais são responsáveis pelos padrões observados e se estes apresentam o mesmo efeito em se tratando de recifes de origem e morfologia diferentes. O capítulo intitulado "Padrões de distribuição de peixes-donzela no Sudoeste do Atlântico: uma comparação entre sistemas recifais tropicais e subtropicais", aborda a distribuição de peixes-donzela, considerando fatores como a exposição a ondas, profundidade e cobertura bentônica em recifes tropicais (Tamandaré-PE) e subtropicais (Arraial do Cabo-RJ). Os principais resultados mostram que a exposição é um importante fator para a distribuição da espécie *Stegastes fuscus*, que em ambos os sistemas apresenta maior densidade em ambientes abrigados, enquanto que o padrão contrário é encontrado para *S. variabilis*. Virtualmente ausente no recife tropical costeiro raso, onde é encontrado em maior abundância em habitats mais profundos, *S. pictus* esteve presente apenas no recife subtropical na faixa de profundidades estudada (até 12 metros). A cobertura bentônica também se mostrou importante considerando a preferência por microhabitats apresentada por cada espécie, o que pode ter mediado diretamente uma mortalidade seletiva. *Stegastes fuscus*, nos dois sistemas estudados, se associou a territórios que lhe ofereceram melhores recursos em relação a refúgio e alimento, como um tamanho de tocas medindo entre 5-10 cm² e uma maior cobertura de algas filamentosas, respectivamente. *Stegastes variabilis*, espécie de menor porte, se distribuiu em áreas menos habitadas por *Stegastes fuscus*, evitando competição, e nos recifes subtropicais se associou a outros atributos que lhe proporcionou maior proteção frente a predadores, como ouriços e maior rugosidade em baixas profundidades. Já em recifes tropicais, fundos dominados por macroalgas foi aparentemente o habitat preferencial desta espécie.

Em relação aos recifes do caribe panamenho, o capítulo “Partição espacial entre peixes-donzela na costa caribenha do Panamá: o papel da preferência do habitat”, aborda a distribuição e uso do hábitat por seis espécies que ocorrem simpatricamente em Bocas del Toro. O objetivo específico deste capítulo foi determinar os padrões de distribuição de peixes-donzela e confrontá-los aos encontrados por trabalhos realizados em recifes caribenhos nos últimos 30 anos para detectar mudanças nos padrões de distribuição devido às mudanças ocorridas nesses recifes. Os mesmos fatores utilizados no capítulo referente à costa brasileira capítulo foram considerados nesse estudo. Uma segregação entre as espécies foi encontrada, e os territórios das espécies mais abundantes (*S. planifrons* e *S. adustus*) nunca se sobrepõem. *Stegastes planifrons* é preferencialmente encontrada em 'patches' com maior cobertura de corais massivos, enquanto *S. adustus* é encontrado em recifes rasos com maior exposição a ondas e maior cobertura do coral-de-fogo *Millepora* spp. Os resultados encontrados são congruentes aos estudos realizados no Caribe nas últimas três décadas, o que indica que apesar de uma alta estabilidade populacional destas espécies, sua resiliência pode ser afetada frente a distúrbios ocasionando perda significativa de habitat.

No que se refere ao estudo da idade e crescimento de *Stegastes fuscus* “Padrões de idade e crescimento em um peixe recifal tropical amplamente distribuído no Atlântico Sul” compara a idade e os parâmetros de crescimento desta espécie em recifes tropicais (Tamandaré-PE) e subtropicais (Arraial do Cabo-RJ) e ainda temporalmente as populações de Tamandaré entre os anos de 1995 e 2011. Os resultados mostraram que a espécie estudada apresenta tendências similares às encontradas para outras espécies de peixes tropicais em estudos anteriores, nos quais foi constatado que os indivíduos apresentam menor longevidade e menor comprimento total em populações de latitudes mais baixas. A estrutura populacional e parâmetros de crescimento também variaram, em menor intensidade, entre os anos estudados em Tamandaré, indicando que a influência de outros fatores, como predação e competição, afetaram a estrutura populacional desta espécie, possivelmente mediadas através de medidas de manejo adotadas localmente.

O último capítulo apresenta as principais conclusões sobre os resultados encontrados nos três principais capítulos desta tese, assim como considerações sobre futuras direções para cada um deles.

Palavras-chave: Pomacentrídeos, Distribuição espacial, Herbívoros territoriais, Uso do hábitat, Crescimento.

GENERAL ABSTRACT

This thesis was organized in five chapters and encompasses the study of distributional patterns of damselfish in different Brazilian systems, as well, as in the Caribbean coast of Panama. It also presents a study on life-history parameters of the widespread Brazilian damselfish, *Stegastes fuscus*. Concerning damselfish distribution along the Brazilian coast, the main goal was to determine which environmental factors are responsible for the patterns observed and if they exert the same effect on distinct systems. The chapter "Damselfish distribution patterns in the South-Western Atlantic: a comparison between tropical and subtropical reef systems", therefore, focuses on environmental features, such wave exposure, depth and benthic cover in tropical (Tamandaré-PE) and subtropical (Arraial do Cabo-RJ) reef systems. Main results showed that wave exposure is an important factor for *Stegastes fuscus* distribution, as in both systems the species presented higher densities in sheltered rocky shores. The contrary was found for *S. variabilis.* Virtually absent in the shallow tropical coastal system studied, *S. pictus* is more abundant in subtropical reefs on deeper sites within the depth range studied (12 m). Benthic cover was an important feature for damselfish habitat selection, which could be a driver of selective mortality. *Stegastes fuscus*, on both systems, associated with territories providing suitable shelter and food, such holes size betweem 5-10m² and higher cover of filamentous algae, respectively. *Stegastes variabilis,* a smaller-sized species, associated with atributes that confered higher protection against predators in subtropical (urchins and rugose shallow habitats) and tropical (macroalgae) reefs.

Considering Panamanian reefs, the chapter “Space partitioning among damselfishes in the Caribbean coast of Panama: the role of habitat preferences”, presents the distribution and habitat use of six sympatric damselfish species in Bocas del Toro. The main goal of this chapter was to determine damselfish distributional pattern and confront them with results found in studies of the last 3 decades, in order to detect alterations on these patterns related to habitat shifts occurring on these reefs. The same environmental factors used on the Brazilian coast were considered here. Segregation among species was found where most abundant territorial species (*S. planifrons* e *S. adustus*) did not overlap with one another. *Stegastes planifrons* is mostly found in 'patch reefs’ with extense massive coral cover, whereas *S. adustus* was found in exposed shallow reefs with high cover of the fire-coral *Millepora* spp. The results found were congruent with previous studies over three decades ago, however microhabitat use shifted for the main species *S. planifrons*, which indicates that although populations present high stability their resilience can be disrupted by significant habitat loss.

In the study referring to age and growth of *Stegastes fuscus* “Age and growth patterns of a widespread tropical reef fish in the Southwestern Atlantic” a comparison between age and growth parameters of the Brazilian damsel is made between tropical (Tamandaré-PE) and subtropical (Arraial do Cabo-RJ) reefs and between different years of tropical poulations (1995 and 2011). Results showed that the studied species are similar to other tropical reef fish, with lower life span and smaller total lengths in lower latitude systems. However, tropical populations also presented different parameters curves, indicating that at a lesser extent, other proccesses as predation and competition may play a role on the population structure of this species. This was possibly mediated through management strategies locally adopted.

Final conclusions on main results found on the main three chapters are made, as well as considerations and further directions for each of them.

Key-words: Pomacentrids, Spatial distribution, Territorial herbivores, Habitat use, Growth.

CAPÍTULO I: **Introdução geral**

O ambiente recifal é o ecossistema de maior produtividade no meio marinho, ocupando até 0.17% da superfície terrestre (SPALDING et al., 2001). Em todo o mundo, este ecossistema vem sofrendo mudanças significativas nas últimas décadas, que se devem principalmente a alterações climáticas globais, sobrepesca, doenças e eutrofização (HUGHES et al., 2003; PANDOLFI et al., 2005). Os efeitos desses impactos são expressos principalmente pela diminuição da cobertura de corais e da biodiversidade nestes sistemas (HOEGH-GULDBERG et al. 2007; HUGHES et al. 2010; DUDGEON et al. 2010) muitas vezes resultando num processo de mudança de fase ("Phase shift"), que consiste na substituição da cobertura coralínea pela dominância de algas na comunidade bentônica (McCOOK, 1999; SCHEFFER et al., 2001).

Estudos recentes indicam que a resiliência dos recifes e o seu retorno à condição inicial de dominância por corais, embora raramente observado (DIAZ-PULIDO et al. 2009), depende não somente do aporte de recrutas de corais nesses sistemas, mas também da pressão exercida pela herbivoria e a condição dos herbívoros na estrutura trófica (MUMBY, 2009; NORSTRÖM et al. 2009; DUDGEON et al. 2010), sendo estes os principais responsáveis pelo controle do crescimento das algas.

A influência de peixes herbívoros sobre as comunidades de algas tropicais não só determina amplamente sua abundância e distribuição (SZMANT, 2001; HUGHES et al. 2007), como também consome uma grande diversidade de macroalgas através de diferentes estratégias alimentares (KLUMPP & POLUNIN, 1990, DUFFY, 2002). Os principais peixes recifais herbívoros no Atlântico Sul são das famílias Acanthuridae (peixes-cirurgião), Labridae (peixes-papagaio), Pomacentridae (peixes-donzela) e Kyphosidae (piranjicas) que compõem a maior parte de biomassa de peixes nesses ambientes (THRESHER, 1980).

Consumindo virtualmente toda a produção primária no ambiente recifal (FERREIRA et al., 1998), ao peixes herbívoros representam o principal elo na transferência de energia para os níveis superiores da cadeia trófica destes ecossistemas. Os herbívoros também agem suprimindo a sucessão de algas através da pastagem (Scaridae, Acanthuridae) e desta forma facilitando o assentamento de corais (BURKEPILE & HAY, 2010) ou podem manter o crescimento de determinadas espécies de algas, e.g. tufos de algas filamentosas, em estágios iniciais de sucessão através de seu comportamento territorial (Pomacentridae) (HATA & KATO, 2003; HATA et al., 2010).

Diversos estudos abrangendo pomacentrídeos territoriais foram realizados em todo o mundo. Desde a década de 70, após o desenvolvimento de técnicas de mergulho autônomo para os estidos científicos, essas espécies foram alvo de estudo de pesquisadores que tentaram aplicar para o meio marinho, teorias ecológicas anteriormente testadas para o ambiente terrestre. Logo, essas espécies se tornaram um modelo para estudos ecológicos voltados a peixes recifais (HIXON, 2011). Os estudos com pomacentrídeos, por exemplo, deram suporte à hipótese da loteria (SALE, 1977; 1978), que sugere que o espaço disponível no recife é compartilhado aleatoriamente por novos recrutas, que futuramente irão competir entre si. O pressuposto seria que as espécies envolvidas são generalistas e com alto poder de dispersão larval. Algum tempo depois surgiu a hipótese da limitação por recrutamento (DOHERTY, 1982), que propõe que as populações são reguladas pelo aporte de recrutamento, que não é o mesmo para todas as espécies, e isto acarretaria a regulação das populações diferentemente, o que seria responsável pela estrutura da comunidade observada. A formulação dessas hipóteses, que são importantes até hoje, foi possível principalmente devido ao comportamento territorial destas espécies e sua forte ligação com o substrato, facilitando a observação em seu ambiente natural.

FUNÇÃO ECOLÓGICA DE HERBÍVOROS TERRITORIAIS

Herbívoros territoriais como os peixes-donzela (família Pomacentridae) são amplamente distribuídos e abundantes em ambientes recifais no mundo (DOHERTY, 1983; MEEKAN et al., 1995; CECCARELLI et al., 2001), podendo ocupar até 80-90% da superfície de alguns recifes (ROBERTSON, 1984; CECCARELLI et al., 2005) e constituindo até 46% da abundância total de peixes (LETOURNEUR, 2000).

Em linhas gerais, os pomacentrídeos são verdadeiros ‘jardineiros dos recifes’, pois podem direcionar a progressão da sucessão ecológica, mantendo uma alta diversidade de algas dentro de seus territórios (HIXON & BROSTOFF, 1996) e seu efeito sobre a comunidade bentônica lhes conferiu um papel de espécie-chave dentro da comunidade recifal. Os principais efeitos observados dentro de seus territórios foram o aumento de algas filamentosas, em termos de biomassa (SAMMARCO, 1983; KLUMPP et al., 1987; FERREIRA et al., 1998; CECCARELLI, 2001; HATA et al., 2002), produtividade

(BRAWLEY & ADEY, 1977; KLUMPP et al., 1987; RUSS, 1987) e percentual de cobertura (SANTANA, 2001; FERREIRA et al., 1998), o que reflete indiretamente sobre a riqueza de invertebrados, aumentando à medida que há maior complexidade estrutural e disponibilidade de microhabitats (HATA et al., 2002; FERREIRA et al., 1998). Mais recentemente, estudos mostraram que os pomacentrídeos territoriais, além de diminuírem a intensidade da herbivoria através da defesa contra seus competidores (HIXON & BROSTOFF, 1996; CECCARELLI et al., 2005), também retiram as algas que não são de seu interesse através do comportamento de "weeding", mantendo uma monocultura de algas selecionadas, geralmente filamentosas (HATA & KATO, 2002; 2006), ou através da retirada de pólipos de corais sadios em colônias utilizadas secundariamente frente à perda de habitats (PRECHT et al., 2010).

No entanto, esses efeitos foram observados para determinadas espécies isoladamente, não se aplicando a todas elas (CECCARELLI et al., 2001). Espécies maiores do grupo podem defender mais eficientemente os recursos em seu território e ingerir até seis vezes mais material vegetal, por área de substrato, do que espécies menores (KLUMPP & POLUNIN, 1990). Ainda, a intensidade em que algumas espécies se alimentam também pode variar extremamente em diferentes épocas do ano (KLUMPP & POLUNIN, 1990; FERREIRA et al., 1998). Consequentemente, sua atuação sobre a estrutura da comunidade bentônica, depende do espaço que ocupam em habitats diferentes de um recife. Considerando necessidades específicas de determinada espécie e a variação no espaço e no tempo da composição da comunidade dentro do seu território, é possível afirmar que nem todas as espécies possuem o mesmo efeito sobre as comunidades bentônicas (CECCARELLI et al., 2004; 2005).

PADRÕES DE DISTRIBUIÇÃO

Uma vez conhecido o papel que uma espécie desempenha em um determinando sistema, também é importante entender como ela se distribui no ambiente e quais os fatores responsáveis pelos padrões de sua distribuição. Atualmente, são aceitas diversas hipóteses, em que diversos fatores atuam em sinergia para os padrões observados. A constatação de que o aporte de recrutas a cada ano seria determinado por fatores estocásticos, deu suporte a teoria que os processos que limitam o número de indivíduos que entram na população (processos pré-assentamento) seriam os principais fatores estruturadores das comunidades de peixes recifais (DOHERTY, 1991). Sabe-se hoje que fatores pós-assentamento, como predação e competição poderm influenciar padrões demográficos, evidenciando a importância da escala espacial e/ou temporal abordadas nos estudos (HIXON & WEBSTER, 2002; HOLBROOK & SCHMITT, 2002; WHITE et al. 2010). Principalmente quando o grupo em questão apresenta grande estabilidade populacional e alta longevidade, como é o caso de muitos pomacentrídeos (DOHERTY & FOWLEY, 1994; MEEKAN et al. 2001; SCHWAMBORN & FERREIRA, 2002), flutuações no recrutamento são absorvidas na estrutura populacional, pois períodos “ruins” com baixas taxas de recrutamento podem ser compensados por anos “bons” de recrutamento em espécies longevas, processo conhecido como “storage effect” (WARNER & CHESSON, 1985).

A seleção de um determinado habitat na fase de recrutamento pode estabelecer os padrões de distribuição dos adultos posteriormente, através da perda pela migração (DOHERTY & FOWLER, 1994; GUTIÉRREZ, 1998). Esta seleção pode ser determinada por diversos fatores, seja através da complexidade do habitat (HOLBROOK et al., 2000), presença de predadores (ALMANY, 2004) e a competição inter- e intra-específica por recursos, como alimento e/ou refúgio (SWEATMAN, 1985). A mortalidade por predação também é outro fator de extrema importância e geralmente ocorre na fase crítica de assentamento no recife, ou seja, determinada pelo tamanho dos indivíduos (BRUNTON & BOOTH, 2003). Desta forma, os processos pós-assentamento se tornam determinantes neste grupo, especialmente frente a mudanças, como a perda de habitat e retirada de predadores e/ou competidores pela atividade pesqueira.

PARÂMETROS POPULACIONAIS

O tamanho de um indivíduo é uma das características morfológicas mais importantes em diferentes fases de vida de peixes recifais, pois pode influenciar desde a sua sobrevivência (e.g. risco de predação; BRUNTON & BOOTH, 2003) até sua posição em uma organização hierárquica (e.g. uso dos recursos, vantagem reprodutiva; BUSTON, 2003; WONG et al., 2007). Embora os peixes recifais ocorram em um amplo espectro de tamanho, ser grande não está necessariamente relacionado à longevidade (ALMEIDA-VAL et al., 2006; HART & RUSS, 1996; NEWMAN et al., 1996, 2000).

Determinar as variações nas taxas de crescimento, reprodução e mortalidade em função da idade de peixes se tornou um dos pilares da biologia de populações. Esses parâmetros em peixes se mostraram bastante valiosos, especialmente se tratando de recursos pesqueiros que representam fonte de alimento e renda para comunidades costeiras de todo o mundo (PAULY et al., 2002). Desta forma, os estoques populacionais necessitam ser avaliados para seu melhor manejo pesqueiro e conservação.

Informações sobre idade e crescimento nos permitem avaliar a estabilidade e explotabilidade de estoques pesqueiros (BROTHERS, 1979; SMITH et al., 1992), assim como a eficiência das estratégias de manejo como, por exemplo, a implantação de reservas marinhas (TREXLER & TRAVIS, 2000). Adicionalmente, a capacidade de se determinar a idade de peixes recifais ao longo de toda a sua distribuição geográfica, nos permite avaliar importantes parâmetros em sua história de vida frente a diferentes condições ambientais, em escalas locais e latitudinais (CHOAT & ROBERTSON, 2002). O conhecimento desses parâmetros se torna importante mesmo quando a espécie estudada em questão não é alvo das pescarias, pois se pode inferir sobre os efeitos indiretos desta atividade em toda a comunidade através de sua função ecológica no ambiente. Por exemplo, a redução de predadores de topo leva à uma redução da taxa de predação sobre níveis tróficos inferiores (SANDIN et al., 2010) e, consequentemente, “liberação das presas”, ou seja, haverá um aumento das populações de presas, resultando numa cascada trófica neste ambiente como sugere a teoria ecológica, em termos gerais.

Uma ferramenta importante para determinação a idade de peixes, são estruturas calcificadas conhecidas como otólitos. Essa estrutura é a mais utilizada em estudos de determinação de idade devido a sua estabilidade em face de variações metabólicas e fornecimento de leituras precisas. A leitura de otólitos foi utilizada inicialmente para estoques de regiões temperadas, pois até algumas décadas ainda acreditava-se que somente a sazonalidade encontrada em ambientes temperados daria a confiabilidade na formação de marcas em estruturas calcificadas (PITCHER & HART, 1982; LONGHURST & PAULY, 1987; FERREIRA & RUSS, 1994), sendo desconsiderada até então para peixes tropicais. Uma vantagem em utilizar otólitos ao invés de outras estruturas é que estes crescem ao longo de toda a vida do indivíduo, sendo isolados de outros tecidos, e desta forma não estã sujeitos aos efeitos de reposição ou reabsorção celular, comum em outras estruturas ósseas (e.g. escamas, vértebras) (GREEN et al., 2009).

ESTUDOS NO BRASIL

No Brasil, a espécie *Stegastes fuscus* é amplamente distribuída e constitui grande parte da abundância total de peixes em ambientes recifais. Consequentemente, está presente em diversos trabalhos ao longo da costa brasileira. Dentre eles, o primeiro realizado por FERREIRA et al. (1998) analisou seu efeito estruturador sobre a comunidade bentônica através de experimentos com gaiolas e trazendo o conhecimento sobre a herbivoria em costões rochosos do sudeste brasileiro. Este estudo indicou sua importância como espécie-chave, promovendo a maior diversidade de algas e invertebrados dentro de seu território. SCHWAMBORN & FERREIRA (2002) realizaram estudo referente à idade e crescimento de *Stegastes fuscus* no nordeste brasileiro e demonstraram a alta longevidade encontrada nesse grupo (15 anos). Estudos comportamentais incluindo territorialismo, interações agonísticas e taxas de forrageamento, foram também realizados em recifes do sudeste (MENEGATTI et al., 2003) e nordeste (OSÓRIO et al., 2006), comprovando que esta espécie defende seu território ostensivamente. Em seguida SOUZA et al. (2007) descreveram os padrões reprodutivos desta espécie no nordeste brasileiro, indicando picos de desova em épocas de temperaturas mais altas. Mais recentemente, comparações feitas entre *Stegastes fuscus* e seu congênere que ocorre simpatricamente *S. variabilis,* viabilizando inferências sobre a exclusão competitiva exercida por *S. fuscus*. Isto porque, a partição de habitats já é observada desde a fase juvenil (MEDEIROS et al. 2010), uma vez que há uma alta sobreposição alimentar entre elas (FEITOSA et al., 2012). Sendo estas espécies amplamente distribuídas em toda a costa e em grande abundância, exercendo forte influência sobre a comunidade bentônica, para entender esta interação é importante conhecer os padrões de distribuição e partição de hábitat, ou seja, interações bióticas e abióticas determinantes. Ainda, é importante observar como estes padrões se mantêm em escala latitudinal, pois nesta escala observamos grandes variações de temperatura e ocorrência de ambientes recifais de origem biogênica e não biogênica.

HIPÓTESES E OBJETIVOS DESTA TESE

O capítulo intitulado "Damselfish distribution patterns in the South-Western Atlantic: a comparison between tropical and subtropical reef systems*",* aborda a distribuição de espécies do gênero *Stegastes* em ambientes recifais tropicais e subtropicais da costa brasileira.

A costa brasileira possui mais de 8000 km de extensão, tendo os recifes como importante componente (aproximadamente 1/3) em sua fisiografia (RANGEL et al., 2007). Recifes coralíneos predominam na costa nordeste central (0º52'N-19ºS), enquanto que costões rochosos dominam ao sul (20ºS-28ºS) (FLOETER et al., 2006). Espécies do gênero *Stegastes* são amplamente distribuídas na costa brasileira e também em ilhas oceânicas, entretanto somente espécies costeiras foram abordadas nesta tese. *Stegastes fuscus*, é uma espécie endêmica da costa brasileira e amplamente distribuída, reconhecida como a mais abundante em diversos trabalhos (FERREIRA et al., 1995, 1998; MENEGATTI et al., 2003; OSÓRIO et al., 2006; HOSTIM-SILVA et al., 2006). Outras duas espécies *Stegastes variabilis* (Castelnau, 1855) e *Stegastes pictus* (Castelnau, 1855) são menos abundantes, mas possuem similar extensão em sua distribuição ao longo da costa. Neste primeiro capítulo pretende-se determinar em escala latitudinal (sistemas tropical e subtropical) a distribuição espacial das diferentes classes de tamanho de espécies do gênero *Stegastes* em habitats sujeitos a diferentes graus de exposição a ondas e profundidades, verificando-se a importância da complexidade estrutural do substrato na partição de habitats entre as espécies.

Este estudo é o primeiro a avaliar a distribuição de peixes-donzela considerando seus diferentes estágios de vida comparativamente em sistema tropical e subtropical da costa brasileira. A hipótese considerada é que o tamanho corporal de um indivíduo e/ou espécie é um indicador da necessidade energética e superioridade inter- e intra-específica e desta forma, é esperado que indivíduos e/ou espécies maiores tenham acesso aos melhores recursos disponíveis (alimento e espaço) (LETOURNEUR, 2000). Havendo uma repartição de nichos entre indivíduos de diferentes espécies e classes de tamanho, como isso ocorre em diferentes habitats de um ambiente recifal (diferentes profundidades, grau de exposição, diferentes micro-habitats)? Este padrão é consistente em diferentes sistemas?

O capítulo intitulado “Space partitioning among damselfishes in the Caribbean coast of Panama: the role of habitat preferences” aborda a distribuição espacial e uso do habitat por seis espécies de peixes-donzela que ocorrem simpatricamente no Caribe Panamenho, em Isla Colón (Colombo), Bocas del Toro. A maioria dos trabalhos envolvendo as populações de peixe-donzela no Panamá foi realizada quando os recifes caribenhos ainda não haviam sofrido mudanças em larga escala como, por exemplo, redução de 50-70% de habitats recifais induzidas por mudanças climáticas e a mortalidade massiva do ouriço *Diadema antillarum*. A perda desta espécie-chave teve um impacto negativo em todo o Caribe, pois era um importante agente controlador do crescimento de algas (HUGHES, 1994; HUGHES & TANNER, 2000; GUZMÁN, 2003). O objetivo deste capítulo foi determinar os padrões de distribuição de peixes-donzela e confrontá-los aos encontrados por trabalhos realizados em recifes caribenhos nos últimos 30 anos de forma a se detectar mudanças nos padrões de distribuição e uso do hábitat devido às mudanças ocorridas nesses recifes.

O capítulo “Age and growth patterns of a widespread tropical reef fish in the Southwestern Atlantic”. Neste capítulo foram analisados os padrões de variação encontrados na idade e crescimento de *Stegastes fuscus* entre populações naturais de recifes tropicais e subtropicais brasileiros. O objetivo desse capítulo é testar diferenças latitudinais e temporais nos parâmetros da história de vida de uma mesma espécie amplamente distribuída, de acordo com o previsto em diversas teorias. A hipótese inicial seria de que as populações em baixas latitudes resultam em maiores taxas de crescimento, tamanhos menores e possivelmente maturação tardia em relação às populações de altas latitudes. Se existe alguma forma de compensação fisiológica, as latitudes mais altas resultariam em taxas de crescimento mais baixas e idades máximas mais altas, resultando em maiores comprimentos. Já através da comparação temporal, esta espécie longeva e com abundância relativamente estável, seria uma boa indicadora de mudanças ambientais, como por exemplo, avaliar os efeitos da criação de uma área com exclusão de pesca.

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CAPÍTULO II: **Damselfish distribution patterns in the South-Western Atlantic: a comparison between tropical and subtropical reef systems**

*Padrões de distribuição de peixes-donzela no Sudoeste do Atlântico: uma comparação entre sistemas recifais tropicais e subtropicais

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RESUMO

A distribuição espacial de espécies simpátricas de peixe-donzela do gênero *Stegastes* foi investigada em relação à exposição de ondas, profundidade e qualidade do substrato, comparativamente em recifes tropicais (08º 44’ S - 35° 05’ W) e subtropicais (22° 59’ S - 42° 00’ W) da costa brasileira. Os estágios de vida (juvenil, sub-adulto e adulto) foram considerados. As densidades de *Stegastes fuscus* e *S. variabilis*, em geral, foram maiores em locais abrigados e expostos, respectivamente e esse padrão foi consistente entre os recifes estudados. A profundidade também foi um forte fator para explicar os padrões de distribuição de peixes-donzela em recifes tropicais, onde as densidades médias de *S. fuscus* foram mais altas em habitats rasos e de *S. variabilis* em habitats mais profundos. Entretando, nos costões rochosos subtropicais, a zonação vertical da comunidade bentônica foi muito variável em escalas de centenas a dezenas de metros. Isto propiciou habitats para *S. fuscus* em todos os estratos de profundidade, embora sua maior abundância tenha sido observada em profundidades intermediárias de locais abrigados. *Stegastes variabilis*, por sua vez, foi mais abundante no raso dos costões expostos ao batimento e *S. pictus* ocorreu em maiores profundidades sem diferenças relacionadas ao nível de exposição, já que nessas profundidades este fator não é tão atuante. Numa escala mais restrita, houve a preferência das espécies em relação a alguns atributos do substrato. *Stegastes fuscus*, nos dois sistemas estudados, se associou a territórios que lhe ofereceram melhores recursos em relação a refúgio e alimento, como o tamanho de tocas medindo entre 5-10 cm² e a maior cobertura de algas filamentosas, respectivamente. *Stegastes variabilis*, espécie de menor porte, se associou a outros atributos que lhe proporcionaram maior proteção frente a predadores nos recifes subtropicais, como ouriços e maior rugosidade em baixas profundidades. Já em recifes tropicais, fundos dominados por macroalgas aparentemente constituíram o habitat preferencial desta espécie. Adicionalmente, os padrões de distribuição observados indicaram que a competição inter-específica também pode ser um fator atuante na partição de habitats entre as espécies, uma vez que a espécie dominante *S. fuscus* possui territórios raramente sobrepostos aos de *S. variabilis*.

Key-words: Pomacentridae, Herbívoros territoriais, partição de habitat, *Stegastes*

Damselfish distribution patterns in the South-Western Atlantic: a comparison between tropical and subtropical reef systems

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ABSTRACT

This study investigated the distribution of sympatric territorial damselfishes, in tropical (Tamandaré - 08º 44' S - 35° 05' W) and subtropical (Arraial do Cabo - 22° 59' S - 42° 00' W) reef systems of the South-Western Atlantic. Tropical reefs sustained higher abundances of damselfish, where several algal groups dominated. However, subtropical reefs presented higher benthic diversity. *Stegastes fuscus* and *S. variabilis* were significantly denser on sheltered and exposed sites, respectively, such pattern being consistent among systems. *Stegastes pictus* was absent from habitats studied in tropical reefs, and not influenced by wave exposure, showing a high affinity with depth, and presenting segregation among life stages. Distribution of *S. fuscus* and *S. variabilis* displayed discrete segregations between life stages conspecifics within microhabitat features. *Stegastes fuscus*, in general, was more abundant where territories presented its optimum attributes, such as holes sizes with 5-10 cm^2 and predominant cover of filamentous algae. *Stegastes variabilis* association with benthic cover indicated flexible and context dependent habitat selection, such as urchins/high bottom rugosity in subtropical reefs and macroalgae in tropical reefs. Moreover, avoidance of competition might play a primary role in species segregation, as dominant adult *S. fuscus* held areas of distribution that rarely overlapped with congeners.

Key-words: Pomacentridae; Territorial herbivores; Habitat partitioning; *Stegastes*

INTRODUCTION

Habitat selection during recruitment is one of the most important driving forces for some reef fish species distribution (Gutiérrez, 1998), however, post-settlement processes (eg. predation) are ever critical affecting spatial distributions at different scales (Jones, 1991; Carr and Hixon, 1995). Space use can be determined by several factors, such as the presence of preferred microhabitats (Holbrook et al., 2000), predator abundance (Hixon and Beets, 1993; Almany, 2004), intra and interspecific competition (Sweatman, 1985; Tolimieri, 1998; Bay *et al*., 2001) and swimming limitations in high-energy environments (Denny, 2005). Reef fish spatial distribution patterns are thus highly variable in scales of tens to thousands of meters (Williams, 1982; Meekan *et al*., 1995; Holbrook *et al*., 2000), (Emslie *et al*., 2012).

Small territorial fish such as damselfish (Pomacentridae) are widely distributed and abundant in shallow habitats (Doherty, 1983; Meekan *et al*., 1995; Ceccarelli *et al*., 2001). They may occupy up to 80% of the reef surface (Robertson, 1984; Ferreira *et al*., 1998; Medeiros *et al*., 2010a) and represent up to 46% of the total fish abundance (Letourneur, 2000). Some species are also known to increase (Sweatman, 1988; Booth, 1992), interfere with (Jones, 1988; Almany, 2004) or have no effect (Doherty, 1983; Jones, 1987) on the abundance of of other damselfish recruits and juveniles. Territory selection by an individual may limit the distribution of a species, thereby providing the opportunity for competing individuals or species to coexist (Gutiérrez, 1998). Though Wellington (1992) showed that settlement of some damselfish species are restricted to conspecific adult habitats, other species avoid conspecific territories (Öhman *et al.,* 1998; Ben-Tzvi *et al*., 2009). It is advantageous to settle in the presence of conspecifics, as suitable habitats and potential mates would be easily spotted, however intraspecific competition could have major effects (positive or negative) on the growth and survival of newly settlers (Sweatman, 1985; Levin *et al*., 2000).

Territorial damselfish usually display marked site fidelity, being capable of significantly modify algae communities inhabiting their territories. Due to these characteristics, they are considered classic models for field manipulation, allowing the test of important hypothesis (Sale, 1977; Doherty, 1982; Ceccarelli *et al.*, 2006). In addition, this group is known to perform farming and weeding behaviour contributing to distinguish territories from nearby areas due to increased diversity, biomass and primary production rates of algae (Hata and Kato, 2003, 2004; Ceccarelli *et al.*, 2005; Jones *et al.*, 2006).

As biomass of algae is augmented inside territories and rates of predation reduced, the abundance of associated cryptofauna is also improved, which is an important resource for abundant invertivores (Brawley and Adey, 1977; Williams, 1980; Hixon and Brostoff, 1983; Horn, 1989; Ferreira *et al.*, 1998; Hata and Kato, 2002). Ultimately, by their abundance and directly use of turf algae, the main bulk of primary production on reef systems, they are potential indicators of phase shifts from coral- to algae-dominated reefs (Ceccarelli *et al.*, 2006; 2011).

Studies dealing with reef fishes and habitat correlations have mostly explored local scales (e.g., microhabitats, reef zones) (Bay *et al.*, 2001; Kawasaki *et al.*, 2003; Kane *et al.*, 2009). For instance, the abundance of fishes has been correlated with gradients of depth (Green, 1996; Richardson, 1999; Medeiros *et al.*, 2010a) and exposure (Russ, 1984; Williams, 1991; Gust, 2002; Depczynski and Bellwood, 2005; Floeter *et al.*, 2007) or live coral cover (Bouchon-Navaro and Bouchon, 1989). The influence of microhabitat availability is expected to influence the spatial and temporal distribution and abundance of habitat-specialised fishes (Munday *et al.*, 1997), including herbivorous damselfishes. Thus, if a particular habitat feature is important for damselfishes' distribution over a broad geographical range, it is important to consider what consistent habitat associations would be found for sympatric species.

Spatial and temporal large-scale consistency have been found for damselfishes, concerning ecological traits, such as feeding rates and body size in respect to temperature (Barneche *et al.*, 2009), modification of benthic communities (Cecarelli *et al.*, 2007), as well as fluctuations in abundance in view of environmental changes (Emslie *et al.*, 2012). The Brazilian coast extends over 8,000 km, and reefs are an important component of its physiographic features (nearly 1/3) (Maida and Ferreira, 1997; Floeter *et al.*, 2001). Coral reefs are the predominant ecosystem on the north and central northeastern coasts (0°52'N-19°S), whereas rocky shores are the main physiographic element southwards (20ºS-28ºS) (Floeter *et al.*, 2001). The scenario established by such an interesting latitudinal gradient from tropical to subtropical reef systems provides unique opportunities to test ecological hypotheses. However, few studies have explored the Brazilian coast as a gradient model (Ferreira *et al.*, 2004; Floeter *et al.*, 2004, 2005; Barneche *et al.*, 2009).

The dusky damselfish *Stegastes fuscus* (Cuvier, 1830) is endemic to the Brazilian coast and widely distributed, except in the oceanic islands, where other endemics or sister species replace it (Sampaio *et al.*, 2006). This species is one of the most abundant fish on the reef systems of the Brazilian coast according to several authors (Ferreira *et al.*, 1995; Ferreira *et al.*, 1998; Menegatti *et al.*, 2003; Osório *et al.*, 2006). Its wide distribution and high abundance provide a unique opportunity to examine the consistency of habitat use and relationship with other sympatric damselfishes along its geographical range, both within and among regions. Two other species, the Cocoa Damselfish, *Stegastes variabilis* (Castelnau, 1855), and the Yellowtip Damselfish, *Stegastes pictus* (Castelnau, 1855), are less abundant, but they co-occur with *S. fuscus* in varied spatial scales along the coast (Ferreira *et al.*, 2001; Floeter *et al.*, 2007; Medeiros *et al.*, 2010; Feitosa *et al.*, 2012). While *S. fuscus* and *S. variabilis* are herbivorous fishes (Ferreira et al., 1998; Feitosa *et al.*, 2012), *S. pictus* is typically omnivorous, feeding both over benthic communities and the water column (Floeter *et al.*, 2007). How they co-exist within and among different systems is an important issue for understanding their different functional roles, as well as their influence on distribution and behaviour of associated reef fish community.

This work is a first approach assessing the extent of spatial distribution among *Stegastes* species at different life phases, comparatively in a tropical and a subtropical reef system in the Brazilian coast. We explored environmental descriptors (wave exposure, depth, benthic cover diversity, rugosity, and hole size) to explain distribution and abundance patterns of the damselfish species studied. The main driving questions were: Is there a major environmental determinant for damselfish distribution among Brazilian reef systems? Are there congruencies concerning their habitat requirements considering different life stages?

MATERIALS AND METHODS

STUDY AREA

Two sites, one encompassing a tropical and another encompassing a subtropical reef, were selected on the Brazilian coast. Both sites harbour special management regimes (Conservation Units or MPAs according to the Brazilian legislation) but in most of their extension, including the studied reefs, they are open-access areas and subjected to fishing. To investigate local and regional patterns of *Stegastes* spp. distribution, it was a sample design that comprised several attributes as both systems present distinct tri-dimensionality, where subtropical reefs are represented by vertical rocky profiles, whereas tropical coral reefs are horizontal lines perpendicular to the coast (see Figure 1).

Subtropical rocky reefs

The subtropical rocky reefs of Arraial do Cabo in the State of Rio de Janeiro (22° 59’ S - 42° 00’), are enclosed in a Marine Extractive Reserve (RESEXMar Arraial do Cabo). The rocky shores formed by granite boulders extend to 25-30 m width, with maximum depths of 15m during high tides. *Stegastes* territories sustain dense algal turfs 1–3 cm high that are dominated by the articulated calcareous algae *Jania* spp. and *Amphiroa* sp. Algal turfs are alternate with colonies of firecoral *Millepora alcicornis*, and the zoanthid *Palythoa caribaeorum* (Ferreira *et al*., 1998). The mean water temperature in the region is about 22ºC year-round, reaching a maximum of 25 ºC (Ferreira *et al*., 2001) and minimum of 18 ºC, where under this temperature indicates that this region is under the influence of a coastal upwelling during the summer/spring periods (Valentin, 1984). The reefs that have been studied here, however, are only sporadically affected by cold waters and typically only in the deeper portions (Ferreira *et al*., 1998).

Tropical reefs

The tropical fringing reefs of Tamandaré in the State of Pernambuco (8º 45' S - 35º W) are located in the upper limit of the Marine Protected Area APA Costa dos Corais, which extends across 135 km of the northeastern coast of Brazil. Coral reefs are composed of three main reef lines parallel to the coast (Maida and Ferreira, 1997). *Stegastes* territories are widespread along reef lines, and benthic cover is mainly composed of thick algae turfs (*Amphiroa* sp.), the calcified algae *Halimeda opuntia*, and other algal groups. The zoanthid *P. caribaeorum* and sparse colonies of the fire-coral *M. alcicornis* are also found. The area has a tropical climate with an established regime of rainy (May to September) and dry (October to May) seasons reaching maximum water temperatures of 26ºC and 30ºC, respectively (Maida and

Ferreira, 1997).

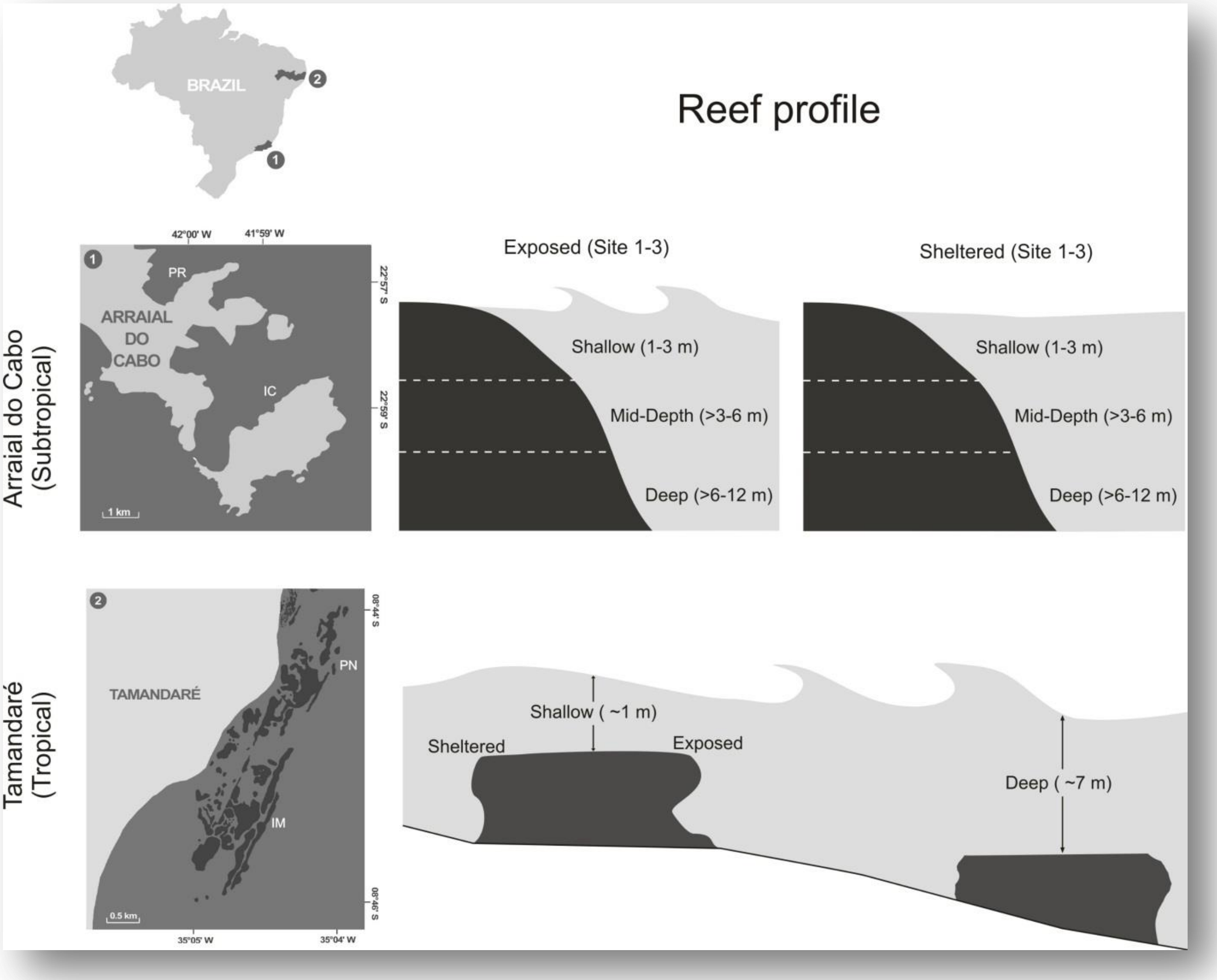

Fig. 1. Map of studied reef systems on Brazilian coast with respective reef profiles. (1) Rocky reefs (subtropical system); and (2) Coral reef formations (tropical system). IC = Cabo Frio Is. (sheltered); PR = Prainha (exposed); PN = Pirambu do Norte Reef; IM = Ilha do Meio Reef.

FIELD SAMPLING

Fish surveys

The distribution of the damselfishes *Stegastes fuscus*, *S. variabilis* and *S. pictus* within systems were examined between Dec 2009 and Feb 2010. Marked color morphs were used to distinguish species' life stages (juveniles, subadults and adults). The Yellowtip Damselfish, *S. pictus*, while conspicuous on Arraial do Cabo reefs, in the tropical northeastern reefs are rarely found in shallow waters, being more common on off shore reefs. Juveniles were only recorded twice during a 3-year period on Tamandare reefs (pers. obs.). Also, individuals of *S. fuscus* are larger in subtropical reefs, apparently related to lower temperatures (Chaves *et al.*, unpub. data), however distinguishing life stages was not compromised.

In the subtropical system, two rocky reefs, Prainha Beach (exposed to wave surge) and Cabo Frio Island (sheltered), were chosen (Fig. 1). In the tropical system, two reefs were selected Ilha do Meio and Pirambu do Norte. These reefs presented the same orientation thus, levels of exposure to wave surge were comparable, where outer and inner reef borders represented the exposed and sheltered habitats. Replicated 10 x 2 meter transects were laid with an overall total of 120 transects (60 for each system) within depths between 1-6 meters. Additional transects (N=60; 30 each system) were laid on deeper reefs (>6m), in order to verify any relationship of bottom cover and fish abundance, however, deeper reefs present very low abundance of damselfishes and were only included on the experimental design to verify whether *S. pictus* (restricted to deeper habitats in subtropical reefs) distribution was influenced by wave exposure.

Samples were collected using a tape measure laid on the reef surface, and the visual census was started after a 3-min period, allowing fish to acclimate with the diver's presence. To avoid edge effects, if a damselfish was not within a given transect, but at least 50% of its territory was inside transect boundaries, it was considered in counts. Fish were counted and grouped into life stages (juveniles, subadults and adults) according to coloration criteria and size. It is worth noting that distinct darker coloration pattern of *S. variabilis* between systems (Souza *et al.*, 2011) is a confusing task to distinguish it among *S. fuscus* individuals, but this matter was circumvented in this study by researchers' experience on these species identification.

Environmental descriptors

On both reef systems, the benthic cover (%) and frequency of occurrence for hole sizes (%) were recorded (N=1080) using 0.40 x 0.40m photo-quadrats (at 0m, 2m, 4m, 6m, 8m and 10m of each 10m-transect). The images were later processed on CPCe 3.5 Software (Kohler and Gill, 2006) using 30 points that were systematically arranged. The major functional groups were defined as massive corals (*Siderastrea stellata*, *Montastrea cavernosa*, *Mussismilia hartii*, *Mussismilia hispida*, *Porites astreoides*), branching corals (*Millepora* spp.), zoanthids

(*P. caribaeorum*, *Zoanthus* spp.), macroalgae (mainly from the genera *Sargassum*, *Caulerpa*, *Codium* sp., *Gracilaria* sp., *Dictyota* sp., and *Dictyopteris* sp.), crustose coralline (crusts), articulated coralline as turfs (*Jania* spp, *Amphiroa* sp.) and *H. opuntia*, filamentous algae (*Gelidium* sp., *Ceramium* sp., *Bryopsis* sp.), urchins (*Echinometra lucunter*, *Lytechinus variegatus*), non-biotic substrate (sand, bare rock, rubble) and other organisms (sponges, ascidians, barnacles and other benthic invertebrates). Size of holes was categorized as areas <5 cm², 5-10 cm², >10 cm².

Depth was also recorded, and the rugosity was measured using a modified chain-link method from Luckhurst and Luckhurst (1978), where a chain was laid along the whole transect line. The rugosity index was obtained from the relationship of the chain length divided by the length of the transect line as the linear distance.

Data Analysis

A two-way ANOVA was performed to test whether systems and wave exposure differed in damselfish distribution. Another one-way ANOVA was used to test specifically the influence of wave exposure on *Stegastes pictus* distribution in subtropical reefs, once it was absent in tropical reefs studied. To ensure that the ANOVA assumptions had been met, we tested for variances homogeneity using the Cochran’s test. A *post hoc* Student–Newman–Keuls (SNK) multiple comparison test was used to separate significantly different means. The data were log (log X + 1) transformed when necessary. The software Statview 5.0 for Windows was employed for these analyses.

Benthic community data was analyzed using PRIMER 6.1.2 (Plymouth Marine Laboratories 2001). Percentage cover estimates for each category within a plot were the basis of this analysis. Similarities in composition between samples (plots) using similarity matrices with log-transformed data for tropical and subtropical systems, respectively were determined through non-metric multidimensional scaling (NMDS) using the Bray-Curtis similarity coefficient. To assess the similarity patterns between samples and the formation of meaningful groups in terms of benthic community for reef systems and wave exposure, two-way ANOSIM was used (Clarke and Warwick, 2001).

The abundance of each life stage of *S. fuscus*, *S. variabilis* and *S. pictus*, and their relationship with percent cover of benthic community, depth, rugosity, and holes size were analyzed using the canonical correspondence analysis (CCA) ordination (ter Braak, 1987). The significant environmental parameters were selected manually with the Monte Carlo permutation test. The data were log-transformed using CANOCO for Windows 4.5.

RESULTS

Damselfish patterns of distribution

Two-way ANOVA tests comparing both systems and wave exposure regimes as factors could only be performed for all *S. fuscus* life stages and juveniles and adults of *S. variabilis*, as juveniles of *S. pictus* and subadults of *S. variabilis* were not recorded (Table I; Fig. 2).

Exposure was an important factor for the distribution of *S. fuscus* and *S. variabilis* (Table I; Fig. 2). *Stegastes fuscus* was always more abundant on sheltered sites, this pattern being more pronounced in the tropical system. Although there was an interaction between factors for juveniles, this is a possible result of the low observation numbers of this life stage. *Stegastes variabilis* had higher densities in the subtropical system, preferring exposed shores in both life-stages examined (Table I; Fig. 2). For *S. pictus*, adults and subadults were restricted to depths below 7 m and presented no significant differences between the exposure regimes analyzed.

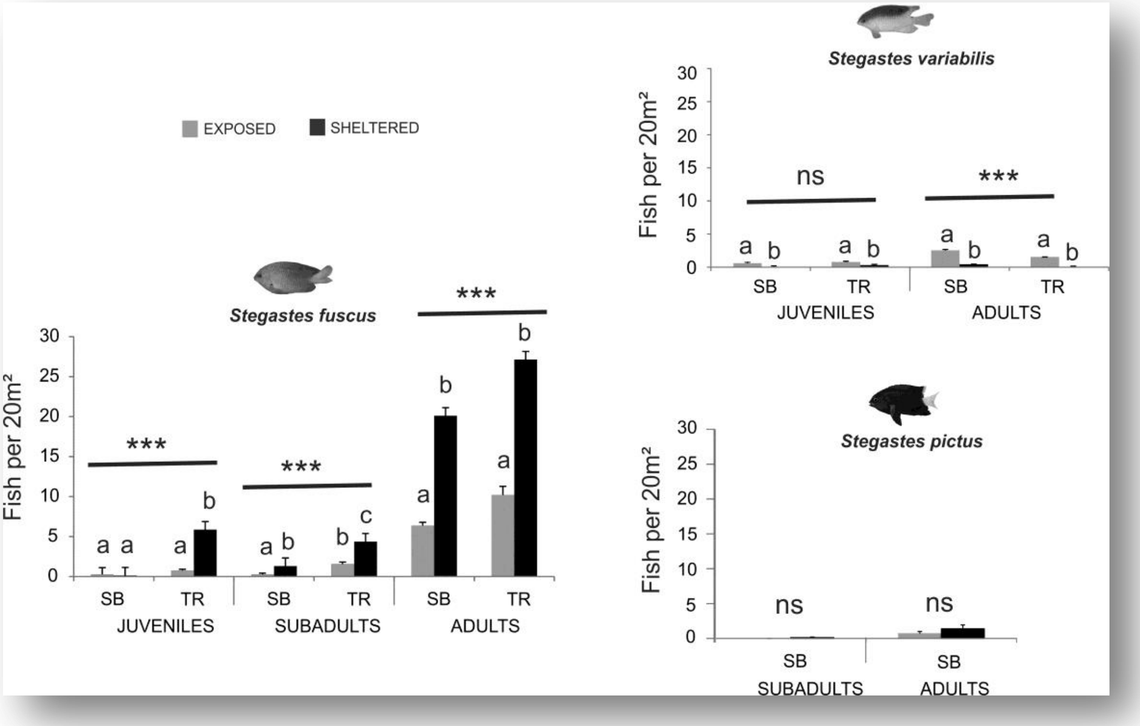

Figure 2. Mean abundance (±Standard errors) for damselfish species within subtropical (SB) and tropical (TR) reefs. (—) represents ANOVA results between systems, where *** p<0.001; ns non significant. Different letters represent homogeneous groups.

Table I. One and Two-way analysis of variance (ANOVA) tests for fish abundance, with reef system (tropical - TR and subtropical - SB systems) and wave exposure (exposed - EX and sheltered - ST shores) as factors.

SOURCE	**N**	**F**	**p**	**Results**
Stegastes fuscus				
Juveniles				
System	60	82.52	**<.001**	TR>SB
Exposure	60	34.55	**<.001**	ST>EX
System x Exposure	120	38.86	**<.001**	*interaction*
Subadults				
System	60	101.04	**<.001**	TR>SB
Exposure	60	23.21	**<.001**	ST>EX
System x Exposure	120	.59	.441 ns	
Adults				
System	60	52.41	**<.001**	TR>SB
Exposure	60	117.12	**<.000**	ST>EX
System x Exposure	120	4.93	.163 ns	
Stegastes variabilis				
Juveniles				
System	60	.732	.063 ns	TR>SB
Exposure	60	15.2	**<.000**	EX>ST
System x Exposure	120	.44	.853 ns	
Adults				
System	60	12.87	**<.000**	TR>SB
Exposure	60	28.20	**<.000**	EX>ST
System x Exposure	120	8.51	.422 ns	
Stegastes pictus				
Subadults				
Exposure	30	1.49	.226 ns	
Adults				
Exposure	30	.54	.472 ns	

Benthic communities and other environmental descriptors

Tropical and subtropical systems presented marked differences with respect to benthic percent cover and other general descriptors of complexity. In subtropical reefs, articulated calcareous and crustose algae, zoanthids (genus *Palythoa*), branching corals (genus *Millepora*) and non-biotic substrate (boulders with no benthic cover and rubble) dominated the benthic substratum. Differently, tropical reefs were characterized by dominance of macroalgae, algal crusts, filamentous and the conspicuous *Halimeda*, indicating an algae-dominated environment. Tropical reefs had also higher values for rugosity than subtropical ones due to the higher frequency of holes in different size categories (Table II).

Confirming such differences the structure of benthic communities, with respect to reef system and wave exposure within and between studied systems, presented significant differences on ANOSIM tests. Two groups on nMDS plots (Fig. 3) were formed with a small degree of overlap were observed considering the reef system (global R = 0.662; p = 0.01). These groups were significantly different from each other with respect to wave exposure; however, there was an overlap among the sheltered sites (global R = 0.347; p = 0.001), indicating possible differential effects of wave surge on both systems. The species that more contributed for such dissimilarity between reef systems and exposure were percent cover of branching corals, zoantids and non-biotic (sand and bare rock, mostly) in subtropical reefs and dominance of macroalgae, zoantids and non-biotic (sand and rubble) on tropical reefs (Table II).

Table II. Benthic composition (Mean percent cover ± S.E.) and general bottom attributes in subtropical and tropical reef systems within wave exposure. Samples of deeper samples are included. N=number of total photoquadrats analysed.

	TROPICAL (N=540)		SUBTROPICAL (N=540)	
	EXPOSED	SHELTERED	EXPOSED	SHELTERED
ALGAE				
% Crustose	4.49±0.03	7.02±0.07	19.52±0.12	12.05±0.10
% Articulated	37.83±0.08	49.72±0.11	19.24±0.12	20.77±0.12
% Filamentous	16.82±0.06	19.06±0.09	2.85±0.06	10.20±0.10
% Macroalgae	25.20±0.09	2.87±0.07	1.65±0.07	1.86±0.08
CORAL				
% Branching	0.02±0.01	1.51±0.07	15.57±0.14	9.54±0.12
% Massive	0.54±0.02	0.77±0.04	0.05±0.02	1.41±0.06
HOLE SIZE				
%<5cm²	1.35±0.02	1.65±0.04	0.43±0.02	0.51±0.03
%5-10cm²	1.17±0.02	1.11±0.03	0.37±0.03	0.40±0.03
%>10cm²	1.40±0.02	1.38±0.04	0.57±0.04	0.89±0.04
% Zoantids	5.82±0.06	3.65±0.07	16.74±0.17	28.5±0.19
% Urchins	1.56±0.02	4.61±0.08	8.34±0.08	4.78±0.08
% Other[a]	0.02±0.01	-	2.01±0.05	1.14±0.04
% Non-biotic[b]	3.70±0.04	6.63±0.08	12.66±0.09	7.85±0.12
H'(diversity index)	0.49±0.01	0.73±0.02	1.16±0.01	0.97±0.02
Rugosity index	1.57±0.01	1.71±0.01	1.59±0.02	1.52±0.02
Depth (m)	3.07±0.02	1.00±0.05	5.07±0.05	4.07±0.05

[a] Sessile invertebrates; [b] sand, bare rock, rubble

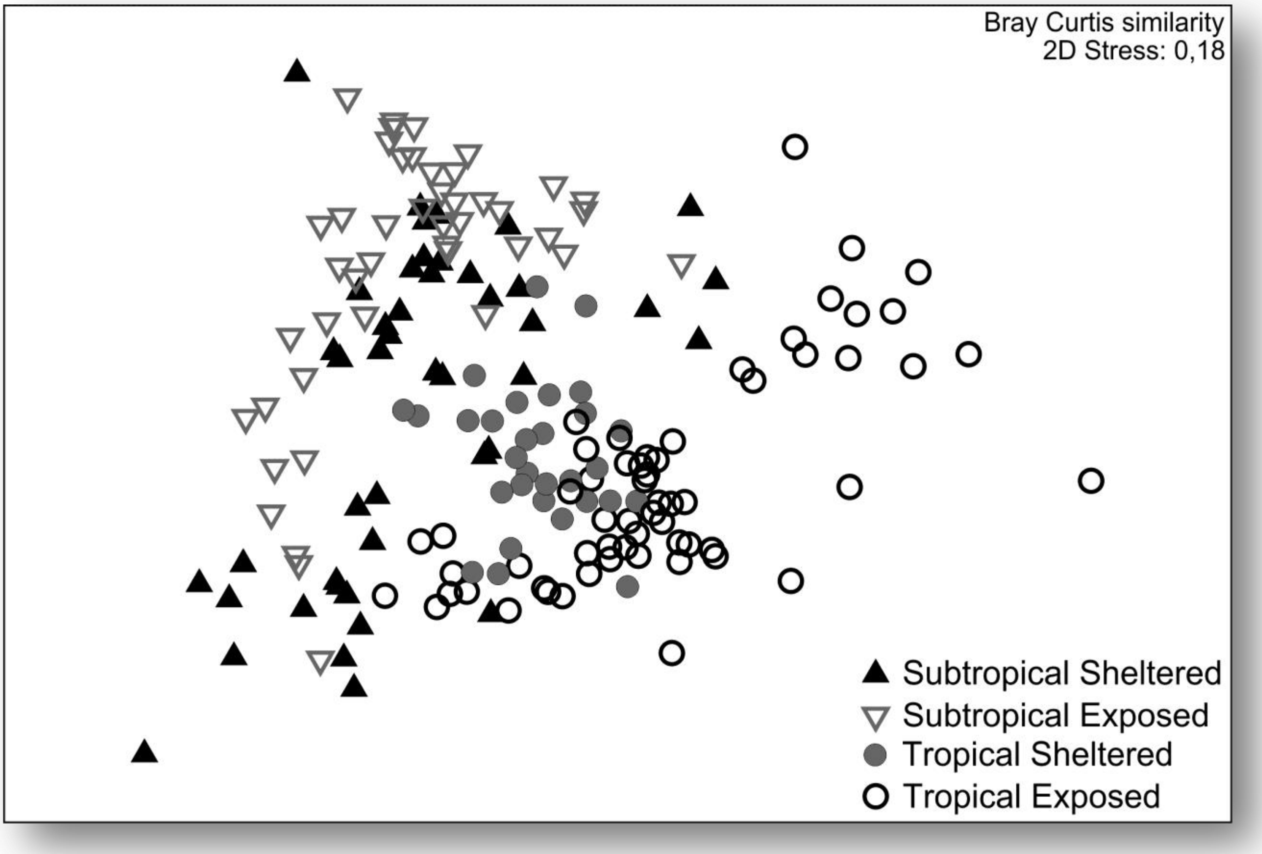

Fig. 3: NMDS plot representing significant groups of benthic community samples formed between reef systems, represented by subtropical and tropical reefs; and wave exposure regimes, represented by sheltered and exposed sites within reefs. Based on photoquadrats (N=)1080 along transects (N=180).

Fish-environment relationships

Although the juvenile and subadult damselfishes were unevenly distributed, it was still possible to assess the patterns of distribution and their relationship with environmental descriptors at a micro-scale (Fig. 4A-B). For subtropical reefs, the first axis explained most of the variance (93.5%; Fig. 4A), and was used then for describing fish-environment relationships. *Stegastes fuscus* showed very discrete life stages segregation compared to the other species. This species is very abundant over shallow and mid-depth transects at sheltered sites. Besides the preference for low water motion environments, it was also associated with sites that had relatively high percent cover of filamentous algae and holes between 5 and 10 cm^2. Subadult *S. fuscus* was associated with deeper habitats. Abundance of adults of *Stegastes pictus* was related to deeper transects. However, subadults were well segregated, facing to the opposite direction of depth and sandy bottoms (non-biotic) and associated with sites presenting hole sizes between 5 and $10cm^2$. *Stegastes variabilis* also presented a discrete segregation between juveniles and adults, however juveniles preferred more rugose and shallow sites with higher cover of urchins.

The distribution of damselfishes on tropical reefs was represented better on two axes that explained together 82% of the variance found. *Stegastes fuscus* displayed once more little segregation among life stages, coinciding with the subtropical system and also associating with very similar bottom attributes such high percent cover of filamentous algae, holes between 5 and 10 cm^2, as well as holes greater than 10 cm^2. *Stegastes variabilis* in tropics also did not presented strong segregation patterns, being closely related to macroalgae dominated bottoms. However, adults and subadults are more pronounced on deep habitats than juveniles, which in accordance with subtropical reefs prefer shallow sites. In general, *Stegastes* spp. elected sites with some cover, as the ones with high percentage of non-biotic descriptors seemed to be avoided.

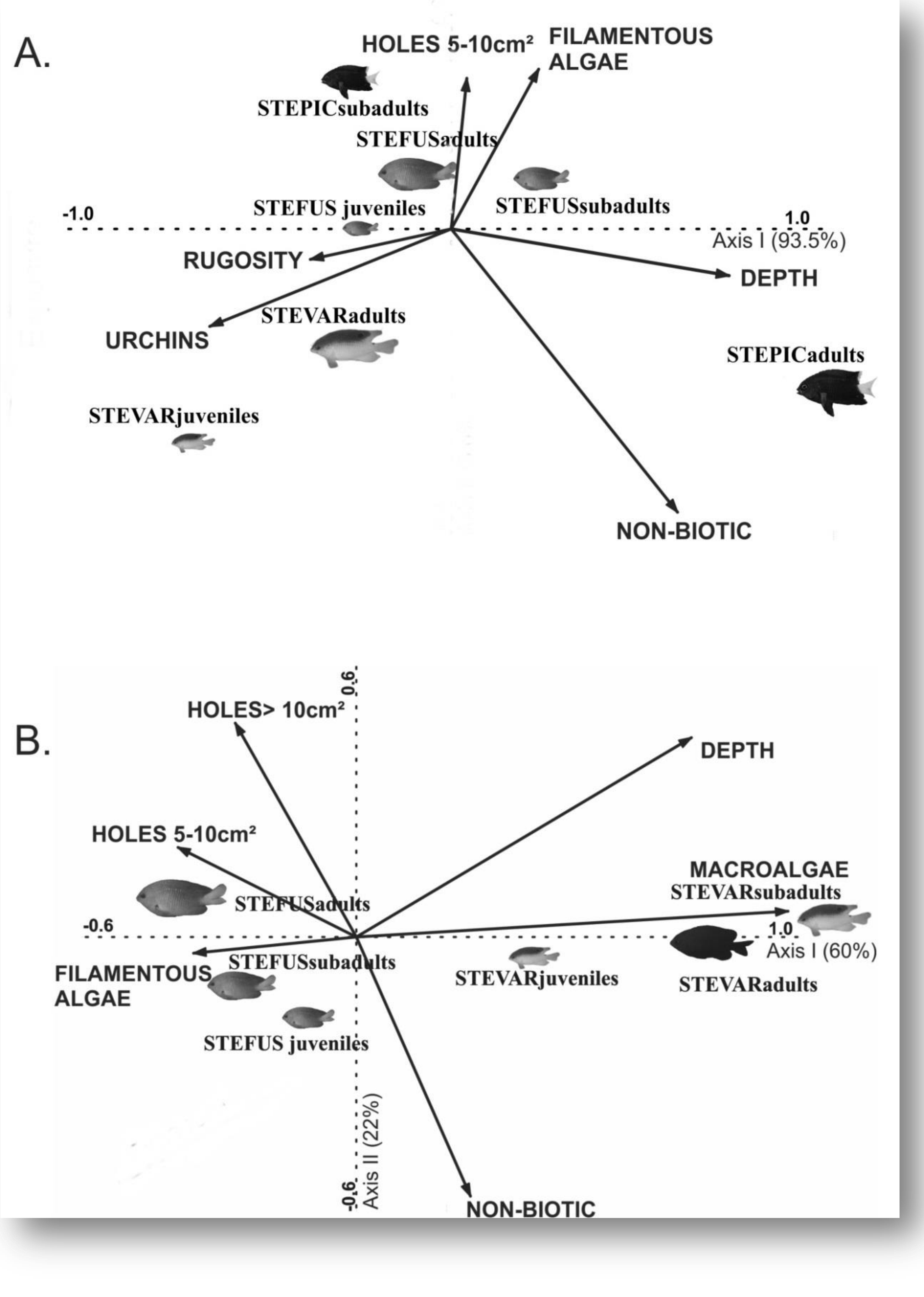

Fig.4. Canonical Correspondence Analysis biplot for different life stages of damselfishes and habitat descriptors in A. subtropical (Arraial do Cabo) and B. tropical (Tamandaré) systems. STEFUS = *Stegastes fuscus*; STEPIC = *Stegastes pictus*; STEVAR = *Stegastes variabilis*.

DISCUSSION

A general comparison between subtropical and tropical systems

This study investigated the abundance and distribution patterns of *Stegastes* spp. as much as benthic communities on distinct reefs distant approximately 2,200 km (1,367 miles) from each other. Despite difference in terms of formation (non-biogenic and biogenic), morphology (steep rock reefs and fringing reefs) and temperature (subtropical and tropical), wave exposure regimes and bottom features that provided shelter and food resources had a similar influence over damselfish either between or within these reefs.

Among studied species, *S. fuscus* was more abundant, as pointed out in several studies along the coast (Ferreira *et al*., 1995; Ferreira *et al*., 1998; Menegatti *et al*., 2003; Osório *et al*., 2006). However, comparatively between the two system studied, this species was more abundant on tropical reefs. The contrary was found for *S. variabilis*, despite being largely less abundant on both systems than *S. fuscus*, it was more abundant on subtropical reefs. Higher depth ranges in the subtropical reefs also provide space for a well-established population of *S. pictus*, obeying a pattern observed also for several species, where distribution is dislocated to higher depths on tropical reefs being observed up to 70 m deep (Feitoza et al., 2005). A corridor of hard bottoms formation between Brazil and Caribbean, also allowed this species to disperse further north in southern Caribbean (Rocha, 2003; Feitoza et al., 2005).

Benthic communities were also very distinct, where an algae dominated component was found for lower latitude, shallow tropical reefs, replaced by a more diverse benthic invertebrate fauna in higher latitudes, dominated by the zoantid *Palythoa caribaeorum* and the firecoral *Millepora alcicornis*, and therefore, forming diverse patchy habitats in subtropical reefs.

Nevertheless, great similarity concerning individual size class structure was found between systems, where smaller sized damselfish (juveniles and subadults) were far less abundant than adults. It is worth noting that juveniles were rare in general between reefs but were almost absent in subtropical systems in the study period. Although there is the possibility of the effect of sampling periods, this species is known to spawn all over the year, despite having reproduction peaks in some periods of the year (Souza *et al*., 2007). It might suggest that recruitment is occurring in habitats not sampled herein, however it is still possible that a recruitment failure occurred in the years preceding this study.

In relatively long-lived fish such as damselfishes, with 15-17 years for *S. fuscus* (Schwamborn and Ferreira, 2002; Chaves *et al.*, unpublished data), the contribution of variable recruitment to population density however, is difficult to detect, due mainly to "storage effects" (*sensu* Warner and Chesson, 1985). It predicts that favorable recruitment inputs could balance periods of low recruitment inputs, and that this would maintain adult densities stable over time. However, *S. variabilis* and *S. pictus* (although absent in the tropical system), presented low adult abundances, which could be attributable to low local retention of larvae from outside sources for replenishment.

The effect of wave exposure

Sheltered reefs yielded densities at least two-fold higher than the exposed reefs for *Stegastes fuscus*, on both reef systems (see Fig. 2). *Stegastes variabilis* and *S. pictus* occurred at much lower densities than *S. fuscus* and were, respectively, inversely affected and unaffected by exposure on subtropical reefs, respectively. The same was observed in tropical reefs, with exception of *S. pictus* that was absent. Exposure to wave surge is then a reliable variable as already reported for the Brazilian coast influencing patterns of abundance of *S. fuscus* and *S. variabilis* (Floeter *et al*., 2007; Medeiros *et al*., 2010).

The observed pattern could be a result of functionally groups that exhibit morphological adaptations to multiple swimming and feeding modes in respect to wave exposure (Fulton *et al*., 2001; Bellwood *et al*., 2002; Johansen and Jones 2011), however, *S. fuscus* and *S. variabilis* are very similar in morphology (Araújo *et al*., 2003), so other traits such as competition and niche displacement are responsible for patterns found. Additionally, *Stegastes pictus* is commonly recorded at deeper and offshore habitats (shipwrecks, oil rigs, oceanic islands).

Limitations in swimming performance may influence the majority of ecological activities of coral reef fishes including settlement, foraging and reproduction from relatively small to large scales (Kawamata, 1998; Fulton *et al*., 2001; Fisher and Bellwood, 2003; Blake, 2004; Denny, 2005; Fisher, 2005; Fulton and Bellwood, 2004; 2005). When considering a gradient of distance from the coast, the most abundant damselfishes, herbivorous together with planktivorous and omnivorous, are characteristically built in a pattern where there is an inverse distribution of herbivorous damselfishes (*S. fuscus* and *S. variabilis*) to planktivorous and omnivorous damsels (*Chromis* spp. and *Abudefduf* spp. respectively) (Ferreira *et al*., 2001; Floeter *et al.*, 2007).

Moreover, wave exposure also exerted influence over benthic communities in this study, with similar sheltered sites communities in both systems, what may also have contributed for *S. fuscus* latitudinal consistency in habitat preferences. However, exposure worked differently and maybe a result of distinct levels of wave surge conferred by reef morphology and orientation in tropical and subtropical reefs, which presents horizontal and vertical profiles, respectively.

Damselfish habitat requirements

Relationships between some environmental descriptors and fish adult abundance have been observed widely among reef fish (Munday *et al.*, 1997; Gutierrez, 1998; Holbrook *et al.*, 2000; Almany, 2004). Many studies described patterns in damselfish distribution on shallow reef zones in the Great Barrier Reef and Caribbean region (Robertson and Lassig, 1980; Waldner and Robertson, 1980; Williams, 1991); however, most of these studies did not consider environmental descriptors, or in many cases they did not use a quantitative approach.

Differently from the Caribbean region, where a diverse community of damselfish co-habit (Chaves *et al.*, 2012), no coral-dependent species was found, what may explain the wide distribution of damselfish species along the Brazilian coast. However, evidence has been given here that damselfishes studied had some habitat requirements where the size and number of available shelter is an important factor in the distribution of the species. Abundance of adult and subadult *S. fuscus* in general were positively correlated to the higher frequency of size holes that matched their estimated total length, while juveniles were more related to rugosity. Also, juvenile *S. variabilis*, although patchily recorded, used urchins and habitats with higher rugosity in the subtropical reef. Reef rugosity and size and shape of holes represent qualified refuges as a mean of predator avoidance before (Hixon and Beets, 1993; Carr and Hixon, 1995, Figueira *et al.*, 2008), indicating that these descriptors are important requirements, especially for small-sized individuals. Additionally, unlike in subtropical reefs, *S. variabilis* was distributed among macroalgae dominated bottoms in tropical reefs, which seemed to be a second choice for habitat in face of its displacement caused by interaction with *S. fuscus*. As juveniles, *S. variabilis* are the second most abundant species on macroalgae beds (mostly composed by *Sargassum polyceratium*) adjacent to the tropical reef studied (pers. obs.) and important as nursery areas for several other species (Rossier and Kulbicki, 2000).

Adult *S. pictus*, on the other hand, was clearly related to the area of reef-sand interface at subtropical systems, relying probably on refuge provided by macroalgae cover at these depths, although the same pattern concerning refuge from predators was observed for smaller individuals.

Moreover, the extent to which the availability of food resources determines the distribution of damselfishes was not investigated. However, correlations were found between the cover of filamentous algae and *S. fuscus* density in both systems, a pattern also found in recent studies both in subtropical and tropical reefs of the Brazilian coast (Ferreira *et al*., 1998; Feitosa *et al*., 2012). It is worth noting that by describing damselfish associations, *S. fuscus* is apparently related to higher quality territories than the other species concerning refuge and food resources (sheltered sites, optimum holes sizes, cover of filamentous algae). Thus, if this reasoning is sound, one would expect that their distributions are a result of higher competitive ability.

The role of interspecific competition

As stated above, a great extent of the distribution dissimilarity found herein is supported by interspecific competition. This hypothesis was tested elsewhere for *S. fuscus* and *S. variabilis* juveniles (Medeiros *et al*., 2010), with findings indicating a competitive segregation exerted by *S. fuscus*. Species segregation forced by territorialism was also reported for their congener *S. planifrons* within its distribution range throughout Caribbean reefs (Robertson, 1996; Almany, 2003; Cleveland and Montgomery, 2003) and that was shown to have also a diplacemente effect on *S. adustus* in Bocas del Toro’s reefs (Chaves et al., 2012).

Stegastes fuscus is widely known for its highly aggressive behaviour (Ferreira *et al*., 1998; Menegatti *et al*., 2003; Osório *et al*., 2006; Medeiros *et al*., 2010) and *S. variabilis* generally does not establish territories close to *S. fuscus*, especially in tropical reefs (Medeiros *et al*., 2010; Feitosa *et al*., 2012). In tropical reefs, *S. fuscus* seems to occur mostly in a gregarious distribution, although juveniles are eventually observed within *S. variabilis* subadult territories. Conversely, *S. variabilis* juveniles are observed to be apart from the adults, especially at different depth gradients. Nevertheless, the stronger evidence of existing hierarchical rules dictated by larger-sized individuals (Forrester, 1991; Booth 1995) is that both species have overlapping feeding habits and rely on similar food resources (Feitosa *et al*., 2012). Also, although the tropical system is dominated by articulated algae (e.g. *Halimeda* sp., *Amphiroa* sp.) not eaten by damselfish, they have the capacity to cultivate filamentous algae on the surface of other structurally complex species (Feitosa *et al*., 2012), food is therefore, not the limiting factor for both species. This consecutively provides the viability of *S. variabilis* to coexist in less qualified habitats. The access to eligible territories becomes the central dispute between these species, where *S. fuscus* displays its competitive superiority. Another clear example of this is that in subtropical reefs, *S. variabilis* maintains higher abundance on exposed shores, but shallow and sheltered habitats sustain optimum territory conditions, and it is where higher densities of *S. fuscus* are observed. In exposed shallow habitats, *S. variabilis* shared space with *S. fuscus* juveniles, however these are less aggressive than adults and may obey to size hierarchical rules.

Distribution of adult *S. pictus* was strongly influenced by depth, or by the reef-sand interface, located at the bottom of the rocky cliff, but it was not a rule of thumb when subadults were considered. This species presents a small size compared to the others, reaching maximum lengths between 7 - 8 cm. In subtropical reefs, *S. fuscus* juveniles, most likely displaced by adults, are occasionally found at deep habitats with *S. pictus*. However, competition for space at these habitats appears to be low, as agonistic encounters have been observed only among *S. fuscus* conspecifics, with larger individuals being more aggressive (pers. obs.). As an omnivore territorial damselfish, *S. pictus* (Floeter *et al*., 2007), commonly recorded at offshore sites (shipwrecks, oil rigs), feeds both upon benthic communities (70% invertebrates and 30% turf – Ferreira *et al*., unpububblished data) and in the water column (plankton pickers). This species is clearly more plastic on feeding behavior resulting in a lesser niche overlap. Nevertheless, the role of interspecific competition cannot be totally excluded, possibly occurring in *S. fuscus* preferential territories.

Further considerations

Data presented herein indicate that wave exposure, suitable habitat as much as interespecific competition are important determinants of the spatial variation in damselfish abundance both on local and regional scales. Furthermore, they bring new insights on how widely-distributed species are predictable, considering such environmental variability (e.g. temperature, reef type, benthic cover) at large scales in the Brazilian coast.

The similarity in patterns observed between the two systems indicates that *S. fuscus*, as a dominant damselfish in subtropical and tropical reef communities, could be an important environmental indicator, as its abundance could be shifting in face of natural and historical anthropogenic disturbances along the coast. Similar variables determining patterns of community structure of these important functional fish for different systems make their distribution quite predictable. However the Brazilian coast harbours other reef systems than those reported herein. Further approaches including as many different reefs as possible will improve our understanding in how these factors (e.g. competition, wave surge, benthic cover) drive territorial damselfish distribution and their possible influence on reef communities.

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CAPÍTULO III: **Space partitioning among damselfishes in the Caribbean coast of Panama: the role of habitat preferences**

***Partição espacial entre peixes-donzela na costa caribenha do Panamá: o papel da preferência do habitat.**

Neotropical Ichthyology, 10(3):633-642, 2012

RESUMO

Este estudo teve como objetivo avaliar a abundância e uso do habitat por juvenis e adultos de peixes-donzela, assim como as comunidades bentônicas em distintos recifes de Isla Colon, Bocas del Toro, Panamá. Os recifes foram escolhidos considerando diferentes níveis de exposição a ondas e profundidade. As comunidades de peixes e bentos estudadas se mostraram distintas. A espécie mais abundante em recifes com maior profundidade e abrigados foi *Stegastes planifrons*, seguida por *S. leucostictus*, que também foi observada em recifes rasos abrigados. As baixas abundâncias de *S. partitus* e *S. variabilis* também foram observadas no primeiro recife citado e estas espécies foram aparentemente restritas a profundidades maiores. Adicionalmente, estes mesmos recifes apresentaram uma vasta cobertura de corais massivos, vivos ou mortos. *Stegastes adustus* apresentou sua maior abundância em baixas profundidades, indicando uma preferência por habitats rasos, aumentando em duas vezes com a exposição a ondas. Os recifes rasos também tiveram maior abundância de *Microspathodon chrysurus*. Além disso, o recife com maior exposição apresentou extenso percentual de cobertura de algas e do coral-de-fogo *Millepora alcicornis*, reconhecido habitat preferencial de *M. chrysurus* e outras espécies de peixes. Neste trabalho, diferentes padrões de uso do habitat foram encontrados, sendo regulados pela profundidade e/ou exposição e ainda a disponibilidade de determinada cobertura bentônica. Para espécies fortemente associadas ao substrato, a especialização, a competição e padrões não aleatórios do recrutamento são conhecidos determinantes dos padrões distribucionais. Este estudo apresentou resultados similares a outros conduzidos há 30 anos no Panamá e outros recifes do Caribe, indicando que as espécies mais abundantes mantêm forte afinidade com o habitat. Entretanto, severas reduções na disponibilidade de habitat, seguidas de eventos de mortalidade em massa de corais, podem ter possivelmente afetado seus padrões de distribuição.

Space partitioning among damselfishes in the Caribbean coast of Panama: the role of habitat preferences

Running head: Damselfish space partitioning in Panama

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Abstract

This study aimed to assess abundance and habitat use by juvenile and adult damselfishes, as much as the benthic cover of different reefs on Isla Colon, Bocas del Toro, Panama. Reefs were selected considering different levels of wave exposure and depths. Damselfish and benthic communities were distinct between reefs. The most abundant species in the sheltered deeper reef was *Stegastes planifrons* followed by *S. leucostictus*, and they were also recorded in the sheltered shallower reef. Low densities of *S. partitus* and *S. variabilis* were also observed in the sheltered deeper reef, as these species are apparently restricted to higher depths. Additionally, these reefs presented patches with high cover of live and dead massive coral. Shallow depths presented high abundances of *S. adustus*, indicating a preference of this species for shallow habitats and exhibiting a two-fold increase in abundance at higher wave surge. Also, *Microspathodon chrysurus* reached higher numbers in shallow depths. Furthermore, the exposed reef presented a high cover (%) of algae groups and the fire-coral *Millepora alcicornis*, acknowledged as a preferred habitat for *M. chrysurus* and other reef fish. In this study, distinct habitat uses were observed, with patterns regulated by depth and/or wave exposure levels and/or availability of specific benthic cover. For site-attached species as damselfish, habitat specialization, competition and/or non-random recruitment patterns have been found to rule distributional patterns. Similar results for damselfish relative abundances were found compared to studies conducted within Panama and other reefs throughout the Caribbean region over three decades ago, indicating strong habitat affinity for the most abundant species. However, severe reductions of habitat availability following coral mass-mortality events may have disrupted their distributional patterns.

Key-words: pomacentrid, territorial herbivores, coral reefs, reef fish, Bocas del Toro

Introduction

Coral reefs are among the most productive systems in the marine environment (Spalding et al., 2001). These systems are changing worldwide in the last decades, due to climate changes, hurricanes, diseases, overfishing and eutrophication (Hughes et al., 2003; Pandolfi et al., 2005). Such disturbances have often resulted in ecological phase shifts, from coral- to macroalgal-dominated reefs (McCook, 1999; Scheffer et al., 2001), which may be observed on many Caribbean reefs (Hughes 1994; McClanahan et al. 2002) and other regions worldwide (Hughes et al. 2007).

Coral cover declined by nearly 80% in the Caribbean in the late 1970s and 1980s (Gardner et al. 2003), with decreases as high as 50-70% recorded in several areas along the coast of Panama (Guzman, 2003). Massive coral loss, in turn, has caused declines in structural complexity, leading to negative consequences to the entire reef community (Alvarez-Filip et al., 2009). Especially when species strongly dependent upon the cover, diversity and complexity of their respective habitat are usually more jeopardized by these natural and/or anthropogenic disturbances (Jones & Syms, 1998, Jones et al., 2004, Graham et al., 2006).

Herbivorous reef fish play major roles in reef resilience, as they control abundance and distribution of macroalgae (Szmant, 2001; Hughes et al. 2007). Territorial herbivores such damselfishes (family Pomacentridae) are capable of modifying algal communities in different ways (Hata & Kato 2003, 2004; Ceccarelli et al., 2005; Jones et al., 2006), such as enhancing the net primary production (Klumpp et al., 1987; Ferreira et al., 1998). Indirectly, territorial herbivores exert significant effects on the foraging activity of roving herbivores through their aggressive territorial defense (Hixon & Brostoff, 1993), and through “weeding” behavior distress coral recruitment, survival, and diversity (Gleason, 1996; Gochfeld, 2010). Overall, these species are considered keystone species in reef systems (Hixon and Beets, 1983).

As widely distributed and abundant on reef systems worldwide (Doherty, 1983; Meekan et al., 1995; Ceccarelli et al., 2001), damselfishes occupy up to 90% of some reef areas (Ceccarelli, 2005; Ilarri *et al.*, 2008; Medeiros *et al.*, 2007, 2010). Thus, by their abundance, behavior and directly use of turf algae, the main bulk of primary production on coral reef systems, they can be relevant actors on phase shifts from coral- to algae-dominated reefs (Ceccarelli et al., 2011). Distribution patterns found for this particular group of species, however, are highly variable at several spatial scales (e.g microhabitats, depth, exposure, reef zones, systems) (Williams, 1982; Meekan et al., 1995; Holbrook et al., 2000; Medeiros et al., 2010). Although pre-recruitment processes are important driving forces in adult abundance and distribution (Doherty, 1983), post-settlement processes such as presence of preferred microhabitats (Holbrook et al., 2000), predator abundance (Hixon & Beets, 1993), intra- and interspecific competition (Sweatman, 1985; Tolimieri, 1998; Bay et al., 2001) are as much as important. Nevertheless, different key mechanisms can be acting synergistically for each species.

This group has been studied throughout the Caribbean, with data available for habitat use, recruitment, behavior, diet and, age and growth of some species (Robertson, 1984; 1996; Gutierrez, 1998; Holbrook et al., 2000; Wilson & Meekan, 2002). However, most of these studies to date focused separately on a single or few species, thus not providing more comprehensive data on damselfish community and their association with environmental descriptors. This study aimed to determine abundance and space use of damselfishes across a coastal island of Panama, as well as their relationship with environmental factors such as depth, wave exposure and benthic cover using a more quantitative approach. We hypothesize that environmental changes, such habitat loss along the Panamanian Coast may have altered damselfish distribution patterns and habitat preferences.

Material and Methods

Study area

The present research was conducted in Bocas del Toro archipelago, Isla Colón, Panama. The whole archipelago comprises an area of ca. 3,500 km², formed by 6 large forested islands and hundreds of small mangrove cays (Guzmán, 2003). Surrounding all these islands and along a large part of the mainland coast, there are fringing coral reefs up to 20 m deep and dozens of shallow reef patches. The whole area represents the second most important contributor on reef formations in the Caribbean coast of Panama with approximately 87 km² of fringing reefs (Guszmán, 2003). The reefs of the archipelago have been evaluated in the past decade and live coral cover up to 50% has been reported, depending on the depth, reaching up to 90% in shallow areas (Guzmán and Guevara 1998a, b, 1999, 2001). Nevertheless, declines on coral cover throughout this area have also been observed in the last decade (Guzmán, 2003).

Three distinct reefs were chosen for this study (Fig.1). Pete's Reef (PT) is a shallow lagoon with patch reefs near mangrove mud flats (~1m). Water motion is low and benthic communities are dominated by numerous species of sponges and the fingercoral *Porites porites* (Pallas 1766). Conch Point (CO) is a wave-protected near-shore fringing reef lined with mangroves (*Rhizophora mangle* L.). Depths range from 0.5 to 1 m at the mangrove edge and increase to approximately 7 m at a 20 m distance from shore. The substratum immediately adjacent to the mangrove edge is covered with turtle grass *Thalassia testudinum* Koenig and green algae, while deeper areas are characterized by the presence of patch reefs and sponges. Shallower (~0.50 m) and relatively more exposed, Lime Point (LM) has a much longer fetch reaching the open waters of the Caribbean; lacking mangroves and characterized by patches of *T. testudinum* and *Syringodium filiforme* Kuetzing (manatee grass), as well as sand alongside its extension. Within this reef, sites closer to the reef edge, and deeper (~1 m) ones showed higher coverage of live coral. On PT and LM observations were done through snorkeling, whereas SCUBA was used in CO.

Surveys

The abundance and distribution of territorial damselfishes and benthic community were assessed in December 2010 and January 2011. Abundance of juveniles and adult damselfishes, as well as habitat use, were assessed using visual census for fish density and percent benthic cover over transects of 10 x 2 m (PT=20; CO=20 and LM=16; N=56). The studied damselfish species are easily distinguishable underwater based on their coloration, both as juveniles and adults. To minimize edge effect, records included damselfishes with at least 50% of its territory inside the transect boundaries.

Depth measures were taken for each transect. Benthic cover was estimated using the linear point-intercept method adapted from Liddell et al. (1984). At each 50 cm interval, substratum was recorded according to the following categories: (1) articulated calcareous algae (algae that project <5 cm above the substratum, mainly branched calcareous forms), (2) macroalgae (algae that project >5 cm above the substratum, mainly fleshy algae), (3) encrusting coralline algae, (4) filamentous algae, (5) branching corals (mainly *Millepora* spp. and *Porites* spp.), (6) massive corals (*Siderastraea* spp., *Montastraea* spp., *Diploria* spp., *Porites* spp.), (7) massive dead corals (overgrown by algae), (8) zoanthids, (9) sea urchins, (10) sponges, (11) sand, (12) rubble (pieces of broken corals), and (13) mud.

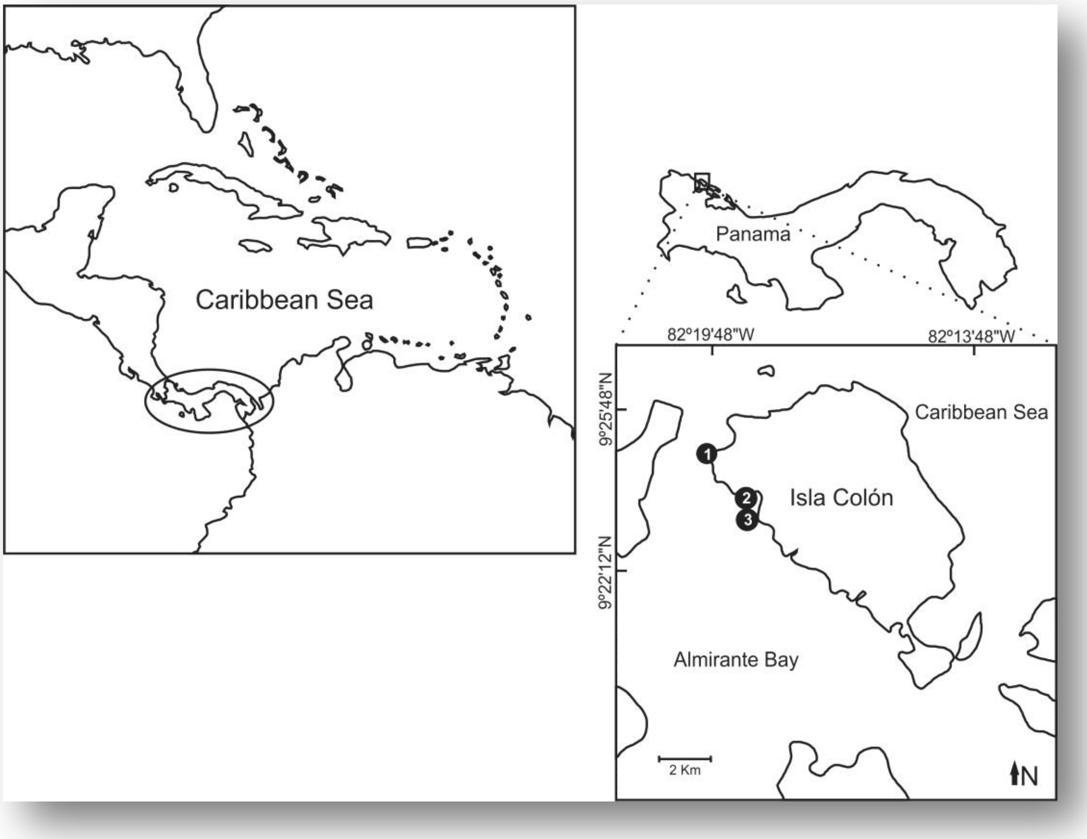

Fig. 1. Map of study area within the Caribbean region. 1-Lime Point; 2-Pete's reef and; 3-Conch Point

Statistical analysis

One-way Analysis of Variance (ANOVA) was used to test differences between species abundance at both life stages (juvenile and adult) and benthic percent cover among reefs. When necessary, data was log10 (x + 1) transformed, and the Student-Newman-Keuls *a posteriori* test was used. The structure of damselfish assemblages (i.e. relative abundance of the different species and life stages) was analyzed using non-Metric Multidimensional Scaling Analysis (MDS), which was later tested for significance of groups formed for exposure and depth factors by the Analysis of similarity (one-way ANOSIM). Separate One-way ANOSIM for these factors was also used to test differences between benthic communities (Clarke & Gorley, 2001). Species' life stages and benthic community relationship was obtained, using the canonical correspondence analysis (CCA) ordination. Significant environmental parameters were selected with the Monte Carlo permutation test. Data were log-transformed and the CANOCO for Windows 4.5 software was used (ter Braak, 1995).

Results

Damselfish distribution among reefs

Fifty-six visual censuses yielded sightings of 1,178 damselfishes belonging to six common Caribbean species: the dusky damselfish *Stegastes adustus* (Troschel 1865), the threespot damselfish *S. planifrons* (Cuvier, 1830), the beaugregory *S. leucostictus* (Müller & Troschel, 1848*)*, the bicolor damselfish *S. partitus* (Poey, 1868), the cocoa damselfish *S. variabilis* (Castelnau, 1855), and the yellowtail damselfish *Microspathodon chrysurus* (Cuvier, 1830) (Table 1). The former two species represented the majority of overall abundance, including adults and juveniles (~90%). *Stegastes adustus* was especially abundant in shallow reefs (PT and LM) (Fig. 2). The abundance of both juveniles and adults from this species were very similar in Pete's Reef, but adult abundance was significantly different between this site and Lime Point (ANOVA; $p<0.0001$) - on the latter it was observed a two-fold increase with wave (Fig. 2). *Stegastes planifrons* presented closer affinity to sheltered reefs (PT and CO), with a significant three-fold increase (ANOVA; $p<0.0001$) in shallow waters (PT). On the exposed reef (LM) juveniles presented very low abundances and adults were absent. The beaugregory *S. leucostictus* was not very abundant when compared with other species, but were observed only in sheltered reefs (PT and CO). Adults from this species were restricted to deeper patch reefs (CO), whereas juveniles did not differed in abundance between depths. Juveniles and adults of *S. variabilis* and *S. partitus* presented very low abundances and were restricted to deeper patches (CO). The yellowtail damselfish *M. chrysurus* was recorded both in the shallow and exposed (LM) and the deeper and sheltered reef (CO), showing no constraint concerning depth or exposure. Adults and juveniles, however, significantly increased 3x and 8x, respectively at LM (ANOVA**;** $p=0.0037$ and $p=0.0002$, respectively) together with the abundance of adult *S. adustus* (Table 1; Fig. 2), indicating preference for exposed reefs.

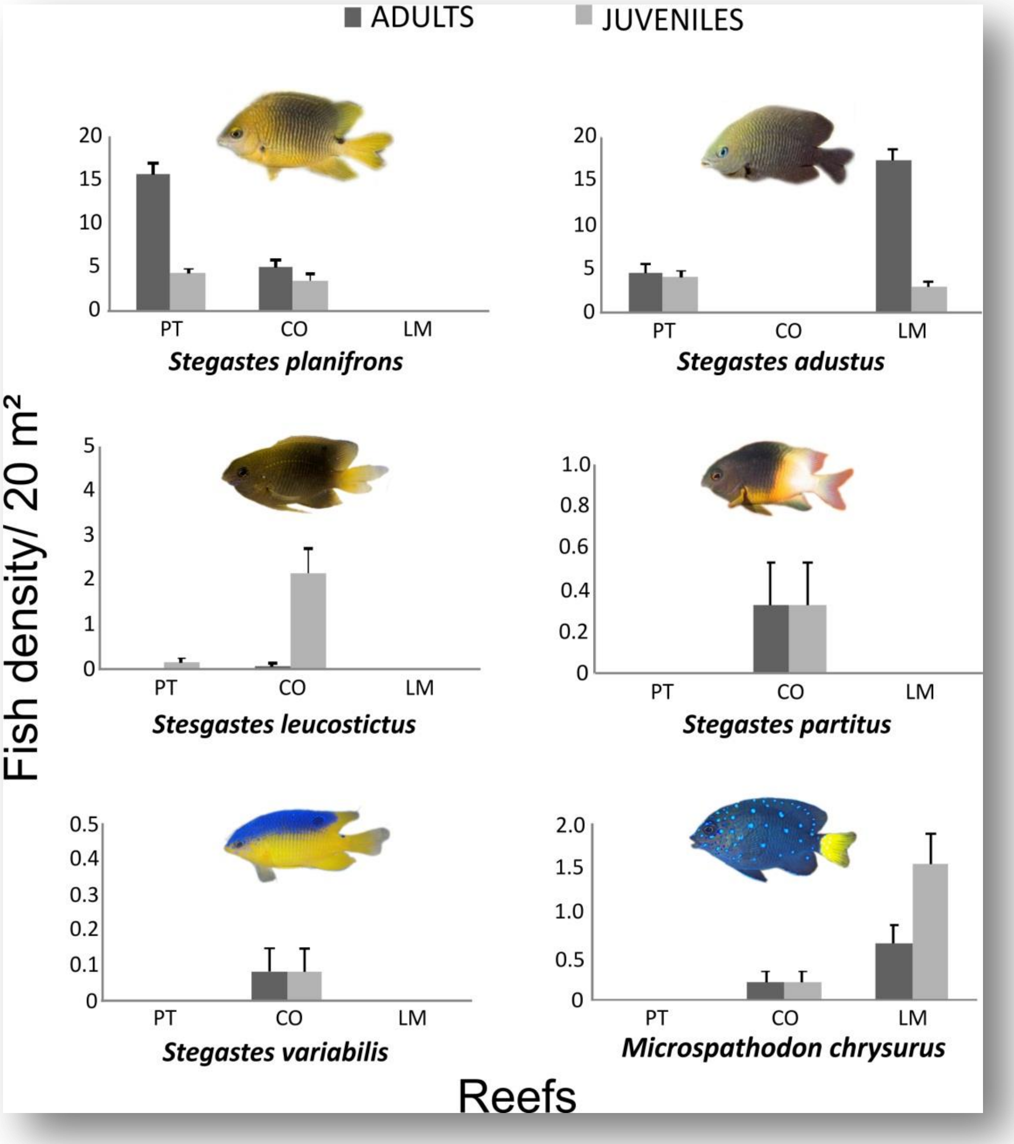

Fig. 2. Mean density per 20 m² (±S.E) of damselfish species observed in Pete's Reef (PT), Conch Point (CO) and Lime Point (LM).

Table 1: Species abundance by life stage and percent composition of substrata (Mean ± SE), plus ANOVA results and Student–Newman–Keuls (SNK) comparison between reefs. ns = non-significant; *p<0.05; **p<0.01; ***p<0.001.

	PETE'S REEF	CONCH POINT	LIME POINT	p	F	SNK
JUVENILES						
S.planifrons	4.05±0.63	4.75±1.01	0.12±0.08	***	10.36	PT=CO>LM
S.adustus	5.75±0.89	0	4.00±0.83	***	19.38	PT=LM>CO
S.leucostictus	0.20±0.11	0.10±0.06	0	***	9.73	PT=CO>LM
S.variabilis	0	0.10±0.07	0	ns	1.89	-
S.partitus	0	0.25±0.16	0	ns	2.18	-
M.chrysurus	0	0.20±0.15	1.62±0.50	***	10.07	LM>CO>PT
ADULTS						
S.planifrons	12.40±1.56	4.55±0.72	0	***	33.59	PT>CO>LM
S.adustus	4.40±0.78	0.05±0.05	17.81±1.11	***	147.69	LM>PT>CO
S.leucostictus	0	1.75±0.48	0	ns	1.89	-
S.variabilis	0	0.05±0.05	0	ns	0.98	-
S.partitus	0	0.45±0.18	0	**	5.32	CO>PT=LM
M.chrysurus	0	0.20±0.15	0.75±0.23	**	6.24	LM>CO>PT
CORAL						
Dead	26.90±2.68	15.48±2.39	0.60±0.41	***	32.98	PT>CO>LM
Massive	43.81±5.46	29.52±2.78	12.80±3.03	***	13.77	PT>CO>LM
Branching	7.86±2.32	0	7.74±2.57	**	5.71	PT=LM>CO
ALGAE						
Turf matrix	0.95±0.56	0.24±0.24	37.80±3.95	**	108.1	LM>PT=CO
Macroalgae	0.24±0.24	0	10.12±2.98	***	14.11	LM>PT=CO
Crustose	0	0.24±0.24	7.74±1.68	***	25.28	LM>PT=CO
Filamentous	8.33±4.09	12.86±1.96	13.10±2.52	ns	0.78	-
OTHER						
Zoantids	0.95±0.56	0.24±0.24	6.25±2.60	**	5.58	LM>PT=CO
Sponges	6.19±1.04	12.62±1.63	0.30±0.30	***	24.98	CO>PT>LM
Urchins	1.90±1.44	0	0	ns	1.56	-
Sand	2.62±0.94	23.57±4.07	0.30±0.30	***	24.99	CO>PT=LM
Rubble	0.24±0.24	1.19±0.59	3.27±1.28	*	4.06	LM>PT=CO
Mud	0	4.05±2.92	0	ns	1.72	-
Depth	1.15±0.02	8.15±0.08	1.34±0.04	**	1.36	CO>PT=LM

Non-metric multidimensional scaling analysis presented in Fig. 3 (a-b) showed distinct groups for damselfish communities, which were separated between wave exposure and depth. The low stress value indicated that the observed sample distribution in the two dimensional space provided a reliable interpretation of the differences among damselfish community structure at the study sites. Separated one-way ANOSIM corroborated the formation of these groups, with low degree of overlap between exposure (global R= 0.654, p=0.001) and depth (global R=0.589, p=0.001).

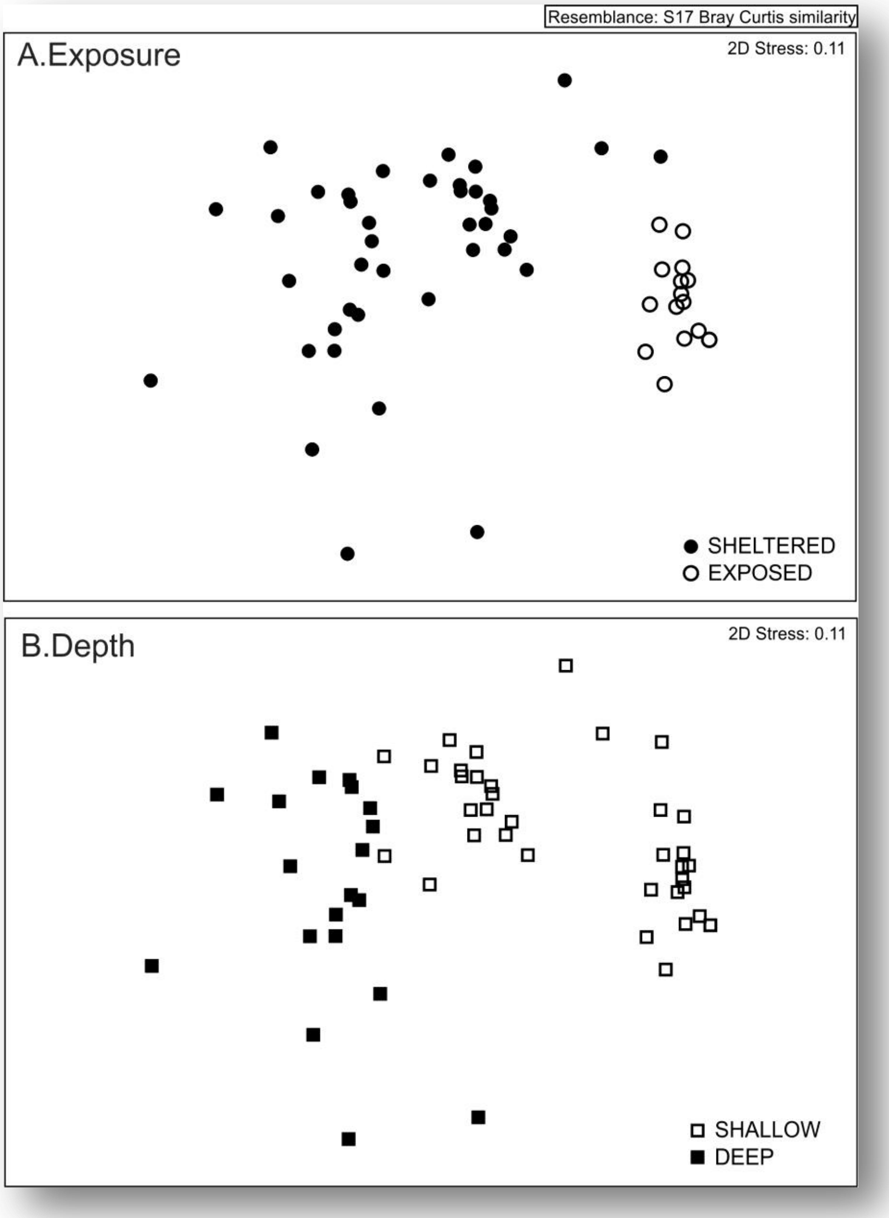

Fig. 3. MDS plots of damselfish community comparison between exposure and depth levels.

Benthic communities

Benthic communities also contributed for differences found among reefs. However, one-way ANOSIM tests detected significant differences among reefs regarding exposure (R=0.655; p=0.001), but not for depth (R=0.092; p=0.055).

Pete’s Reef (PT) and Conch Point (CO), both being sheltered reefs, presented higher cover of live or dead corals, including massive corals (mainly brain corals) and the branching finger coral *Porites* spp. (Table 1). Coral cover was always higher on the shallower reef (PT). Particularly, the deeper reef (CO) presented higher cover of sponges and sand, the latter being a consequence of more dispersed patch reefs. The exposed reef (LM) was an algae-dominated reef, comprising crustose, articulated and macroalgae. Also, colonies of the firecoral *Millepora alcicornis* Linnaeus, 1758, zoanthids and rubble were commonly observed.

Fish-habitat relationships

Habitat relationships for damselfish and benthic descriptors using the canonical correspondence analysis are presented on Fig. 4 (a-b). The first two axes were significant (p=0.001) and accounted for 61.4% and 21.6%, respectively, of the relationship between species and explanatory variables. The first axis, responsible for most of explained variation, was positively related to habitats that presented high cover of branching corals, macroalgae and articulated calcareous algae (Fig. 4a). Such descriptors represented samples of Lime Point (shallow and exposed), which *S. adustus* and *M. chrysurus* were more associated with (Fig. 4b). A discrete segregation between juvenile and adult conspecifics from these species was observed, where *S. adustus* juveniles were strongly associated to the complex structure of fire-corals. This Axis was, in the other hand, negatively represented by deeper patch reefs, contributing to high records of sandy bottoms, together with a high cover of live and dead massive corals. Such descriptors represented mostly Pete’s reef and Conch Point samples (Fig. 4b). Axis I drove most of the juveniles of S. *leucostictus*, *S. partitus* and *S. variabilis* abundance, as they were found associated with depth. *Stegastes planifrons* (juveniles and adults) showed a close relationship with massive and dead coral cover, together with adult *S. partitus* and *S. leucostictus*, showing preference for sparser patch reefs with higher cover of massive corals interspersed with sandy bottoms. Adult *S. variabilis* presented a distinct segregation from juveniles, but also associating with deeper patch reefs, explained by Axis II.

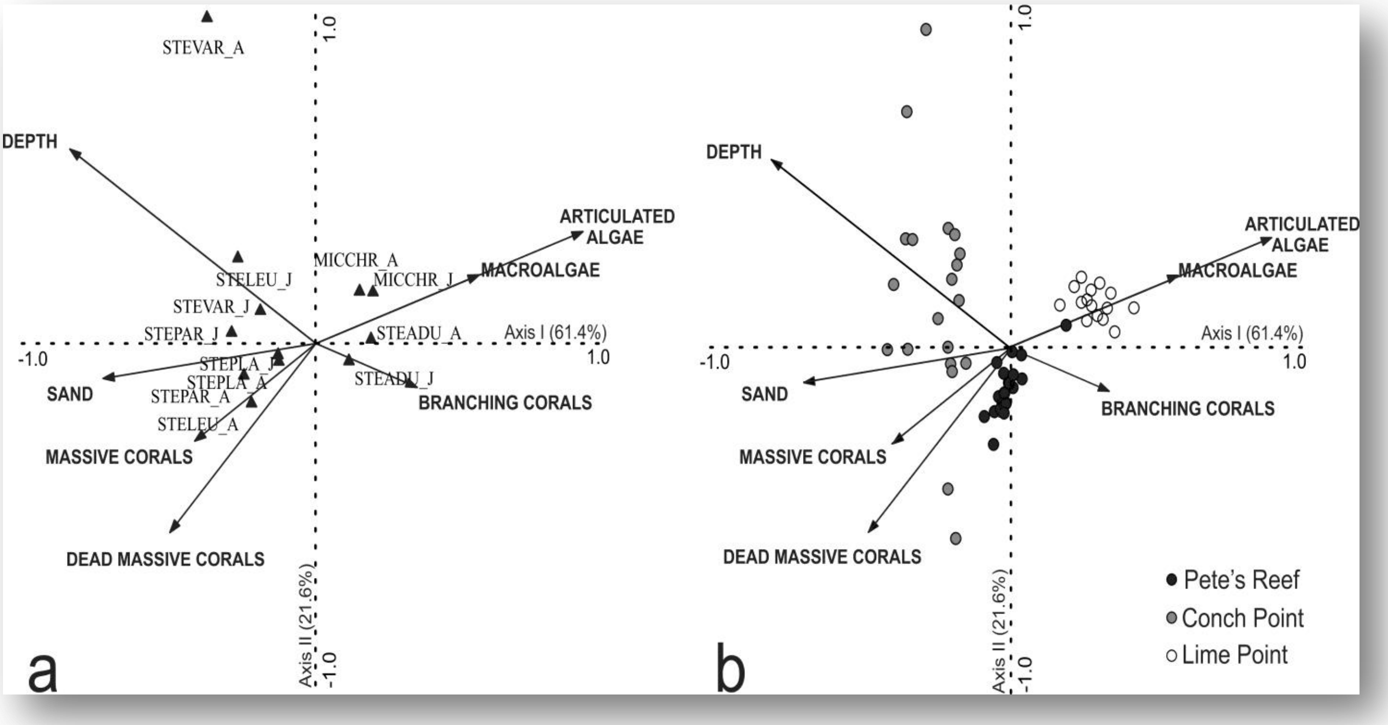

Fig. 4. Canonical correspondence analysis plot showing the correlations of the most significant variables (arrows) with fish species (a) and samples (b). Species codes: STEPLA = *Stegastes planifrons*; STEADU = *Stegastes adustus*; STELEU = *Stegastes leucostictus*; STEVAR = *Stegastes variabilis*; STEPAR = *Stegastes partitus*; MICCHR = *Microspathodon chrysurus*. The letters (J and A) following the species code names denote juvenile and adult, respectively.

Discussion

Habitat use

Although this work used a more quantitative approach than previous studies, damselfish distribution seemed to follow the prevailing patterns of habitat use found for this group of fishes throughout the Caribbean Sea in the last decades (Itzkowitz, 1977; Waldner & Robertson, 1980; Robertson, 1981; 1984; 1996). However, differences were found in respect to benthic cover they associated to. In addition, it was possible to detect the habitat partitioning and segregation among different species.

At a broader scale, differences regarding reefs were found not only for damselfish species composition, but also for benthic communities. These differences may be due to the influence of wave energy. It has been demonstrated that wave-stressed habitats are dominated by organisms with life histories adapted to a disturbance regime, presenting high resistance, such as coralline algal communities (Witman, 1992). In this study, reefs with more pronounced wave surge allowed a diverse algal community, including crutose types, as much as the encrusting and heavily calcified firecoral *Millepora alcicornis*, with a major contribution to bottom cover. In the other hand, sheltered reefs had a more prominent colonization of massive corals, such *Montastraea* spp. and *Diploria* spp.

Considering damselfish abundance, the dusky damselfish *S. adustus* presented higher abundances on Pete's reef and Lime Point, indicating a preference of this species for shallow habitats, but it exhibited a two-fold increase in abundance at higher wave surge. This species is not particularly abundant in other Panamanian reefs (Robertson, 1996), but has been already recognized to prefer shallow and high wave energy habitats (Waldner & Robertson, 1980; Gutierrez, 1998; Dominici-Arosemena & Wolff, 2005). It also refuges on structural complex colonies of the elkhorn coral *Acropora cervicornis* (Waldner & Robertson, 1980). However, in this study, this species associated with colonies of the firecoral *Millepora alcicornis*, very resistant to water motion. As this hydrocoral presents a ramified hard structure, it apparently sustained the high abundance of *S. adustus*, as in many other reef fish species (Pereira et al., 2012; Coni et al., 2012). Moreover, wave exposure and any branching coral seem to be habitat requirements to the dusky damselfish, which should increase their vulnerability to habitat loss considering the massive mortality of Acroporid species throughout the Caribbean (Precht et al., 2002; 2010). Colonies of *M. alcicornis* seem to be also a preferred substrate for *M. chrysurus*, such as on Jamaica, Florida, Bahamas and Panama (see Waldner & Robertson, 1980; Robertson, 1984), and also on Brazilian tropical reefs (Ferreira et al., 2005). This study found that highest abundance of juvenile *M. chrysurus* followed this association and fish may use *Millepora* spp. not only for shelter, but perhaps also for feeding on the soft tissues, mucus or small epibionts (Ciardelli, 1967; Pereira et al., 2012).

In contrast, *Stegastes planifrons* was highly abundant in sheltered reefs, as previously noticed in other studies (Waldner & Robertson, 1980; McGehee, 1994; Dominici-Arosemena & Wolff, 2005). It was correlated especially with cover of live massive and dead corals, where its abundance increased. As past information on benthic cover is lacking one could not confirm pervasive habitat loss, however it is strong evidence that a habitat shift have occurred already for *S. planifrons*, as recently described by Precht et al., (2010). This author provided valuable information on the lethal consequences of habitat shifts of this species, from branching forms (*Acropora* spp.) to massive corals (*Montastraea* complex) and *Porites porites*, which are the main corals found in sheltered reefs of Isla Colón. *Stegastes planifrons* predation on living tissue and consequent extensive coral mortality, benefits the proliferation of algal gardens (Precht et al., 2010), and its association also with dead corals could be an indication of this activity by *S. planifrons*. Such relationship should be specifically addressed at this point.

The role of interspecific interactions

Size and aggressiveness differences are among the most important factors driving the outcomes of competition for space in damselfish (Robertson & Lassig, 1980; Robertson, 1984; Danilowicz, 1997). Damselfish of the genus *Stegastes* are relatively small territorial fish and some are considered extremely aggressive (Itzkowitz, 1977; Robertson, 1984; 1996; Menegatti et al., 2003; Osório et al., 2006; Medeiros et al., 2010). An invasion of territory usually results in aggressive responses towards both conspecifics and heterospecifics, including individuals two or three size bigger (Pereira & Ferreira, 2012).

Adults of *S. adustus* and *S. planifrons* are more strongly dependent on benthic algae for food than *S. partitus*, which commonly feeds on both planktonic and benthic material, or *S. leucostictus* and *S. variabilis*, which are more omnivorous benthic feeders (Emery, 1973; Robertson, 1984), indicating that coinciding food resource use would only be compensated with less territory overlapping. Direct causal relationships between fish abundances are hard to detect and not always clearly evident, as they are highly dependable on the fluctuations in recruitment and adult populations. However, the effects of interspecific competition on demographics and distribution were already detected in damselfish (Robertson, 1996). *Stegastes planifrons*, by its aggressiveness and population numbers, is known to have a negative influence on *S. partitus* and *S. variabilis* abundance, assuming an asymmetric competitive relationship (Robertson, 1996).

Stegastes adustus is also abundant and aggressive (Robertson, 1996), but both species are known to show little overlap in their distribution (Waldner & Robertson 1980; Robertson

1984; Gutiérrez, 1998). Herein they clearly followed the same trend in relation to adults of one another. The absence of *S. planifrons* on LM reefs and presence in lower abundance of *S. adustus* in PT indicate that the latter, at some level is a more habitat generalist in shallow depths, whereas *S. planifrons* seems to be more specialized, occurring generally only over live massive coral colonies, as described previously. These distributions indicate that interspecific competition could have strong effects on abundances of species in shared habitats of *S. adustus* and *S. planifrons*. However, habitat preferences would be the primary factor responsible for segregation, and that is observed since very early stages of life (Gutiérrez, 1998).

Furthermore, habitat partitioning by territorial herbivores brings also light to other interactions than competition. *Stegastes adustus* and *M. chrysurus* reached higher abundances when sharing habitats at Lime Point reefs. In fact, this association was reported over three decades ago by other authors (Clarke, 1977; Itzkowitz, 1977; Waldner & Robertson, 1980; Robertson, 1984), indicating an interesting pattern of behavior. The exclusion of *M. chrysurus* by adult *S. planifrons* is usually expected, due to the high aggression of the latter (Robertson, 1984). It has been argued that *M. chrysurus* may benefit from the smaller-sized *S. adustus* for its higher ability of territory defense, which may allow then to take long distance movements for reproduction (Sikkel & Kramer, 2006) or feeding activities.

Adults of *M. chrysurus*, although also associated with *Millepora* colonies on this study, are less dependent of shelter, attaining larger shared territories with *S. adustus* (LCTC, pers. obs.), and taking advantages of co-defense of their boundaries. Regardless of the fitness costs for the "host" *Stegastes*, this relationship indicates high stability of damselfish behavioral traits.

Further considerations

In spite of small-scale variability, similar trends were found for damselfish habitat use compared to previous studies. Although pre-recruitment processes are likely to play an important role, the high longevity of this group known to be over a decade long (Kohda, 1996; Schwamborn & Ferreira, 2002), probably confers some population stability and contributes for the maintenance of their distributional patterns over a large time span. This stability, however, may be disrupted by major environmental changes such as the mass mortality of important structuring corals during disturbances (e. g. El-Niño events, hurricanes, diseases).

At a local spatial scale the presence of preferred habitats, such as live corals, is of major importance and a massive coral cover loss (almost 80%) throughout the Caribbean in the last decades (Aronson & Precht, 2001; Gardner et al., 2003; Guzman, 2003; Edmunds & Elahi, 2007; Alvarez-Filip et al., 2009) may have resulted in lower recruitment and associated reduction in damselfish population size. For instance, *S. planifrons* faced decreased adult abundance after declines of *Acropora* spp. throughout Caribbean reefs, which represented negative consequences for secondary preferred habitats, such algae overgrowing massive corals (Precht et al., 2010).

Although the reefs studied are not yet considered algae dominated systems and past data are lacking, they have probably suffered modifications in the last decades due natural and land based impacts. Bocas del Toro has been subjected to several anthropogenic disturbances due to the increasing tourism activity. This came together with other human impacts such as artisanal fisheries, sport fishing and the environmental stresses resulting from diving activities (Dominici-Arosemena & Wolff, 2005). Yet, we have no knowledge on how damselfishes responded in a pervasive manner to these changes.

Damselfish patterns of local distribution may be good indicators of health on coral reef systems. As well adapted species to present conditions and in a scenario of community homogenization due to overfishing, hurricanes and other stressors along the Caribbean, the abundance patterns of *S. planifrons* and *S. adustus* in Isla Colón may be an important reference point. Moreover, understanding how these fish are facing changes and how good indicators they are would be a useful tool to become aware of such environment modifications.

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CAPÍTULO IV: **Age and growth patterns of a widespread tropical reef fish in the Southwestern Atlantic**

***** Padrões de idade e crescimento em um peixe recifal tropical amplamente distribuído no Atlântico Sul

Formatado para submissão na revista científica "Marine Ecology Progress Series"

RESUMO

Análises de idade e crescimento foram utilizadas para verificar diferenças nos parâmteros de crescimento, mortalidade e longevidade entre populações do peixe-donzela *Stegastes fuscus* (Pomacentridae) com exemplares coletados em recifes tropicais (Tamandaré - 8º 45' S; 35º W) e subtropicais (Arraial do Cabo - 23º 44’ S; 42ºW) da costa brasileira. As populações tropicais também foram comparadas entre os anos de 1995 e 2011 para verificar mudanças temporais nos mesmos parâmetros. Os indivíduos alcançaram comprimentos maiores, assim como maior longevidade com o aumento da latitude. Nos recifes subtropicais, o maior comprimento furcal foi 138 mm, enquanto que nas populações tropicais, este alcançou o máximo de 105 mm FL. A classe etária mais velha em adultos, no recife subtropical foi de 17 anos, diminuindo para 15 anos em 1995 e 16 anos em 2011 no recife tropical. As curvas de crescimento também foram significativamente diferentes, particularmente entre diferentes latitudes. Isto vai de acordo à regra de Bergman, que sugere que indivíduos maiores em uma espécie ocorrem em altas latitudes/menores temperaturas e que a tendência de maior longevidade é inerente de taxas fisiológicas mais baixas. Entretanto, outros processos, como a competição e predação podem ser uma importante fonte de variabilidade local quando medidas de manejo são adotadas. No caso deste estudo, foi criada uma área de proteção integral, e isso se refletiu numa menor condição atual de indivíduos no sistema tropical. Esse estudo sugere que o uso de parâmetros demográficos agregados para uma espécie obtidos em diferentes escalas deve ser feito com cautela.

Age and growth patterns of a widespread tropical reef fish in the Southwestern Atlantic

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Running-head: Age study of a tropical damselfish

ABSTRACT

Age-based analyses were used to demonstrate consistent differences in growth, mortality and longevity between populations of *Stegastes fuscus* (Pomacentridae) collected at tropical (Tamandaré - 8º 45' S; 35º W) and subtropical reefs (Arraial do Cabo - 23º 44’ S; 42ºW) along the Brazilian coast. Tropical populations were also compared between the years of 1995 and 2011 to verify temporal changes on life history parameters. Fish had significantly greater maximum lengths and reached larger life span in higher latitudes. In subtropical reefs fish reached maximum fork length of 138 mm, whereas in the tropics they reached maximum of 105 mm FL for populations in both periods. The largest age class of adult-size fish collected from subtropical location comprised 17 year-olds, while in tropical reefs ranged between 15 in 1995 and 16 year-olds in 2011. These results extend the validity of Bergmann’s rule, which states that larger individuals within species occur towards higher latitudes and/or lower temperatures, as to get older at higher latitudes could be an inherent tendency when physiological rates are slower. Other density–dependent interactions, such competition and predation are also important sources of local variability between populations on tropical systems, especially when management actions are observed. In the present study the creation of a no-take may resulted in fish condition decrease. Our study suggests that pooling demographic parameters over large streches of coast may result in increased error, particulartly on the spatial scale.

Key-words: life history trait, damselfish, otoliths, growth parameters

INTRODUCTION

In reef fish populations, the study of age and growth brings important information on basic life-history parameters, such as estimates on recruitment, growth rates, spawning seasons, longevity and mortality (Choat & Robertson, 2002). These data have been a useful tool for fisheries and ecosystem management, as they aid managers to assess how a given level of fish stock exploitation is sustainable and how its life-history has been affected by fisheries (Brothers, 1979, Smith et al., 1992). It is also important to understand the demography or life histories of non-target species, which can be affected indirectly by this activity (Heithaus et al., 2008). For instance, changes in size and longevity of herbivores can strongly influence grazing rates, which can in turn influence abundance of some groups of algae that compete with corals for space on the reef (Paddack et al., 2006, Hughes et al., 2007). In addition, it can provide fishery independent insights in population dynamics, and is a valuable measure of the effectiveness of marine reserves and other specific management strategies (Trexler & Travis 2000, Murie & Parkyn, 2005).

Many species of fish have broad geographical distributions, spanning a wide range of habitats (Gillanders, 1995, Meekan et al. 2001, Gust et al., 2002, Jones et al. 2002). However, fish exhibit considerable plasticity in demographic features associated with locality and habitat variables (Gust et al., 2002). Several factors may account for the variability among populations. At the local scale conspecifics' density, predation rates, competition, resource availability and wave exposure are of fundamental importance (Atkinson & Sibly, 1997, Holbrook & Schmitt, 2002, Ackerman, 2004, Fulton & Bellwood, 2004). For this reason geographical variation in population size and age structure has been shown for a number of coral reef fish species at different scales (Meekan et al., 2001, Robertson et al., 2005, Trip et al., 2008).

Along these lines, both the quality and magnitude of demographic variation and the spatial scale in which it occurs can be measured by assessing populations from different locations and/or habitats (Gust et al., 2002), and possibly also at a temporal scale on a particular location where management actions have taken place or different levels of fishing are observed through time (Ruttemberg et al., 2011, Walsh et al., 2012). Nevertheless, temperature is thought to be the most significant factor affecting fish at a larger scale, indicated by several studies. Bergmann's rule, for example, states that larger species or larger individuals within species (see Gaston et al., 2008) occur towards higher latitudes and/or lower temperatures, and this is well described for several vertebrate groups (Lomolino et al., 2006); also for marine fishes (Choat & Robertson 2002; Barneche et al., 2009).

As other ectotherms, fish have no or a limited ability to control their body temperature (Henderson, 2005). Many studies demonstrated that even small increases in temperature cause large increases in energetic costs for body maintenance, as metabolic rate increases exponentially with temperature (e.g. Fry, 1971, Brett, 1979, Jobling, 1994, Jobling, 1996). These costs diminish their virtual energy for allocation to other life history traits such as growth and/or reproduction in fish (Brett, 1979, Yamahira & Conover, 2002). For circumventing the associated fitness loss, fishes underhigher temperatures tend to eat more, which in turn increases their exposure to predators and substantially reduces their survival (Biro et al., 2004, Biro et al., 2007, Stamps, 2007). Following this argument, organisms living in colder, higher latitude environments should have lower growth rates, higher age at maturity, and higher longevity, since physiological processes would be desacelerated. Growth rates are thus important parameters to be monitored for climate variations, as those have been reported to change the hydrographic and productivity delimitations of large marine ecosystems (Sherman et al., 2009). At the temporal scale, changing environmental conditions and the influence of strong cohorts (Ferreira & Russ, 1995; Russ et al., 1996) may be accountable for the differences. Additionally, one of the main ways in which predator–prey interactions of non-target species may be indirectly affected is through fishing activities (Heithaus et al., 2008). Therefore, growth parameters and fish condition would allow inferences on local historical events regulating populations, such as the creation of no-take zones.

The dusky damselfish *Stegastes fuscus* (Cuvier, 1830) is endemic to the Brazilian coast and it is widely distributed with exception of oceanic islands, where other endemics or sister species prevail (Sampaio et al., 2006). This species is the most abundant fish in Brazilian reef systems

(Ferreira et al., 1995, Ferreira et al., 1998, Menegatti et al., 2003; Osório et al., 2006, Chaves et al., Chapter 2) but not a fishery target, and despite of its ecological importance as a key-stone species (Ferreira et al., 1998), little is known about its life-history traits (but see Schwamborn & Ferreira, 2002, Souza et al., 2007). Its large extension of distribution plus high abundance provides an interesting scenario to examine variation in age-based parameters across its geographical range.

As an ectothermic animal, temperature changes are expected to influence its physiological responses in behaviour, growth and reproduction, as found by many studies (Wood & McDonald 1997, Munday et al. 2008, Barneche et al., 2009, Johansen & Jones, 2011). We hypothesize then, that as populations of *Stegastes fuscus* grow to smaller adult sizes at tropical reefs, they would also have lower survival rates and shorter life spans at lower latitudes than those living at higher latitudes. Additionally, we compare populations parameters obtained for the tropical system in 2011 with those derived from samples collected in 1995 at the same study site (see Schwamborn & Ferreira, 2002). Since then, the entire area was declared a Marine MPA in 1997 and a no-take area has been created in 1999, near the study site. So, if a non-target species is released from indirect effects of fishery activities, populations in the same local would present changes on growth parameters, as the contrary situation would have favoured the the population in the past, by increased condition (e. g. higher longevity, lower predation, larger total length/weight) (Ruttemberg et al., 2011, Walsh et al., 2012), when released from predators and/or competitors targeted by fisheries. Thus, the specific questions posed herein were: 1) Are there differences in growth parameters and age structure in *Stegastes fuscus* between reef systems separated by 15 degrees of latitude?; 2) Are differences in size structure observed among sampling localities driven by growth or mortality patterns, or a combination of these?; 3) Are changes in life history parameters and population structure detectable over a 16-year interval?

MATERIALS AND METHODS

STUDY AREAS AND FIELD SAMPLING

This investigation examined otoliths of *Stegastes fuscus* at two localities along the Brazilian Coast; including Tropical (Tamandaré, Pernambuco State: 8º 45' S 35º W) and Subtropical reefs (Arraial do Cabo, Rio de Janeiro State: 23º 44’ S; 42ºW), spanning 15° of latitude (FIG.

1). The tropical reefs of Tamandaré are located within the MPA Costa dos Corais created in 1997, and the study site is close to a well established no-take zone operating since 1999. The subtropical rocky reefs of Arraial do Cabo, in the other hand, are influenced by coastal upwelling during the summer/spring periods (Valentin, 1984), however, the reefs that have been studied are only sporadically affected and typically only in the deeper habitats (Ferreira *et al*., 1998).

Reefs within each system were selected to obtain a representative sample of the local population between NOV 2010 and MAR 2011, where this species was observed to be abundant in several size classes (Chaves et al., unpub. data). A total of 175 individuals were collected from Tropical reefs and 143 from Subtropical rocky reefs. Collection sites at Tamandaré comprised the reefs of Igrejinha as in Schwamborn & Ferreira (2002) for further temporal comparisons between years 1995-2011 and in Arraial do Cabo, included Prainha and Forno Beaches, both locations sheltered from wave surge, a factor known to widely influence *Stegastes fuscus* abundance in both systems (Chaves et al., Chapter 2), thus avoiding differences related to this factor. Using SCUBA and snorkeling, individuals were collected covering both the juvenile and adult size ranges, which were 45-125 mm Total length (TL) for Tamandaré reefs and 65-157 mm TL Arraial do Cabo. Sea urchin was used as bait to attract specimens out of their territories. Once attracted, fish were caught with spears, cast and/or hand nets.

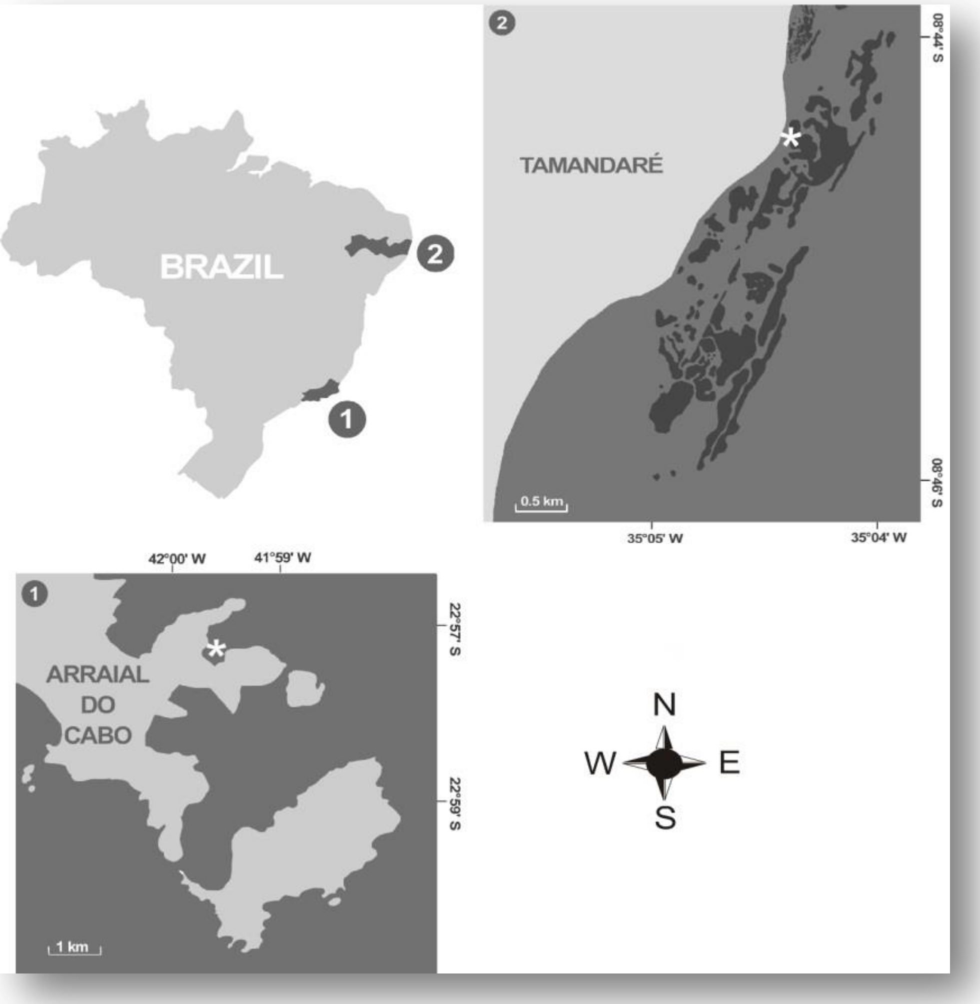

Figure 1. Study areas: (1) subtropical reef; (2) tropical reefs. * represents sample sites

AGE DETERMINATION

Immediately prior to dissecting, the fish were weighted (g) and standard length (SL), total length (TL) and fork Length (FL) were measured to the nearest 0.1mm. To assess age of the fish both sagittal otoliths were removed, cleaned in distilled water, and stored dry. Schwamborn & Ferreira (2002) validated the formation of annual increments in *S. fuscus*, and this validation was used herein for aging fish of both systems. One sagitta from each pair was used for section readings and the other was used for readings of whole otolith. The otoliths were embedded in an epoxy resin and sectioned transversely (approximately 100-150 μm thick) with a Buehler® Isomet low-speed saw. Then they were polished using 600-2000 grit sandpaper, sanding in a circular motion, which kept polishing even. Sections were mounted on glass slides with Entellan© and examined and counted from the primordium to the rim along an axis for opaque bands. White incident light under a dissecting microscope was used for readings.

Transverse sections of sagittae from both systems contained an alternating sequence of opaque and translucent zones that formed an interpretable pattern of increments, although opaque zones were more evident on subtropical samples. Each otolith was read at least two times for annuli to assess the index of average percentage error (IAPE) between readings (Beamish & Fournier, 1981). If counts varied more than 10%, the readings were repeated. If necessary a second reader was used to assess the IAPE between readers. If the readers diverged by more than 10% for a given otolith section, the readings were repeated by a third. The data were included by consensus, considering also the readings of whole otoliths for younger ages.

AGE AND SIZE STRUCTURE

Age and size frequency distributions, were constructed and compared between the tropical and subtropical systems, and between 1995 and 2011 in the tropical system, using Kruskal-Wallis and all-pairs multiple comparisons through the Steel-Dwass *a posteriori* test. Adittionally, as morphometric condition indices are inexpensive, mostly non-destructive, and easily calculated from historical datasets that describe the length and weight of individuals (Lambert and Dutil, 1997), condition factors between years of the tropical system were used as life history proxies at each size class and, compared to detect changes in the population in a 16-year interval. For this comparison, we only used individuals within the same period of the year from both populations in order to minimize reproduction-induced variations. The Fulton’s condition factor (K) was obtained for each size class by the expression:

$$Kmean = 100W/FL^{(b-3)}$$

where W is the mean total weight (g) at each size class, FL is the mean Fork Length (mm) at each size class, and b is the coefficient obtained from the length-weight relationship curve obtained for each sample.

GROWTH CURVES

Growth was investigated by fitting the von Bertalanffy (1938) growth function (VBGF) to size-at-age data using the nonlinear optimization method on the Kaleidagraph 4.0 software. The model was fit for each system and year separately. The growth function is defined as Lt = $L\infty \ (1 - e^{-k(t\ -\ t0)})$, where Lt is length at time t, L∞ is asymptotic length, k is the growth coefficient and t0 is the hypothetical time at which length is equal zero. Because the VBGF parameters can be sensitive to range of ages and size used, t0 was constraint to 0 for all populations, as it is often small and has little effect (Roff, 1984). To determine significant differences between mean lenghts for each age class of both populations, F-tests were performed to test for equal variances. Following this either t-tests for unequal or equal variances were performed (Zar 1996). All tests of significance were at $\alpha = 0.05$.

Additionally, VBGF for *S. fuscus* from Tamandaré and Arraial do Cabo reefs were tested for statistically significant differences as well as for *S. fuscus* from Tamandaré populations between 1995 and 2011. Two non-linear comparisons of growth curves were performed: a) Analysis of the residual sum of squares (ARSS) (Chen et al., 1992), and b) Likelihood ratio test (LRT) (Kimura, 1980, Haddon, 2001). For the ARSS the following procedures were employed: a) VGBF parameters for each sample (Tamandaré 1995 and 2011, and Arraial do Cabo 2011) was estimated as already described, b) residual sum of squares (RSS) and an associated degree of freendom (DF) of VBGF were calculated for each sample, c) the resultant RSS and DF of each sample were added to produce a summed RSS and DF, c) data of all samples were pooled to calculate the RSS and DF of a total VBGF and d) the Fisher statistic was calculated as:

$$F = \frac{\frac{RSS_p - RSS_s}{DR_{RSS_p} - DF_{RSS_s}}}{\frac{RSS_s}{DF_s}} = \frac{\frac{RSS_p - RSS_s}{3(K-1)}}{\frac{RSS_s}{N-3.K}}$$

where RSSp = RSS of each VBGF fitted by pooled growth data, RSSs = sum of the RSS of each VBGF fitted to growth data for each individual sample, N = total sample size and K = number of samples in the comparison.

The LRT was performed through a code developed for running it at the Fish Methods Package to the R software (Nelson, 2013). The results for linear constraints under each testing hypothesis are given.

LONGEVITY, MORTALITY AND SURVIVAL

Two types of longevity measurement were assessed. The oldest individuals found (maximum age), and the mean age of the oldest 10% (mean maximum age) of each population (Gust et al., 2002; Buechler, 2005). This maneuver was made because longevity estimates based on only the oldest specimen in a population may over-emphasize the age of outliers in local age distributions.

An estimate of total mortality (Z) was obtained by using the age-based catch-curve method of Beverton & Holt (1957). The natural logarithm of the number of fishes within each age class was plotted against their corresponding age, and Z was estimated from the descending slope, b, and as this species is not commercially exploited, total mortality was considered equal to natural mortality (Z=M). Catch curves were then compared in pairs through the two slope comparisons method (Zar, 1996). Survivorship (S expressed as %.year^{-1}) for each population was calculated from the above estimates of mortality following $S=e^{-M}$.

RESULTS

OTOLITH READINGS

There were notable differences in the clarity of the incremental macrostructure of otoliths between locations. The otoliths from subtropical reefs were easier to interpret than those from the tropics. However it was possible to obtain estimates of growth of tropical and subtropical individuals of *Stegastes fuscus* based on otolith readings (FIG. 2).

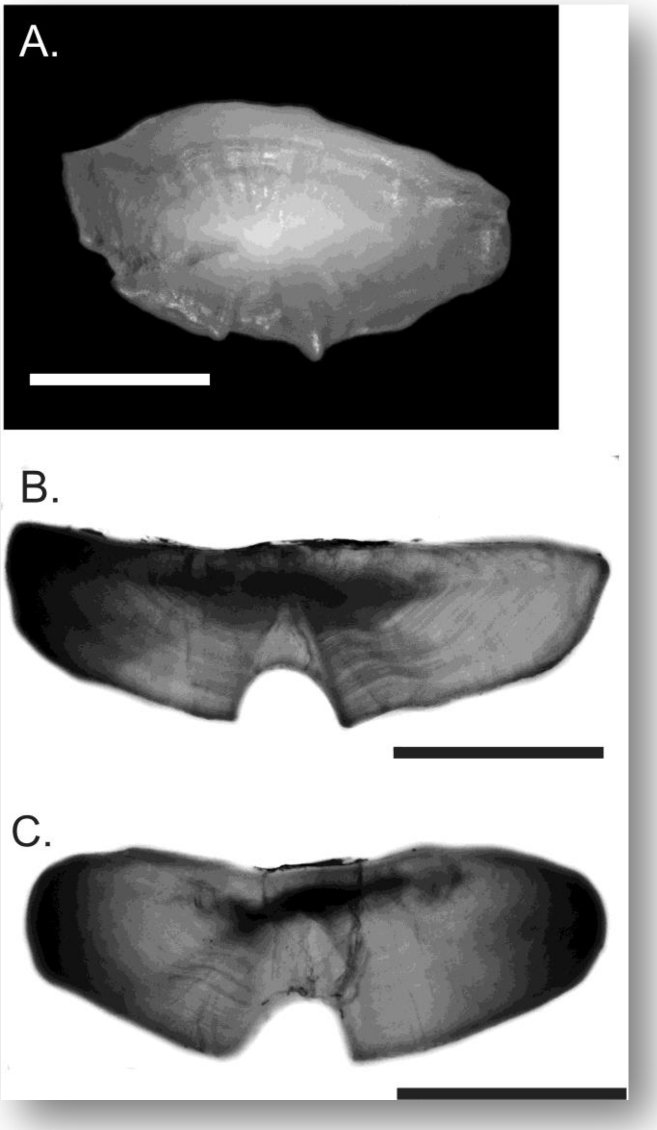

Figure 2. Whole and sectioned otoliths of a (a) 4 and a (b) 7 year old *S. fuscus* in the subtropical system and a sectioned otolith of a (c) 9 year old individual in the tropical system in year 2011, showing a dense central opaque region and a subsequent alternating sequence of opaque and translucent bands (Scale bar = 0.5 mm).

COMPARISON OF AGE STRUCTURES

As all damselfish collected were aged and measured we were able to construct age and size frequency distributions from both studied systems and years. Individuals in the 0+ age group were underestimated in the population age structure because the collection method was unable to capture recruits or juveniles around 30-40 mm. Thus, information on age “0” is not presented here in any of the analyses performed.

The age and size structure of the tropical system population was unimodal and skewed toward the younger age classes (3-7 years) (FIG.3). The modal age was 5 years and 7 cm FL but there were also substantial numbers of 0-4 year old and 4-6 and 9 cm FL fishes. Over 65% of damselfish sampled were 6 years of age or less and over 88% were 5-9 cm FL. From 5 years of age and 9 cm FL the frequency of individuals declined with individuals older than 12 years and larger than 9 cm FL relatively rare, with 7% and 6.2%, respectively. The oldest individuals recorded were 16 years of age and the largest 11 cm FL. The subtropical system age frequency distribution differed significantly from that at the tropics (KW, $p<0.0001$; DS, $p=0.0012$), as it was weakly unimodal with the sample dominated by 7 year-old individuals. However, as with the tropical system, older individuals (from up to 7 years) rapidly declined in the sampled population; yet individuals older than 10 years comprised 28% of population. The size frequency distribution was strongly unimodal, skewed towards the largest individuals (12-13 cm FL) and also significantly different from the tropical system (KW, $p<0.0001$; DS, $p<0.0001$), where individuals reached maximum lengths faster than in the tropics.

The age and size structures of the same tropical system compared between the years of 1995 and 2011 (16 years) allowed us to infer on differences between age and size structures after the creation of a no-take zone and after the population turnover, as according to Schwamborn & Ferreira (2002), they live 15 years. As shown on FIG. 4, during both periods the tropical population presented unimodal distributions for size classes (FL) and age. Size frequency distributions differed significantly among populations (KW, $p<0.0001$; DS, $p=0.0003$) with a modal size around 7-9 cm FL, but higher for 2011. Age distributions were not different in the post-hoc test (SD; $p=0.659$), however, both were skewed toward younger age classes, with the population of the year 2011 presenting a more flattened distribution while in 1995 class modes for 5 and 6 years were more pronounced. The population of 1995 also presented more individuals with age "0" distributed within smaller size classes. More than 77% of population was between 3 and 8 years and 63% between 7 and 10 cm FL.

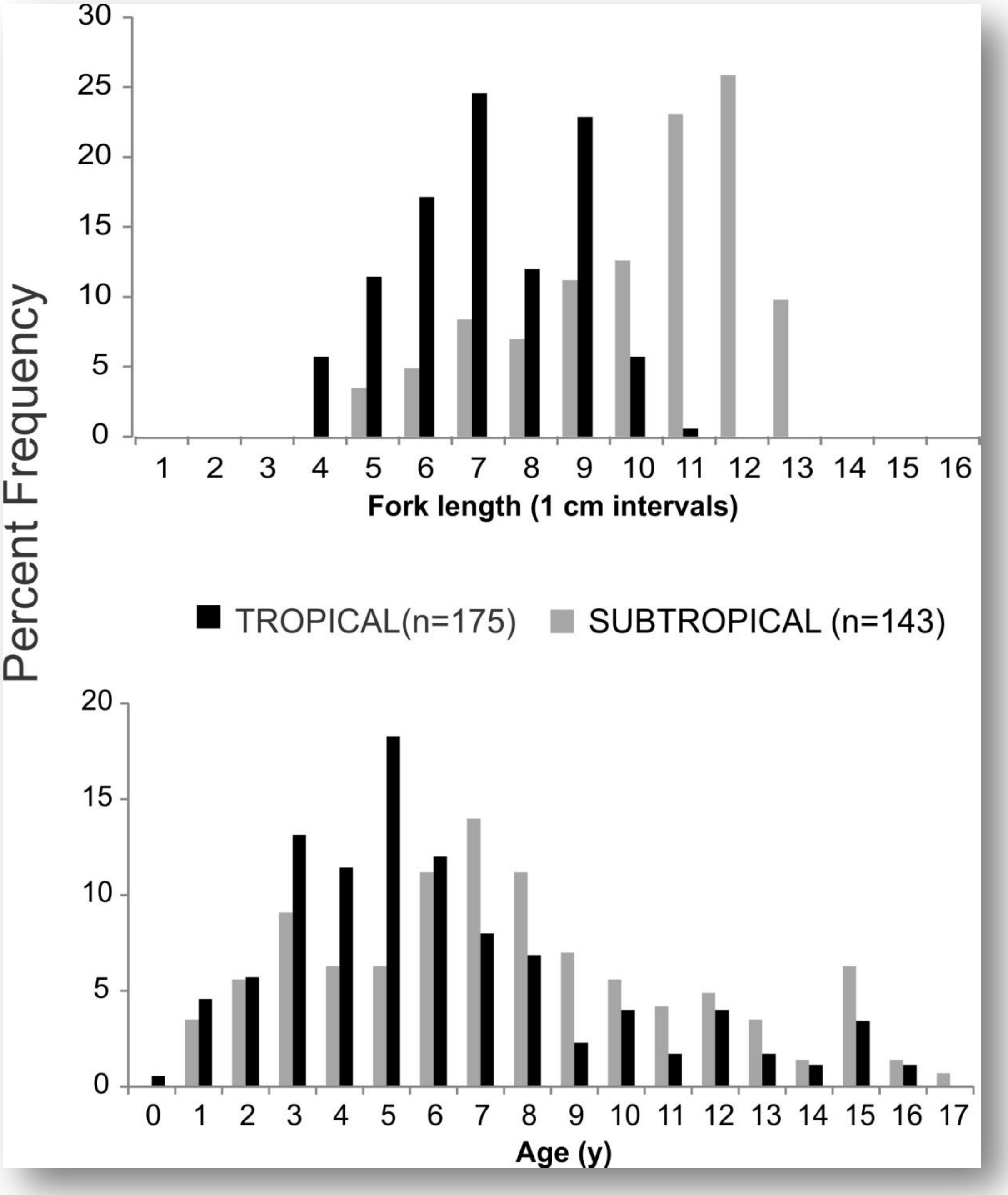

Figure 3. Age and size frequency (%) distributions of damselfish collected from the subtropical and tropical systems in 2011.

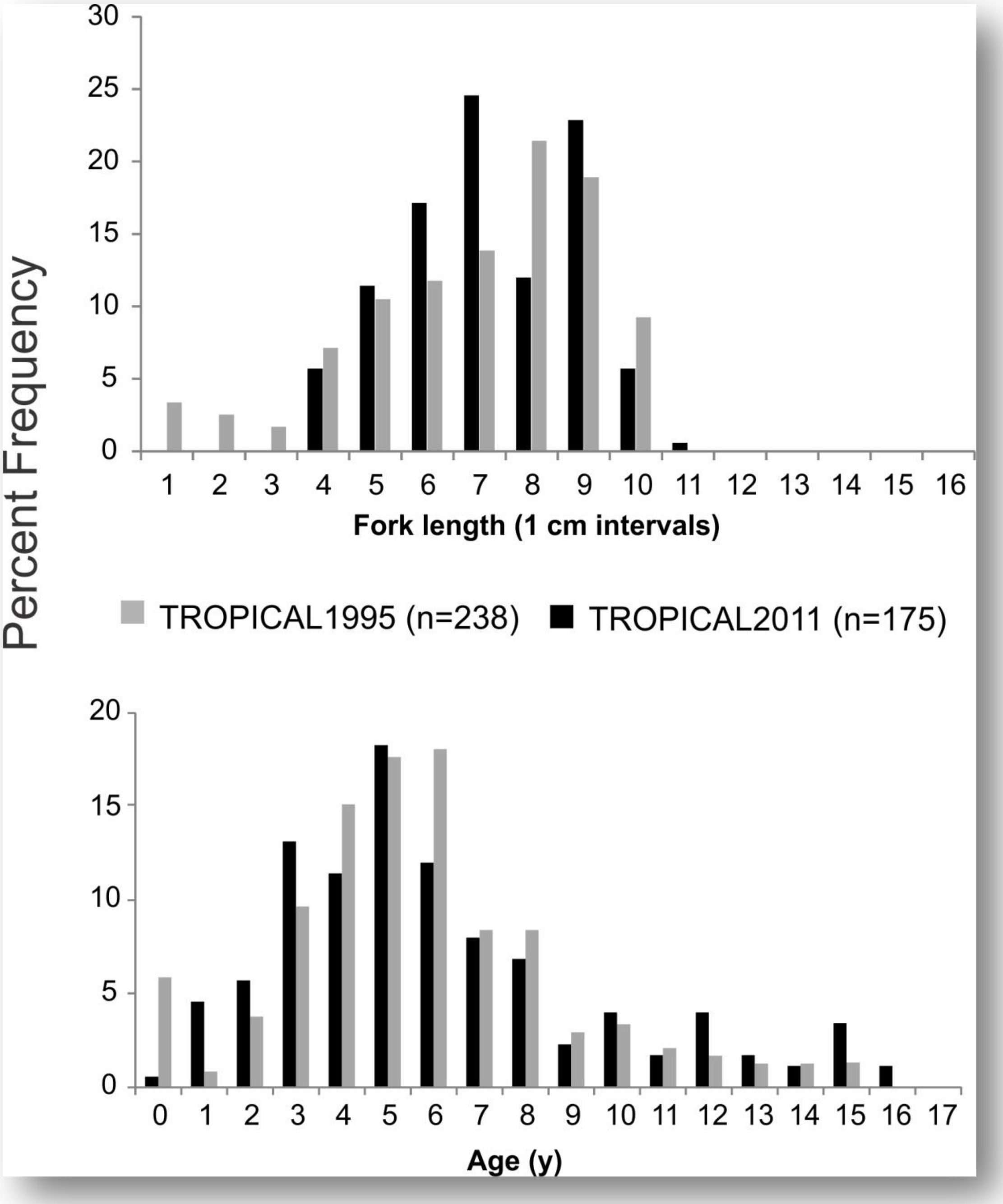

Figure 4. Age and size frequency (%) distributions of damselfish collected from the tropical systems in 1995 and 2011.

The condition factor (K) was higher for the tropical population in 1995 for every size class (Fig. 5), indicating that individuals although attaining the same length, reached higher body mass (g) in the past, with individuals of large size classes presenting continuously increasing condition with size.

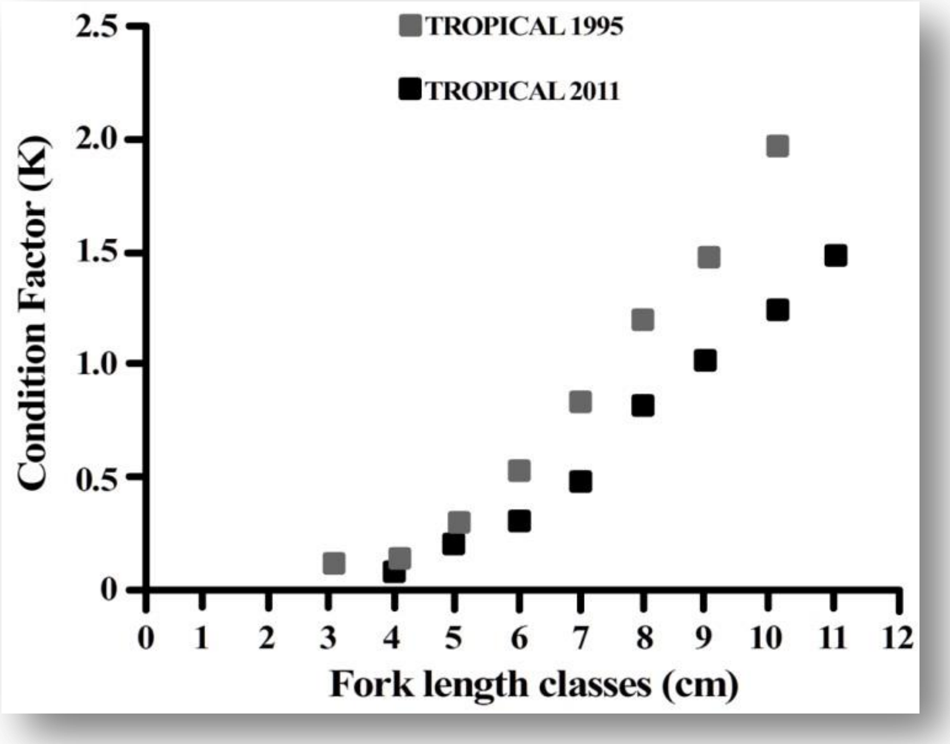

Figure 5: Condition Factor (K) of tropical populations in 1995 and 2011.

COMPARISON OF GROWTH CURVES

The VBGF shown in FIG. 6 point out that growth of the tropical population year 1995 and 2011 were slower than the subtropical one, as indicated by the growth coefficient K (Tropical 1995=0.21; Tropical 2011=0.15; and Subtropical=0.30). The differences among all classes between the tropical and subtropical system were mainly due to individuals being larger at every age class for the subtropical system (All classes; t tests, p<0.005). However, populations of tropical system did not differed for size classes between years, except for the 15 cm class, which was greater in 1995 (p=0.03) due to great individual variability.

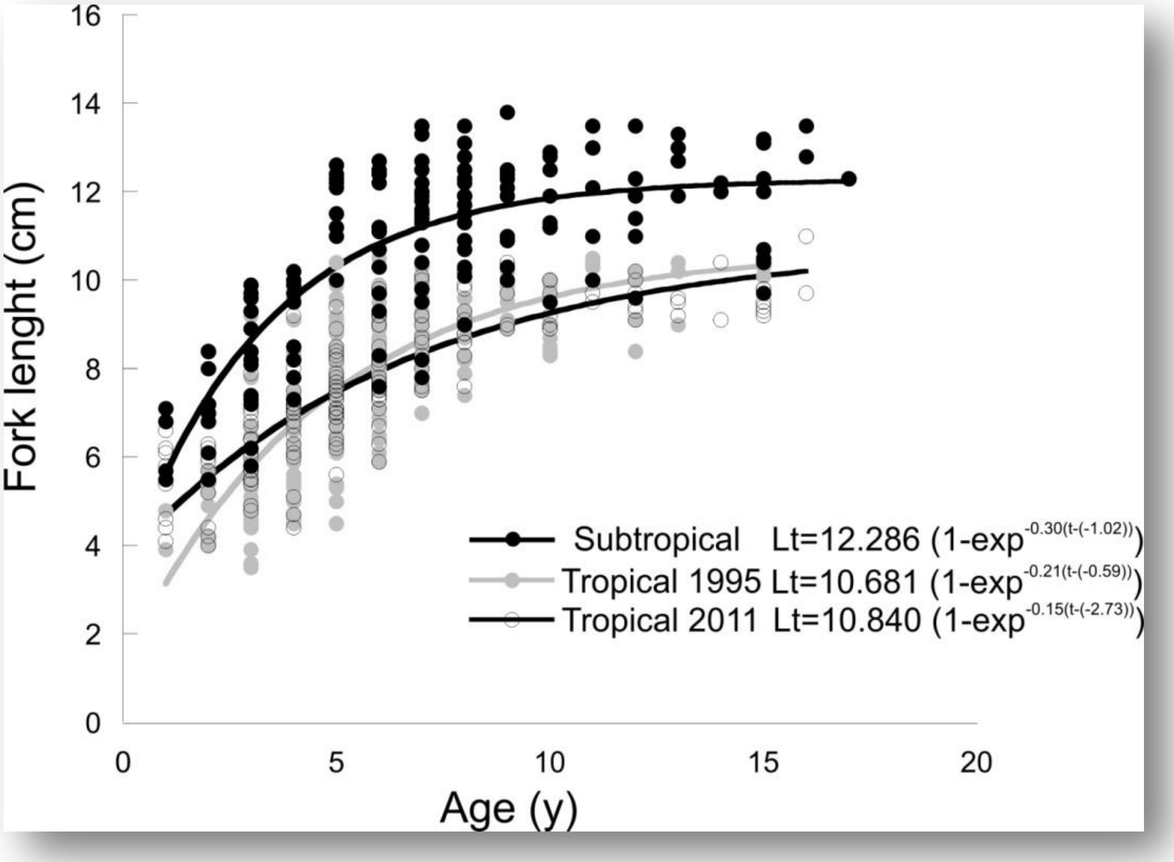

Figure 6. The von Bertalanffy growth curve fitted to length at age data of tropical reefs year 1995 (n=238), tropical reefs year 2011(n=175) and subtropical reefs (n=143) of *Stegastes fuscus*. Age “0” was excluded from all dataset.

In addition, both tests used to compare growth curves indicated significant differences between years and systems. The ARSS on the VGBF for *S. fuscus* growth data from 1995 and 2011 differed significantly (F = 8.84; p < 0.0001; Table I-a) as well as there were significant differences in growth between Tamandaré reef and Arraial do Cabo *S. fuscus* populations (F = 141.99; p < 0.0000001; Table I-a). Comparison through LRT also showed that *S. fuscus* growth curves differed between years (χ2 = 17.01; p = 0.001; table I-b) as well as among locations (χ2 = 274.53; p < 0.0001; Table I-b). Despite of that, no significant differences were observed for asymptotic length and K between years (χ2 = 0.02; p = 0.888 and χ2 = 1.89; p =0.169). Among locations, all growth parameters showed significant differences (Hypothesis H1, H2 and H3; table I-b).

Table I. VBGF parameter comparison: a) Analysis of the residual sum of squares (ARSS); b) Likelihood Ratio tests (LRT).

a)ARSS results

Comparison	**RSS_s**	**RSS_p**	**F**	**p**
Years	426.09	454.69	8.840	<0.00001
Systems	379.38	894.05	141.990	<0.00001

b)LRT results

Temporal comparison

Hypothesis	**Linear constraints**	**Residual sum of squares**	**Qui value**	**p**
Ho vs H1	Linf 1 = linf 2	426.61	0.02	0.888
Ho vs H2	K1 = K2	433.38	1.89	0.169
Ho vs H3	t01 = t02	443.08	8.17	0.004
Ho vs H4	Linf 1 = linf 2; K1 = K2; t01 = t02	443.08	17.01	0.001

Latitudinal comparison

Hypothesis	**Linear constraints**	**Residual sum of squares**	**Qui value**	**p**
Ho vs H1	Linf 1 = linf 2	384.71	4.85	0.028
Ho vs H2	K1 = K2	390.31	9.48	0.002
Ho vs H3	t01 = t02	385.12	5.19	0.023
Ho vs H4	Linf 1 = linf 2; K1 = K2; t01 = t02	893.58	274.53	0.000

LONGEVITY, MORTALITY AND SURVIVAL

The mean maximum age (T*max*) calculated for *S. fuscus* was significantly lower at the tropical 2011 (mean of 13.83 yrs) compared to the subtropical system (mean of 15 yrs) (p=0.03). Also, when comparing the tropical populations of 1995 (mean of 11.5 years) and 2011, longevity was significantly lower in 1995 (p=0.00004). The observed maximum ages for *S. fuscus* were 15, 16, and 17 years in Tropical 1995, Tropical 2011 and Subtropical populations, respectively. Mortality rates estimated from catch curves showed a general trend of decrease between tropical populations of 1995 and 2011, however it was not significantly different (p>0.05). Between tropical and subtropical systems there was also a slight trend to increased mortality with latitude, however once again it was not significantly different (FIG. 7). Survival rates (% per year) were 73.53%, 80.06% and 78.54%, in populations of tropical 1995, tropical 2011 and subtropical systems, respectively.

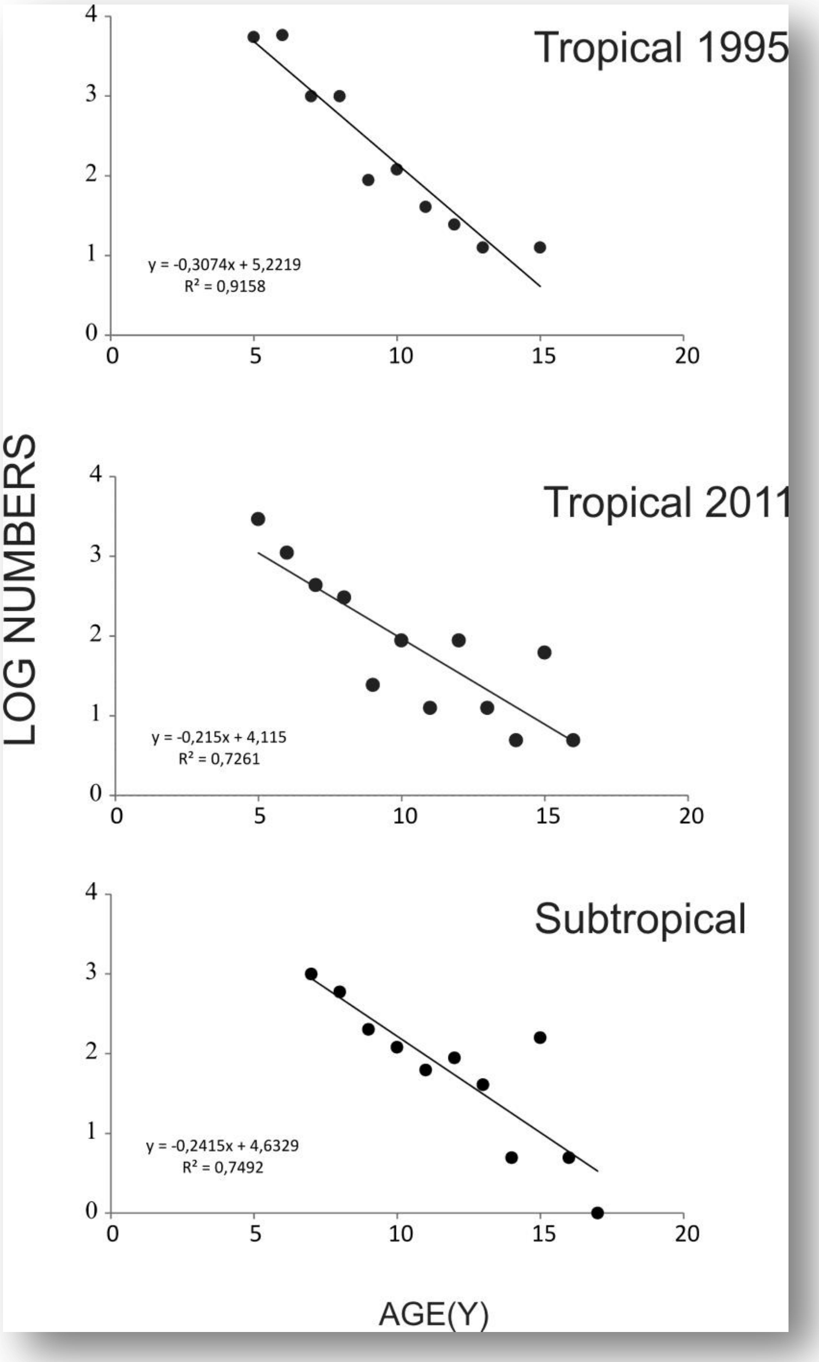

Figure 7. Age-based catch curve estimates of *Stegastes fuscus* mortality rates for populations in tropical reefs (years 1995 and 2011) and in subtropical reefs.

DISCUSSION

The abundance of *S. fuscus* reported for several coastal Brazilian reef systems (e.g. Ferreira et al. 1995; Ferreira et al., 2001; Chaves et al., 2010; Medeiros et al., 2010) indicates that the environmental conditions are highly favourable for sustaining the populations of this damselfish. Comparisons of densities of *S. fuscus* between the localities studied, however, revealed significant variation in density and size structure between tropical and subtropical reefs with greater density on tropical reefs (Chaves et al., Chapter 2). These findings raise intriguing questions, as if the higher quality of the territory, expressed by more abundant food and refuges in the tropics, increase the number of conspecifics that can optimally coexist (Chaves et al., Chapter 2).

In relation to otolith quality, differences in sharpness and contrast of translucent and opaque bands between locations were observed. Although for both sets of samples it was possible to obtain reliable readings, the otoliths from subtropical reefs were easier to interpret than those from the tropics. Individuals from higher latitudes had more defined bands in otoliths, as previously described for the congeneric species *Stegastes planifrons*, *S. partitus*, and other pomacentrids (Caldow & Wellington, 2003, Fowler & Doherty, 1992), being associated to factors such as seasonal environmental conditions or differences in length and timing of reproductive season.

A latitudinal variation was then found for other several key life traits for *S. fuscus*. Significant differences of growth curves were found between locations, with all growth parameters showing significant differences. *Stegastes fuscus* attains a large size at age, larger mean asymptotic size, and longer maximum life span in subtropics. These finding are in congruence with other studies concerning life history changes on coral reef fish, resulting in differential physiological rates in response to variations in temperature (Meekan et al. 2001, Choat & Robertson 2002, Choat et al. 2003, Caldow & Wellington 2003). The main process driving differences is a local upwelling in the subtropical system (Arraial do Cabo), which directly influences primary productivity and availability of food resources through nutrient-rich waters. This is possibly reflected in the observed differences in growth rates, which were greater in subtropical low temperature contrarily to the expected. However, establishing the effects of water temperature on growth requires observational time series of sufficient length to ensure adequate statistical power, as well as to capture reasonable range of the historical variability inherent to that system.

In addition to the positive size-latitude relationship that would be predicted for ectotherms (and for endotherms more) in general, fish at higher latitudes also tend to live longer and have lower mortality rates than fish at lower latitudes (e.g., Choat et al., 2003; Robertson et al., 2005). The trends found herein coincided with longevity patterns, as subtropical population was significantly older than those in the tropics. This extends the validity of Bergmann's rule, which states that larger individuals within species occur towards higher latitudes and/or lower temperatures, as to get older at higher latitudes could be an inherent tendency when physiological rates are slower.

Although differences of growth curves generated from samples collected in the tropical system with a 16 year interval also differed significantly, this difference was caused by the parameter t0, with no significant difference found for K or Loo. This parameter is influenced by the presence of small-sized individuals in the sample, what by the other hand may result from sampling methods or availability linked to recruitment period. Thus, the lack of significant overall comparative differences in size at age after 16 years in the tropics, indicates a remarkable stability of population parameters. Furthermore, differences found between locations seem to be indeed related to lower temperatures in the subtropics.

When comparing the age structure sets, it was possible to make further inferences, where a clear latitudinal significant difference was due to a shift of the modal classes to older ages in the subtropics. Between the two tropical data sets, the sample from 1995 had a stronger 6 year old class, while in 2011 it was weaker. This could be attributed to a higher mortality affecting 5 years old age class in 2011 as opposed to 1995. Strong year classes either were absent in 2011 or predation could have operated disproportionately removing them, as to flatten the age distribution. Strong year classes are commonly observed on fish population as a result of variable rates of replenishment (Doherty, 1982, Ferreira & Russ, 1995; Russ et al., 1996). Also, variations in the age structure could have other causes (Morgan et al., 2007), such as changes in age at maturation and sex ratio and truncation of the age structure caused by size-selective predation. A stronger pulse of recruitment, however, generating a stronger year class in 1995 but not in 2011 seems to be a more plausible explanation even if the age structures were not significantly different among populations. Other plausible explanation could not be found to this age-class specific mortality.

Our estimates of mortality (Z), which in the case of *S. fuscus* can be considered equal to M (natural mortality) did not vary between systems or years, and were considered low, given higher survival rates (~70-80%). Mortality rates as calculated by catch curves are sensitive to recruitment variations, as one of the obvious assumptions of the method is constant recruitment (Allen, 1997, Russ et al., 1996). As for Tamandaré populations of 1995 and 2011 age structures were very similar, no difference in mortality rates would be expected. In either case, the non-significant differences in mortality rates, as inferred from the descending slope of the catch curve, represents an acceptable level of mortality that can be accommodated within the species' life history strategy. A possible recruitment variation was then counter balanced by an overall stability, achieved by long lived populations in both systems.

After the creation of a no-take zone in 1999 this system had a fishery pressure release, with a study in the area showing that just after a year of creation, targeted top-predators abundance increased between four and 11 times (Ferreira et al., 2000). This may have contributed to predator movement to fished areas, through a “spillover effect” (see Russ, 2002). However, after attaining a certain size, *S. fuscus* is naturally less susceptible to predators, and it is known that mortality rates are usually higher over smaller individuals within reef fish populations (e.g. recruits, juveniles) (Hixon & Carr, 1997). Thus higher mean longevity and larger individuals would be justified. If not due to lower susceptibility to predators of larger individuals, size-selective predators are removing smaller individuals from population in 2011 also, suggesting a selection pressure in favour of increased body size under conditions of high predation (see Hill & Dunbar, 1998), also sustained by condition increasing with size.

It is expected that the effects of predation risk should be more important than direct effects of predation in more complex habitats with longer lived prey species (Heithaus et al., 2008). Even though population of 2011 lived significantly longer, condition factors showed that individuals reached lower body mass. Fish condition is frequently considered to measure the extent of an individual's stored energy, in our case, body mass representing the integrated energetic history of the fish (Gagliano & McCormick, 2004). For instance, in a situation of predator scarcity, as ours in 1995, it has been found that prey can direct energy to growth, storage and reproduction instead of predator avoidance (Lima, 1986), as much as forage more regularly and beyond territory boundaries (Madin et al., 2010, Jones & Dornhaus, 2011). In the other hand, body mass loss and decreased feeding rates had also been linked to the cost of antipredatory defence (Perez-Tris et al., 2004). Following this reasoning, higher somatic body weight in individuals of the population of 1995 can be accounted for lower predation risk before the no-take area was created and despite higher values of fish condition are usually attributable to reproductive fat reserves in fish (Lambert & Dutil, 1997, 2000), data compared were from the same period of year (January and February), known to be a spawning peak in the area for *S. fuscus*.

Conversely, the no-take area also released fishing pressure over roving herbivores (parrotfishes and surgeonfishes) (Ferreira & Maida, 2007). The effects of competing roving herbivores on the foraging activity of *S. fuscus*, which would lead to pervasive impacts on life traits are, however, poorly known and somewhat controversial. The main source of competition for this damselfish species is caused largely by conspecifics (Osório et al., 2006, Medeiros et al., 2010). The algal gardens created by this territorial damselfish have higher algal biomass and primary productivity than neighboring areas (Ferreira et al., 1998), what generally encourage roving herbivores to intrude them in order to access better quality resources; yet, such interactions were not frequently observed in the field. It may be that similar strategies are being employed to circumvent competition, in a way that roving herbivores are excluded from areas occupied by damselfishes, as reported by Ceccarelli et al. (2006) in the Great Barrier Reef.

Furthermore, general low natural mortality rates coupled with the relatively high longevity found for this species resulted in a certain stability of the studied populations. This aspect could be reflected in the high abundance of adults detected, due to a process known as "storage effect" (*sensu* Warner & Chesson, 1985). One single favorable recruitment input of this species can balance several periods of low recruitment rates, and this would maintain adult densities until circumstances are favorable again. Regardless of higher predation risk and/or predation rates over recruits and smaller individuals, population numbers are compensated by this effect at both scales (latitudinal/temporal).

FURTHER CONSIDERATIONS

Large Marine Ecosystems (LMEs) have been used as a framework for the assessment and management of marine resources (Sherman, 1991). Divisions are established to capture ecosystem variability in productivity, fish and fisheries, pollution and ecosystem health, socioeconomics and governance (Duda & Sherman, 2002). Emerging trends, however, induced by global warming have been observed (Sherman et al., 2009; Gherardi et al., 2010). Between Brazilian tropical and subtropical systems, there is a 15 degree span in latitude, and each is located in one LME (East and South) with Arraial do Cabo (subtropical) located further south of the boundary of the two LME. Therefore, it provided an exceptional opportunity to compare populations of the widespread and abundant Brazilian damsel *S. fuscus*, which is expected to have pervasive effects on the diversity of reef communities along the Brazilian coast.

Likewise, this study along with information of spatial differences in life history traits provided evidence of the indirect effects of the creation of a no-take zone in tropical reefs, using a proxy of condition in damselfish inhabiting fished coral reefs. Our study therefore cautions against pooling demographic parameters over broad spatial and temporal scales without considering these variations. Furthermore, studies on the effects of fishing predators and herbivory of large targeted species (parrotfishes and surgeonfishes) will bring out important information of the direct and indirect effects of fishing in the context of management and conservation. Although a number of studies have documented changes in individual traits in target fishery species worldwide (Jennings et al., 1998, 1999, Fromentin & Fonteneau, 2001), understanding how fishing indirectly affects life history traits of non-target species will lead managers to take effective protection measures on Brazilian reef systems.

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CAPÍTULO V: **Considerações finais**

Um dos objetivos desta tese foi avaliar padrões de distribuição das espécies de peixe-donzela do gênero *Stegastes* em diferentes sistemas recifais da costa brasileira (sumarizados na figura 1 deste capitulo). Foram comparados dois sistemas recifais bastante distintos em relação à formaçao (não-biogênico e biogênico), morfologia (costões rochosos verticais e recifes de coral em franja) e temperatura (subtropical e tropical).

A espécie mais amplamente distribuída e abundante na costa brasileira, *Stegastes fuscus*, demonstrou grande afinidade com ambientes de baixa energia, abrigado de ondas e em baixas profundidades, onde a produtividade primária é ótima. A presença de recursos preferenciais também indicou uma seleção do hábitat. Por exemplo, esta espécie foi mais abundante em locais onde os territórios apresentaram maior incidência de abrigos, tocas entre 5-10 cm², ideais para o porte da espécie. Também a maior cobertura de algas filamentosas, conhecido grupo de algas na preferência alimentar da espécie (FERREIRA et al., 1998, FEITOSA et al., 2012), que é cultivada amplamente dentro dos seus territórios. Por outro lado, também pode-se concluir que esta espécie costeira é mais habitat generalista que as espécies caribenhas, uma vez que sua distribuição não é condicionada à cobertura coralínea, mas sim ao ambiente recifal, seja ele de origem biogênica ou não. As outras duas espécies foram menos abundantes, mas apresentaram uma distribuição bastante característica. *Stegastes variabilis*, de certo modo, apresentou uma distribuição inversa à de *S. fuscus*, evidenciando que interações interespecíficas são importantes em sua distribuição. Sabe-se que *S. fuscus* é uma espécie bastante agressiva (MENEGATTI et al., 2003) e possui maior porte em relação à *S. variabilis*. Entretanto, há uma grande sobreposição no uso de recursos (FEITOSA et al., 2012), o que sugere mais uma vez que esta espécie sofre uma competição assimétrica (ROBERTSON, 1984). Desta forma, *S. fuscus* possui territórios ótimos, abrigados de ondas e com concentrados recursos preferenciais, enquanto *S. variabilis* é marginalizado a territórios expostos e com recursos dispersos. *Stegastes pictus*, por sua vez, apresenta baixa sobreposição de nicho, se alimentando de invertebrados e também na coluna d’água. Sua plasticidade no uso de recursos lhe permite uma distribuição em hábitats mais profundos e/ou distantes da costa (e.g. naufrágios, plataformas de petróleo, ilhas oceânicas).

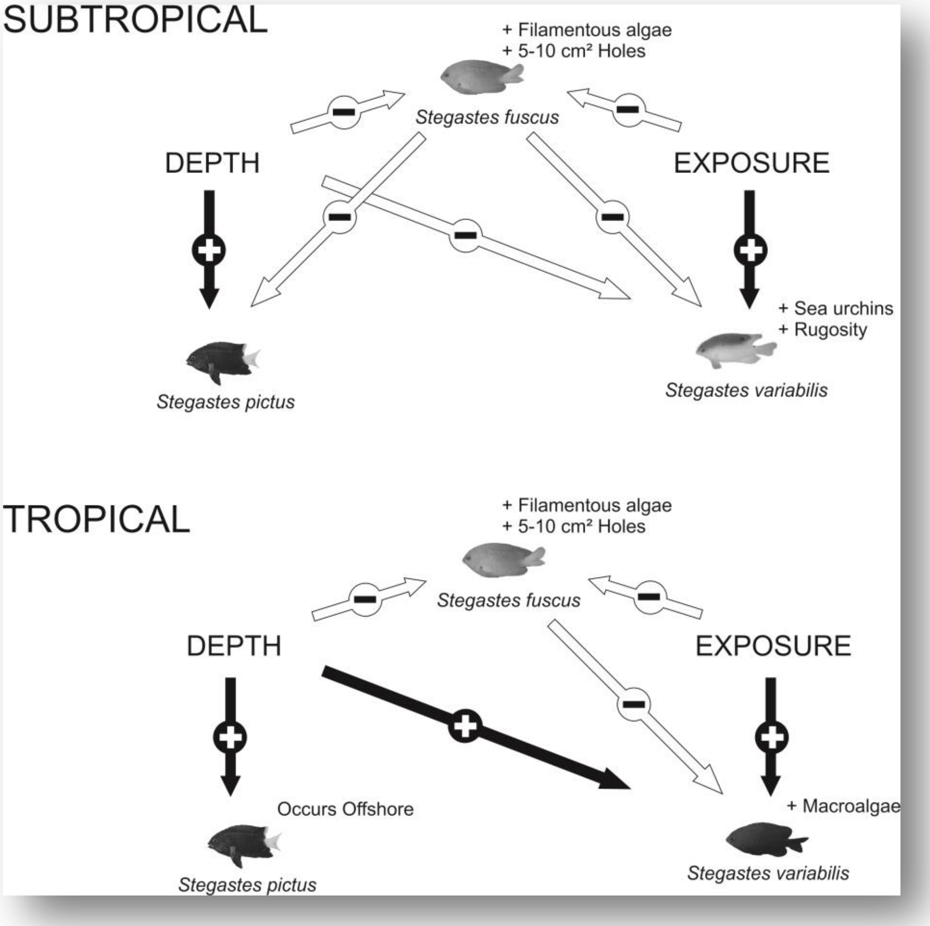

Fig.1. sumário geral dos padrões observados de distribuição das espécies de peixe-donzela nos sistemas estudados.

Os resultados encontrados são muito semelhantes aos apresentados por MEDEIROS (2010), em que comparam o uso do habitat por juvenis de *Stegastes fuscus* e *S. variabilis*. A superioridade competitiva de *S. fuscus* foi aí primeiramente evidenciada já na fase juvenil, podendo ser extrapolada a um padrão consistente ao longo de toda a costa brasileira em habitats onde estas espécies co-habitam.

No geral, este estudo indica que fatores como exposição às ondas e seleção do hábitat, assim como a competição por espaço são determinantes na distribuição espacial de peixes-donzela na costa brasileira. Isso demonstra uma alta previsibilidade, em espécies amplamente distribuídas, considerando uma grande heterogeneidade ambiental (e.g. temperatura, tipo de recife, cobertura bentônica). E ao contrário de algumas espécies encontradas no Caribe que são associadas à distribuição de determinadas espécies de corais, podemos concluir que *Stegastes fuscus* não é dependente da cobertura de corais e sim de ambientes recifais.

A similaridade encontrada entre os dois sistemas estudados indica que *S. fuscus*, como uma espécie dominante em comunidades tropicais e subtropicais, pode ser uma importante espécie indicadora, pois sua abundância pode estar sendo modificada frente às alterações ambientais (naturais e antrópicas) ao longo da costa brasileira. Sob este ponto de vista, embora sua distribuição seja bastante previsível, deve-se considerar que além destes sistemas, o Brasil apresenta uma grande diversidade de hábitats. Entretanto, devido a limitações orçamentárias, este trabalho selecionou somente dois sistemas ao longo da costa, e futuros estudos, incluindo a maior diversidade de recifes possível irão aprofundar o nosso conhecimento em torno de como a competição, a exposição a ondas, e a cobertura bentônica influenciam a distribuição de peixes-donzela, assim como seus efeitos sobre toda a comunidade recifal.

Foi feita uma reavaliação dos principais fatores determinantes na distribuição das espécies de peixe-donzela que ocorrem em Isla Colón, Bocas del Toro, na costa caribenha do Panamá. Recifes distintos foram escolhidos de forma a abranger a maior variedade de habitats (e.g. recifes abrigados ou expostos a ondas, rasos, fundos, e com variada cobertura bentônica) permitindo determinar se houve preferência no uso do hábitat por estas espécies, que ocorrem em toda a região do Caribe (ver Fig. 2). Em relação às espécies mais abundantes, *Stegastes planifrons* e *S. adustus*, houve uma segregação bem clara em sua distribuição, com uma intensa competição previamente observada nos recifes em que cohabitam. *Stegastes planifrons* mostrou maior afinidade com recifes abrigados que apresentaram maior percentual de cobertura de corais vivos ou recobertos por algas. Entretanto, as espécies de coral às quais *S. planifrons* se associou foram diferentes de outros trabalhos, o que acredita-se ser consequência de perda de hábitat ocorrido na região. Esse efeito já foi observado em estudo recente relatado por PRECHT (2010). O deslocamento de *S. planifrons* para hábitats não preferenciais resulta em uma situação prejudicial à saúde das espécies de corais colonizadas, uma vez que para manutenção de seus territórios, a espécie retira pólipos da colônia para o assentamento de algas. Fato observado no local deste estudo. *Stegastes adustus*, por sua vez, utiliza preferencialmente hábitats rasos, aumentando consideravelmente sua abundância em recifes expostos ao batimento de ondas. Nestes recifes, a cobertura do substrato é em sua maioria, representada por macroalgas e turf de algas articuladas. Entretanto, os juvenis desta espécie mostraram grande afinidade a territórios apresentando grande cobertura do coral-de-fogo *Millepora alcicornis*, cuja ramificação lhes confere abrigo contra predadores em potencial. Já foi relatado que o uso desta espécie de coral também se estende à alimentação

(PEREIRA et al., 2012; CONI et al., 2012), o que merece um estudo mais aprofundado na área de estudo. *Stegastes adustus* também mostrou uma associação com a espécie *Microspathodon chrysurus*, que possui maior porte, observado anteriormente por outros autores (CLARKE, 1977; ITZKOWITZ, 1977; WALDNER & ROBERTSON, 1980; ROBERTSON, 1984). Acredita-se que *M. chrysurus* utiliza a capacidade de defesa de *S. adustus* para maior aproveitamento de outras atividades fora de seu território, seja para visitação de estações de limpeza, para alimentação, ou para reprodução (SIKKEL & KRAMER, 2006). As outras espécies observadas do gênero *Stegastes* (*S. partitus*, *S. leucostictus* e *S. variabilis*), juntas apresentaram uma abundância muito baixa (~10% da abundância total), o que não permitiu estabelecer padrões muito claros de distribuição, entretanto observou-se uma tendência de ocorrência em recifes mais fundos (acima de 6 m). *Stegastes partitus*, por exemplo, é a espécie de peixe-donzela mais abundante em ilhas do norte caribenho, e.g. Cuba (GONZALEZ-SANSON et al., 2009), Ilhas Virgens (TOLIMIERI et al., 1998), Hispaniola e Mona Passage (SCHMITT et al., 2002; DENNIS et al., 2005) entre outras. Entretanto, esta espécie é planctívora, o que lhe traz limitações quanto à ocorrência em locais com fortes correntes (NEMETH, 1997). Os recifes estudados, por sua vez, são muito próximos à costa e relativamente protegidos de massas d'água que lhe trariam alimento.

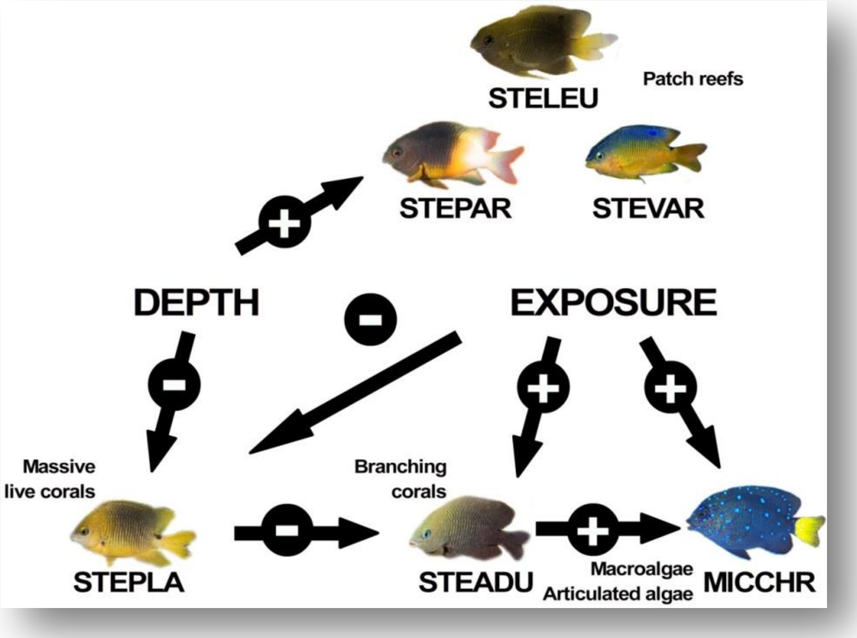

Fig.2: Sumário dos padrões observados na distribuição de espécies de donzela ocorrentes na costa caribenha do Panamá.

Este estudo, além de confirmar padrões descritos em trabalhos anteriores, feitos há até três décadas, etambém nos traz evidências de que os peixes-donzela podem ser indicadores ambientais úteis em relação à perda de hábitat, um problema detectado amplamente na região do Caribe desde a década de 80. Sua importância como espécies-chave em ambientes recifais, nos permite prever possíveis cenários frente a processos de mudança de fase (phase shift) de recifes dominados por cobertura coralínea a um estado de dominância por algas. A limitação de dados pretéritos sobre a ocorrência de mudanças locais nos impede de tecer conclusões mais profundas, entretanto esforços devem ser feitos para um maior conhecimento sobre a relação destas espécies de peixe e hábitats disponíveis para sua colonização.

Esta tese abordou ainda parâmetros da história de vida da espécie endêmica de peixe-donzela *Stegastes fuscus* na costa brasileira. Os parâmetros avaliados se referem à idade e crescimento desta espécie em diferentes sistemas recifais, representando um ambiente tropical e um subtropical. Uma comparação em diferentes anos (1995 e 2011) em Tamandaré também foi feita (ver sumário na Fig. 3). As idades máximas observadas para *Stegastes fuscus* (15, 16 e 17, para Tamandaré em 1995, Tamandaré em 2011 e, Arraial do Cabo em 2011, respectivamente) são comparáveis às encontradas em outras espécies de pomacentrídeos, como *P. moluccensis* e *P. wardi*, alcançando 10 e 12 anos, respectivamente (FOWLER, 1990, FOWLER & DOHERTY, 1992) e também *Hypsypops rubicunda*, com 12–13 anos (CLARKE, 1970). Ainda, uma espécie congênere, *Stegastes altus*, com dados obtidos pela observação em campo, alcançou 15 anos (KOHDA, 1996). Isto demonstra que este grupo apresenta uma longevidade relativamente alta. Em espécies com alta longevidade, pode ocorrer um processo conhecido como efeito de estocagem (storage effect *sensu* WARNER & CHESSON, 1985), o que indica que embora possa ocorrer baixo recrutamento em algumas temporadas, o número de indivíduos na população será compensado em outros anos de bom recrutamento. Desta forma, se a alta longevidade pode fornecer estabilidade à sua população, a persistência e dominância de *Stegastes fuscus* possuirá um relevante efeito sobre a diversidade na comunidade recifal dos sistemas estudados.

BRAY (2001) encontrou um efeito latitudinal significativo sobre as idades máximas encontradas para *P. moluccensis*, em que altas latitudes apresentaram indivíduos mais velhos. Embora as idades máximas alcançadas nas populações analisadas tenham sido pouco diferenciadas, a longevidade média (Tmax) foi significativamente maior em maiores latitudes. Isto ocorreu em relação às populações tropicais de 2011 e 1995. O mesmo foi evidenciado em relação aos comprimentos máximos, em altas latitudes, onde os indivíduos foram significativamente maiores, e isso ocorreu para todas as classes etárias estabelecidas, entretanto não entre os anos em Tamandaré, o que indica que além do fator temperatura, outros processos estruturantes como a competição por territórios e a predação devem exercer diferentes papéis nestas populações. Algumas hipóteses levantadas são que um aumento na condição dos indivíduos adultos tenha sido consequência da retirada de predadores (WALSH et al., 2012) pela pesca no passado, ou até o alívio da competição, embora não avaliados neste trabalho diretamente. A retirada de predadores naturais e competidores pela pesca no passado pode ser a explicação mais plausível neste caso. Uma vez que uma zona de exclusão da pesca foi estabelecida em 1999 em Tamandaré, há indícios de que os estoques de predadores mostraram significativa recuperação no entorno desta área.

Este trabalho foi ao encontro do que já foi encontrado em outros estudos sobre a história de vida de peixes recifais em resposta a mudanças de temperatura (MEEKAN et al., 2001; CHOAT & ROBERTSON, 2002; CHOAT et al., 2003; CALDOW & WELLINGTON, 2003), entretanto as variações nos parâmetros de idade e crescimento não são obrigatoriamente devido a diferenças genéticas entre as populações, principalmente quando diferenças podem ser encontradas mesmo em populações muito próximas geneticamente, no caso populações tropicais em 1995 e 2011. Uma vez que a temperatura pode não ser o único fator a explicar a variação nos parâmetros de vida entre populações, estes devem ser analisados separadamente em se comparando diferentes escalas sejam elas, espacial ou temporal.

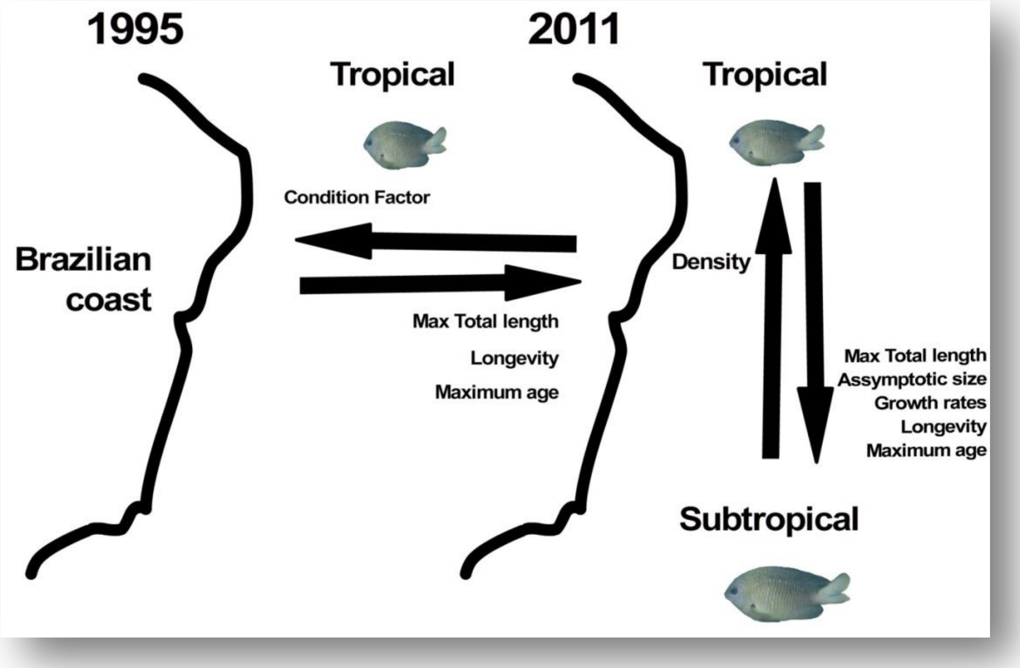

Fig. 3: Sumário dos padrões encontrados nos parâmetros da história de vida de *Stegastes fuscus*. A direção das setas indica onde foram encontrados valores mais altos.

Devido primeiramente a restrições orçamentárias e esforço temporal dedicado às análises de amostras, a replicação dos locais ao longo da costa foi limitada. Algumas considerações, entretanto devem ser feitas quanto aos locais de amostragem. Arraial do Cabo, sistema escolhido para representar altas latitudes, sofre a influência de uma ressurgência no período de primavera-verão (VALENTIN, 1984). Isso pode levar a diferenças em parâmetros da história de vida desta espécie, causadas por outros fatores que extrapolam o fator latitudinal e/ou baixas temperaturas. A maior disponibilidade de recursos, provenientes de águas enriquecidas por nutrientes, ocorre a partir do momento em que a produtividade primária dentro do território da espécie possivelmente aumenta. Surge desta forma um interessante ponto a se averiguar de modo a eliminar o possível efeito da ressurgência: As populações mais ao sul, como Santa Catarina (27°30'S; 48°W), por exemplo, apresentariam as mesmas características? Por outro lado, sabe-se que o efeito da ressurgência ocorre em áreas externas ao Arraial do Cabo, como apontado por FERREIRA et al. (1998), e a diferença encontrada entre a produtividade encontrada dentro e fora dos territórios, se deve exclusivamente ao comportamento de "gardening" da espécie, tanto no inverno, quanto no verão.

Diferenças nos parâmetros de vida referente à sazonalidade, variabilidade local na disponibilidade de alimento (e.g. conteúdo estomacal e análise de lipídios), diferenças latitudinais em relação a estágios iniciais de vida e esforços reprodutivos são alguns aspectos a se entender futuramente. A obtenção do máximo de informações de espécies tropicais amplamente distribuídas latitudinalmente, nos permitirá avaliar impactos decorrentes de mudanças climáticas globais sobre os ambientes recifais. Ainda, uma vez que foram encontradas evidências de que a pesca pode afetar indiretamente espécies não-alvo, se faz necessário estudo mais aprofundado incluindo dados de abundância de predadores e compreender as possíveis estratégias anti-predatórias adotadas por *Stegastes fuscus* e outras espécies. Desta forma, poderá se avaliar o nível do risco de predação e a extensão de seus efeitos sobre seu comportamento.

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ANEXO

Ministério do Meio Ambiente - MMA
Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio
Sistema de Autorização e Informação em Biodiversidade - SISBIO

Autorização para atividades com finalidade científica

Número: 17829-2	**Data da Emissão: 06/12/2010 18:05**

Dados do titular

Nome: Laís de Carvalho Teixeira Chaves	CPF: 088.469.887-44
Título do Projeto: Idade e crescimento de Stegastes fuscus em diferentes sistemas recifais da costa brasileira	
Nome da Instituição : UFPE - UNIVERSIDADE FEDERAL DE PERNAMBUCO	CNPJ: 24.134.488/0001-08

Cronograma de atividades

#	Descrição da atividade	Início (mês/ano)	Fim (mês/ano)
1	Coleta de peixes na RESEX Arraial do Cabo	11/2010	12/2010
2	Coleta de peixes na APA Costa dos Corais	01/2011	03/2011
De acordo com o art. 33 da IN 154/2009, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto.			

Observações e ressalvas

1	As atividades de campo exercidas por pessoa natural ou jurídica estrangeira, em todo o território nacional, que impliquem o deslocamento de recursos humanos e materiais, tendo por objeto coletar dados, materiais, espécimes biológicos e minerais, peças integrantes da cultura nativa e cultura popular, presente e passa da, obtidos por meio de recursos e técnicas que se destinem ao estudo, à difusão ou à pesquisa, estão sujeitas a autorização do Ministério de Ciência e Tecnologia.
2	Esta autorização NÃO exime o pesquisador titular e os membros de sua equipe da necessidade de obter as anuências previstas em outros instrumentos legais, bem como do consentimento do responsável pela área, pública ou privada, onde será realizada a atividade, ou do proprietário, arrendatário, posseiro ou morador de área dentro dos limites de unidade de conservação federal cujo processo de regularização fundiária encontra-se em curso.
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6	Este documento não dispensa o cumprimento da legislação que dispõe sobre acesso a componente do patrimônio genético existente no território nacional, na plataforma continental e na zona econômica exclusiva, ou ao conhecimento tradicional associado ao patrimônio genético, para fins de pesquisa científica, bioprospecção e desenvolvimento tecnológico.
7	Em caso de pesquisa em UNIDADE DE CONSERVAÇÃO, o pesquisador titular desta autorização deverá contactar a administração da unidade a fim de CONFIRMAR AS DATAS das expedições, as condições para realização das coletas e de uso da infra-estrutura da unidade.
8	As atividades contempladas nesta autorização NÃO abrangem espécies brasileiras constante de listas oficiais (de abrangência nacional, estadual ou municipal) de espécies ameaçadas de extinção, sobreexplotadas ou ameaçadas de sobreexplotação.

Outras ressalvas

1	A pesquisadora e sua equipe devem respeitar a possível presença de pescadores nos pontos de coleta. As capturas subaquáticas devem ser realizadas apenas nos momentos em que não haja, no ponto, a prática da pesca artesanal.

Equipe

#	Nome	Função	CPF	Doc. Identidade	Nacionalidade
1	Beatrice Padovani Ferreira	Orientadora do Projeto de Doutorado	702.596.317-87	048210082 IFP-RJ	Brasileira
2	CARLOS EDUARDO LEITE FERREIRA	Co-orientador do Projeto de doutorado/Coleta de Material	010.539.867-50	10152716-6 IFP-RJ	Brasileira
3	SIMONE MARQUES	Coleta e transporte de Material	003.844.226-40	MG-7.297.034 SSP/MG-MG	Brasileira
4	Andreza Cecília Gomes Pacheco	Coleta e transporte de Material	269.202.468-05	287179254 SSP-SP	Brasileira
5	João Lucas Leão Feitosa	coleta e transporte de marerial	059.363.214-10	7153420 sds-PE	Brasileira

Locais onde as atividades de campo serão executadas

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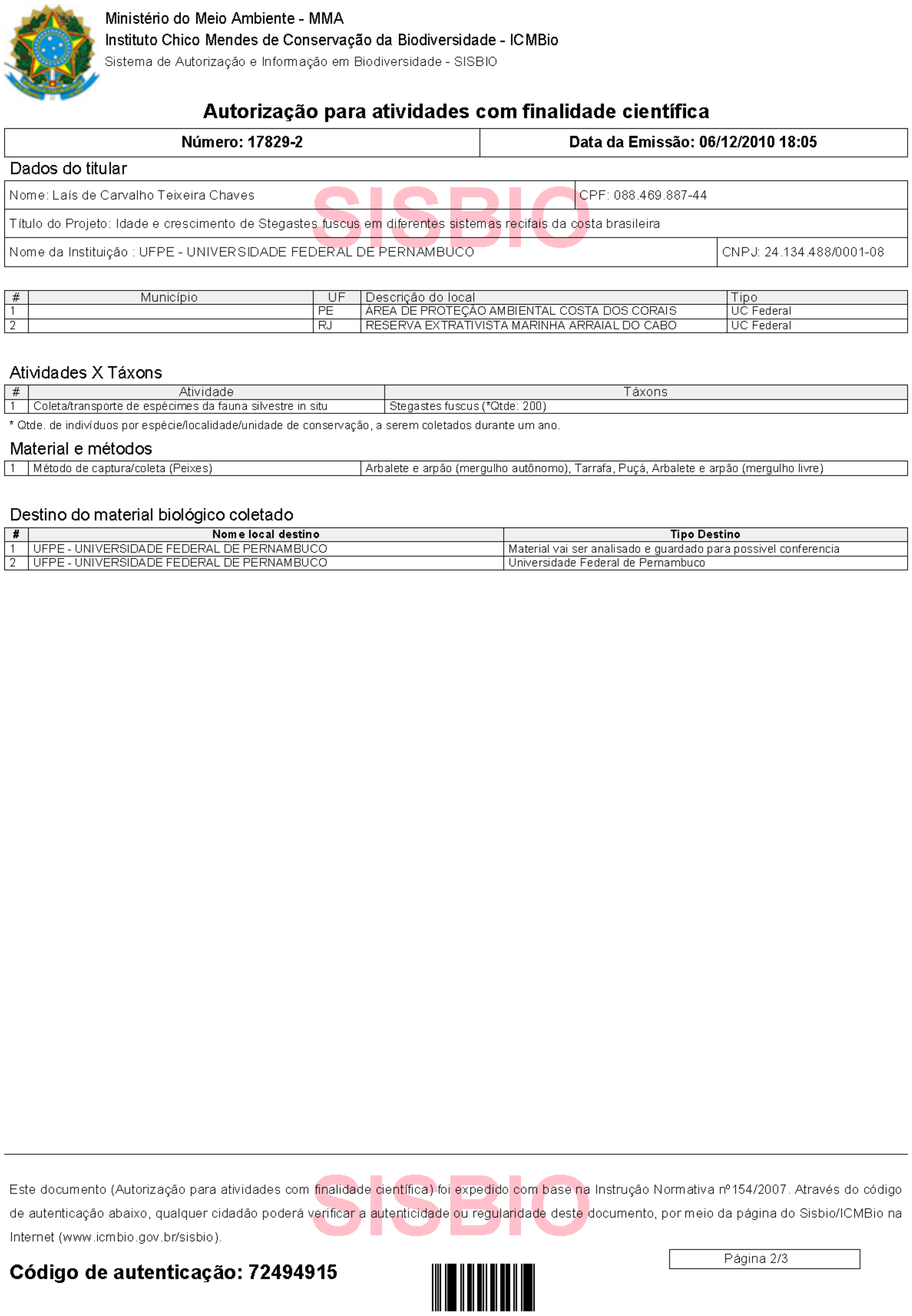

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#	Município	UF	Descrição do local	Tipo
1		PE	ÁREA DE PROTEÇÃO AMBIENTAL COSTA DOS CORAIS	UC Federal
2		RJ	RESERVA EXTRATIVISTA MARINHA ARRAIAL DO CABO	UC Federal

Atividades X Táxons

#	Atividade	Táxons
1	Coleta/transporte de espécimes da fauna silvestre in situ	Stegastes fuscus (*Qtde: 200)

* Qtde. de indivíduos por espécie/localidade/unidade de conservação, a serem coletados durante um ano.

Material e métodos

1	Método de captura/coleta (Peixes)	Arbalete e arpão (mergulho autônomo), Tarrafa, Puçá, Arbalete e arpão (mergulho livre)

Destino do material biológico coletado

#	**Nome local destino**	**Tipo Destino**
1	UFPE - UNIVERSIDADE FEDERAL DE PERNAMBUCO	Material vai ser analisado e guardado para possivel conferencia
2	UFPE - UNIVERSIDADE FEDERAL DE PERNAMBUCO	Universidade Federal de Pernambuco

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Dados do titular

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Nome da Instituição : UFPE - UNIVERSIDADE FEDERAL DE PERNAMBUCO	CNPJ: 24.134.488/0001-08

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