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PROGRAMA DE PÓS-GRADUAÇÃO EM OCEANOGRAFIA AMBIENTAL

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PEIXES RECIFAIS: COMPARAÇÃO ENTRE AMBIENTES ARTIFICIAIS E NATURAIS

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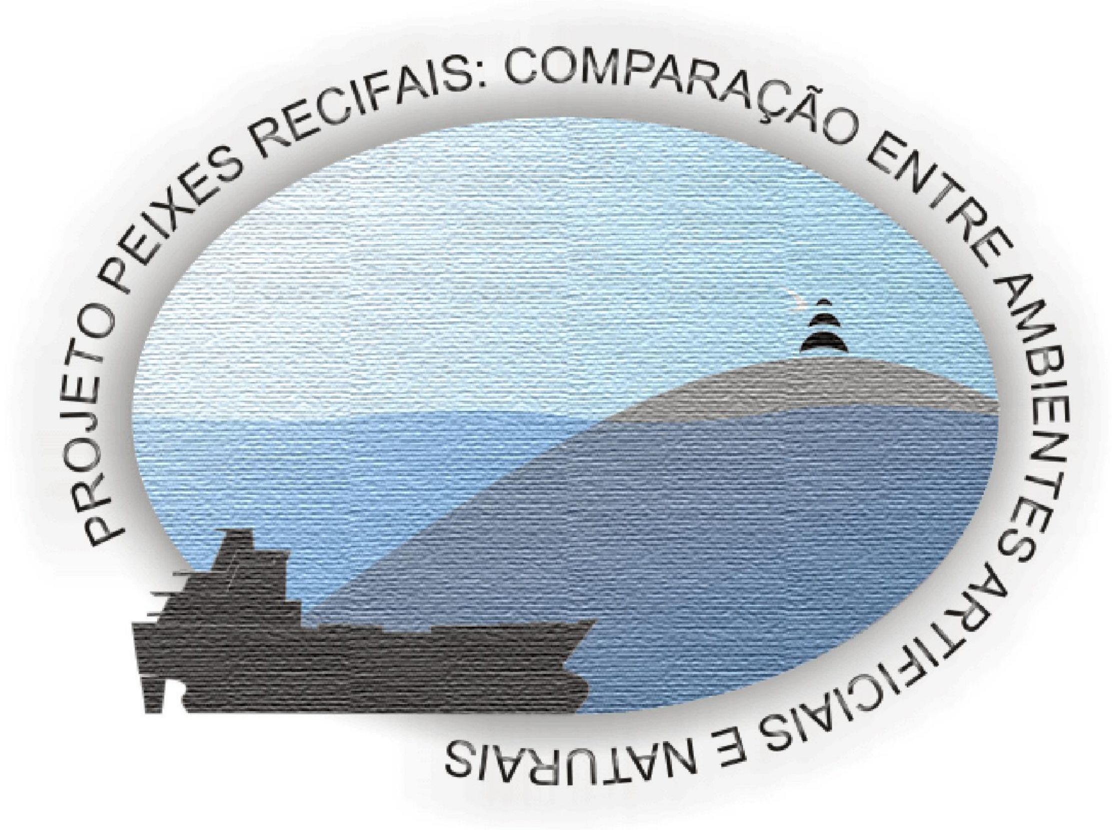

A minha Madalena, por sua força e garra.

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“[...] I fear that too often the actual objective [of artificial reefs] is simply to put more fish in the cooler.”

William J. Lindberg

RESUMO

A presente dissertação foi elaborada a partir dos resultados do projeto "Recifes artificiais e naturais no Espírito Santo: uma análise da comunidade de peixes", financiado pela Fundação de Apoio à Ciência e Tecnologia do Espírito Santo (FAPES). O projeto envolveu duas vertentes, uma relativa ao levantamento da estrutura e composição das comunidades de peixes e outra relativa ao levantamento da riqueza de espécies criptobênticas. Os ambientes estudados foram os recifes artificiais Victory 8B (um navio afundado intencionalmente em 2003) e Bellucia (um navio naufragado em 1903) e as ilhas Rasas e Escalvada. Estes recifes se encontram a cerca de 10 km da costa de Guarapari, estado do Espírito Santo. Os trabalhos de campo foram realizados em 2008 e 2009. A estrutura e composição das comunidades de peixes foram acessadas através de censos visuais (transects de 20 x 2 m). Adicionalmente, foram realizados levantamentos das comunidades bentônicas (grupos funcionais) e da rugosidade superficial dos recifes para avaliar a importância do substrato nos padrões encontrados. Os peixes criptobênticos foram capturados usando puçás manuais.

A dissertação está dividida em cinco capítulos, um introdutório e quatro compostos por um manuscrito cada. Esta formatação foi escolhida por ser adequada à heterogeneidade dos assuntos abordados e por tornar mais rápido o processo de divulgação da pesquisa realizada (publicações de artigos em revistas científicas). O Capítulo 1 traz uma introdução geral sobre recifes artificiais e sobre os fatores que motivaram a realização do estudo proposto. No Capítulo 2, a estrutura trófica das comunidades de peixes é comparada entre (e dentre) os recifes artificiais e naturais e os fatores que causam as diferenças observadas são identificados. A freqüência de comprimento, biomassa e freqüência de ocorrência de quatro gêneros de peixes de importância econômica para a pesca local são comparadas no Capítulo 3 para avaliar o potencial de atração e produção dos recifes artificiais. Equações de relação peso-comprimento de oito espécies criptobênticas capturadas nos recifes artificiais e naturais são apresentadas no Capítulo 4. Por último, no Capítulo 5 são apresentadas observações comportamentais realizadas no Victory 8B, um cardume de *Decapterus macarellus* utilizando um mero *Epinephelus itajara* como refúgio durante ataques predatórios de *Caranx latus*.

Palavras-chaves: Naufrágios • Recifes artificiais • Estrutura trófica • Impactos • Atração-produção

ABSTRACT

The present thesis was elaborated from the results of the project “Recifes artificiais e naturais no Espírito Santo: uma análise da comunidade de peixes”, financed by Fundação de Apoio à Ciência e Tecnologia do Espírito Santo (FAPES). The project focussed on (a) the structure and composition of fish communities and (b) the diversity of cryptobenthic fishes. The study sites were the artificial reefs Victory 8B (one derelict ship intentionally sunk in 2003) and Bellucia (one shipwreck that sunk in 1903) and the Rasas and Escalvada islands. These reefs are 10 km off Guarapari, state of Espírito Santo, Brazil. The field work was done in 2008 and 2009. The structure and composition of fish communities were accessed trough underwater visual census (20 x 2 m-belt transects). Additionally, the benthic communities (functional groups) and the reef rugosity were accessed in order to determine the importance of the substrate to the found patterns. The cryptobenthic fishes were captured using hand nets.

The thesis is divided in five chapters, one introductory and four composed of an equal number of manuscripts. This formatting was chosen because it is suitable to the heterogeneity in topics and also makes the scientific divulgation process (formal publication) faster. Chapter 1 is a general introduction on artificial reef research and factors that motivated the development of the proposed study. In Chapter 2, the fish trophic structure is compared between (and within) artificial and natural reefs and difference-causing factors identified. The length frequency, biomass and occurrence frequency of four fish genera targeted by local fisheries are compared, in Chapter 3, to evaluate the potential of artificial reefs for production and attraction. Length-weight relationship equations of eight cryptobenthic species captured at artificial and natural reefs are presented in Chapter 4. Finally, in Chapter 5 are presented behavioural observations realized on the Victory 8B, a *Decapterus macarellus* school using a Goliath grouper *Epinephelus itajara* as a refuge during *Caranx latus* predation attacks.

Key-words: Shipwrecks • Artificial reefs • Trophic structure • Impacts • Attraction-production

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CAPÍTULO 1

Introdução geral

Origem e definição de recifes artificiais

No início do século XVIII, pescadores japoneses descobriram que a captura de peixes era mais produtiva ao redor de naufrágios, o que levou ao afundamento deliberado de estruturas fabricadas com madeiras e pedras. Esta abordagem passou a ser chamada de recifes artificiais e foi amplamente difundida, estando em uso extensivo em muitos países costeiros, os quais utilizam uma grande variedade de materiais, técnicas e configurações (Clark, 1995).

Atualmente, recifes artificiais têm sido definidos como objetos depositados propositalmente no ambiente aquático de modo a influenciar processos físicos, biológicos e/ou sócio-econômicos relacionados aos seus recursos. No entanto, estruturas afundadas acidentalmente (e.g., naufrágios) e desenvolvidas com outros objetivos primários (e.g., píers e quebra-mares) muitas vezes são considerados como recifes artificiais por disponibilizarem novos habitats no ambiente aquático (Seaman & Jensen, 2000).

O concreto tem sido o material mais utilizado na construção de recifes artificiais. Porém, materiais de oportunidade como rochas, madeiras, pneus, plataformas de petróleo, navios e automóveis também são freqüentemente empregados (Baine, 2001). Embora o uso mais abrangente dos recifes artificiais seja o incremento da pesca comercial, artesanal ou recreacional (Woodhead et al., 1982; McGlennon & Branden, 1994; Watanuki & Gonzales, 2006; Leitão et al., 2008; Whitmarsh et al., 2008), estas estruturas podem ser instaladas com objetivos variados, incluindo o desenvolvimento de atividades de aqüicultura (Fabi et al., 1989), turismo subaquático (Morgan et al., 2009), manejo de recursos naturais (Guillén et al., 1994), conservação da biodiversidade (La Mesa et al., 2008), reabilitação de ecossistemas degradados (Clark & Edwards, 1994; Seaman, 2007) e experimentação científica (Beets, 1989; Hixon & Beets, 1989; Rilov & Benayahu, 2002; Sherman et al., 2002).

Debate atração *vs.* produção

Enquanto a pesca tem levado a um forte declínio dos estoques pesqueiros marinhos (Myers & Worm, 2003), a implantação de recifes artificiais tem sido promovida com o objetivo de incrementar as mais diversas pescarias. Taxas de captura favoráveis e elevada densidade de peixes são freqüentemente utilizados como provas de que os recifes artificiais beneficiam os estoques pesqueiros. Segundo Lindberg (1997), esta suposição tem sido amplamente aceita por tornar o desenvolvimento de recifes artificiais compatível com a ética conservacionista.

Embora o aumento inicial na produção pesqueira total devido ao estabelecimento de recifes artificiais seja freqüentemente explicado pela rápida colonização e elevada densidade nestas estruturas (Bohnsack, 1989), muitas questões envolvendo o debate atração *vs.* produção permanecem em discussão (Stone et al., 1979; Bohnsack et al., 1997; Lindberg, 1997; Powers et al., 2003). Atualmente, quando muitos dos estoques encontram-se sobre-explotados e, portanto, abaixo da capacidade de suporte dos recifes naturais, sabe-se que a produção pesqueira não é limitada pela disponibilidade de habitat (Lindberg, 1997). Segundo Bohnsack (1989), o dilema atração *vs.* produção não é um problema dicotômico, estes são apenas os dois extremos de um gradiente que pode variar entre diferentes espécies e dentro de uma mesma espécie, ou seja, algumas espécies podem ser atraídas de recifes naturais e outras produzidas nos recifes artificiais, enquanto outras podem ainda ser parcialmente atraídas e produzidas. A atração em si não é considerada um problema, desde que o nível de pesca não coloque em risco a manutenção dos estoques. Porém, para populações em estado de sobrepesca, a atração pode concentrar os indivíduos restantes em áreas pequenas e conhecidas por pescadores, tornando-os mais vulneráreis e acelerando o processo de declínio populacional (Bohnsack, 1989).

Recifes artificiais não são panacéias para os problemas e conflitos da pesca e, portanto, seu uso deve ser considerado somente como parte de um programa de manejo pesqueiro maior. Na maioria das vezes, os projetos de implantação de recifes artificiais falham na elaboração de um planejamento que garanta que estes sirvam como efetivas ferramentas ecológicas e econômicas. Somente quando os programas são cuidadosamente planejados, manejados e mantidos é possível alcançar os benefícios pretendidos (Clark, 1995).

Uso de recifes artificiais na costa brasileira

No Brasil, o uso de recifes artificiais iniciou-se no estado do Rio de Janeiro na década de 1980 e, desde então, expandiu-se por toda a costa. Esses projetos, os quais têm sido propostos tanto pelo setor público quanto privado, têm utilizado, além de concreto, diversos materiais obsoletos (e.g, navios, pneus, contêineres e restos de plataformas de petróleo descomissionadas). Segundo Buckley (1989), embora os recifes artificiais sejam sempre apresentados como projetos para melhorar a pesca, a verdade é que muitos são pouco mais que disfarces para programas de descarte de materiais obsoletos, projetos para obtenção de isenção de impostos ou jogadas políticas para promover alguma companhia, grupo ou causa. Desta forma, é essencial que os atuais e futuros projetos de implantação de recifes artificiais na costa brasileira sejam analisados rigorosamente por gestores da pesca e pesquisadores em sua essência e necessidade, para que não se repitam os erros cometidos em outras ocasiões.

Embora a realização de pesquisas envolvendo recifes artificiais no Brasil seja muito recente, o número de trabalhos publicados vem crescendo rapidamente (Brotto & Araujo, 2001; Faria et al., 2001; Gomes et al., 2001; Godoy et al., 2002; Zalmon et al., 2002; Cunningham & Saul, 2004; Jardeweski & Almeida, 2005; Brotto et al., 2006; Conceição & Pereira, 2006; Krohling et al., 2006; Brotto et al., 2007; Brotto & Zalmon, 2008; Krohling & Zalmon, 2008; Santos et al., 2008). No entanto, grande parte destes é composta por pesquisas experimentais de curta escala (máximo de dois anos), sendo insuficientes para diagnosticar as alterações causadas no ambiente marinho e avaliar o desempenho dos projetos quanto ao alcance de seus objetivos. Além disso, a maior parte dos projetos promovidos pelo setor privado não tem sido corretamente avaliada e monitorada e, portanto, não são conhecidos seus impactos nos meios físico, biológico e sócio-econômico. Mesmo quando acompanhados por pesquisadores, as informações permanecem, em geral, dispersas e pouco acessíveis.

Diante do uso crescente e desregulado de recifes artificiais na costa brasileira e considerando que estes podem ser causadores de significativo impacto ambiental, o Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA) decretou em 2006 a Instrução Normativa N° 125 (Brasil, 2006). Esta legislação estabeleceu procedimentos rigorosos quanto ao licenciamento ambiental para a implantação de recifes artificiais no âmbito da gestão dos recursos pesqueiros. Em 2009, a Instrução Normativa N° 125 foi revogada e a implantação de recifes artificiais passou a ser regulada pela Instrução Normativa N° 20 (Brasil, 2009).

Motivações da presente pesquisa

Em 2003, o Victory 8B, um navio cargueiro de bandeira grega abandonado em condições precárias no Porto de Vitória, ES, foi transformado em recife artificial e afundado na costa de Guarapari, sul do Estado. Para implantação deste recife artificial foi selecionada uma área de fundo arenoso entre as ilhas Rasas e Escalvada, cerca de 10 km da costa. Apesar de o projeto ter sido coordenado pelo órgão ambiental estadual, o ambiente marinho onde foi implantado o recife artificial não foi adequadamente monitorado. Em primeiro lugar, não foi realizado monitoramento pré-implantação, impossibilitando a avaliação dos reais impactos causados por esta estrutura na área de influência direta. Segundo, o monitoramento pós-implantação foi iniciado tardiamente, somente 2 anos após o afundamento. Além disso, como o monitoramento ambiental deste recife artificial não incluiu a avaliação da comunidade de peixes associada a ele (foi realizado somente o monitoramento das capturas na área ao seu entorno), não foram determinadas as importâncias relativas do recrutamento e da atração de indivíduos adultos de recifes naturais adjacentes no processo de colonização. O projeto também apresentou falhas quanto à escolha do local e preparação da estrutura. Em relação à escolha do local, foram priorizadas a segurança da navegação e a viabilidade logística para a realização de operações de mergulhos. Apesar de o recife artificial ter sido implantado em uma área de fundo arenoso, a existência de ilhas e recifes submersos de elevada relevância ecológica em áreas muito próximas faz com que o local seja inadequado para este tipo de empreendimento, uma vez que pode tornar o recife artificial um importante atrator de peixes dos recifes naturais. Quanto à preparação da estrutura, apesar de ter sido retirado todos os equipamentos e materiais poluentes, a tinta não foi removida, dificultando o processo de colonização por organismos bentônicos.

A ausência de um monitoramento adequado da comunidade de peixes presentes no Victory 8B e a existência de um naufrágio verdadeiro, o Bellucia, afundado em uma área próxima (adjacente as Ilhas Rasas) 100 anos antes da implantação do Victory 8B, nos motivaram a realizar a presente pesquisa. Esta foi financiada pela Fundação de Apoio à Ciência e Tecnologia do Espírito Santo – FAPES (Projeto “Recifes artificiais e naturais no Espírito Santo: uma análise da comunidade de peixes”; Processo Nº 38854660/2007). O objetivo principal foi comparar a estrutura e composição das assembléias de peixes entre estes recifes artificiais e dois recifes naturais próximos (ilhas Rasas e Escalvada) para avaliar quais características dos “naufrágios” os tornam similares ou distintos dos ambientes naturais e quais possíveis impactos podem ser detectados nas comunidades de peixes dos recifes naturais. Outro objetivo desta pesquisa foi comparar os dois naufrágios para avaliar se após um longo intervalo de tempo (100 anos) as comunidades de peixes associadas a eles se tornam mais similares às dos ambientes naturais. Estes resultados ajudarão na avaliação de futuros projetos de implantação de recifes artificiais na costa brasileira, para que estes não sejam utilizados com o único propósito de lançamento de materiais obsoletos ou exploração desordenada dos recursos marinhos.

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CAPÍTULO 2

Trophic structure of reef fish assemblages in south-eastern Brazil: a comparison of artificial and natural environments

Thiony Simon, Jean-Christophe Joyeux and Hudson Tercio Pinheiro

Abstract

Comparisons of reef fish assemblage trophic structure on artificial and natural reefs are rare but useful because they permit an assessment of ecological function beyond taxonomic composition. The present work compares the trophic structure of reef fish assemblages on artificial (one old and one recent shipwreck) and natural reefs (two coastal islands) with the aims to determine if trophic structure differs between and within artificial and natural reefs and if, as time passes, artificial reefs would tend to support assemblages of trophic structure similar to that of natural reefs. Two artificial structures, the shipwrecks Bellucia (an iron freighter that sunk in 1903) and Victory 8B (a derelict freighter intentionally sunk in 2003), and two natural rocky reefs, Rasas and Escalvada islands, in south-eastern Brazil were examined. Two hundred and thirty-nine underwater visual censuses (20 x 2 m belt-transects sample unit) were realized in natural and 81 censuses in artificial reefs between January and April 2008. The censuses were distributed among four sectors and three subsectors in natural reefs and in three sectors and two subsectors in artificial ones in order to warranty that all habitats in these reefs were sampled. Abundance data (ind. m^{-2}) were transformed to biomass data (g m^{-2}) through length-weight relationship equations. Species were grouped in eight trophic guilds (roving and territorial herbivores, omnivores, sessile and mobile invertebrate feeders, planktivores, carnivores and piscivores) based on the main diet of adults. To assess the importance of substrate characteristics to the trophic structure, benthic composition and rugosity were determined. The reef fish trophic structures were found to be strongly different between artificial and natural reefs and between artificial reefs, but very similar between natural reefs. The mainly factors driving the differences between artificial and natural reefs were carrying capacity of mobile invertebrate feeders, vertical relief, reef size, structural complexity and behavioural preferences. Between artificial reefs, depth, adjacent bottom (presence of rock outcrop), benthic cover and ecological interactions such as predation caused the most important differences in trophic structure. After a century, the Bellucia shipwreck still appears to support a fish fauna of trophic structure strongly dissimilar to that of adjacent natural reefs.

Keywords

Fish guilds • Shipwrecks • Artificial reefs • Ecology

Introduction

The knowledge of how natural communities are organized is a constant search of ecologists, and this information collaborates to the development of monitoring programs, impact analyses and management initiatives. In marine reef environments, structural complexity and long evolutionary history influenced an important diversification of trophic guilds, especially for fishes, who occupy a wide variety of niches (Bellwood & Wainwright, 2002). Species diversification peaks in coral reefs of the Indo-Pacific and the Caribbean (Hughes et al., 2002; Floeter et al., 2008), but tropical marginal reefs, oftentimes composed of rocky shores and reefs, also can support similar communities (Ferreira et al., 2001; Floeter et al., 2007).

While marine natural resources decrease (Myers & Worm, 2003) due to the continuous increase of consumption by coastal human populations, options that offer sustainability or improvement of the yields are well perceived by people in general. Thus, artificial reefs have been suggested by many corporations as a solution for the economic maintenance of reef fisheries (Lindberg, 1997). However, the real benefits brought by artificial reefs are an issue much debated among scientists and researchers (Stone et al., 1979; Bohnsack et al., 1997; Lindberg, 1997). In a reality were reef environments aren’t primary limiting factors for fish presence or abundance (because fisheries are the regulating factor), lack of management policies for artificial reefs can be prejudicial to all reef communities, artificial and natural alike (Capítulo 3).

Many works comparing fish communities between artificial and natural reefs have been published (e.g., Randall, 1963; Stone et al., 1979; Rooker et al., 1997; Rilov & Benayahu, 2000; Terashima et al., 2007), but very few have attempted to contrast the trophic structure between environments (e.g., Arena et al., 2007). This is unfortunate because such functional approach provides an ecological rather than taxonomic description of the assemblages and thus permits to infer general evolutionary trends (Ferreira et al., 2004; Floeter et al., 2004). In the present work we compare the trophic structure of reef fish assemblages among artificial and natural reefs in south-eastern Brazil to respond the following questions: (1) does the trophic structure differ between artificial and natural reefs, between artificial reefs and between natural reefs? What factors could be causing the differences observed? (2) Do artificial reefs (accidental or intentional shipwrecks) evolve with time toward supporting a fish assemblage with a trophic structure similar to assemblages on natural reefs?

Material and methods

Study sites

The present work was performed at replicated artificial and natural reefs, located 10 km off Guarapari, south-eastern Brazil (Fig. 1). The two artificial reefs are steel-hulled freighters differing in origin and age. The Bellucia sunk in 1903 after colliding against a rock outcrop near Rasas Islands. In the collision, the ship broke in two parts; these now are 150 m from each other. The wreck maximum depth is 27 m and remains of the superstructure reach 20 m below the surface. The Victory 8B (or, simply, Victory) was purposely submerged in 2003 to combine waste disposal and touristic purposes after being stripped of everything but paint. Maximum depth is 35 m and the top of the funnel is at 18 m below the surface. Due to their difference in age, the structural condition of the two artificial reefs is very contrasting. The Bellucia's structure is much crushed and complex while that of the Victory still is relatively conserved and so less complex. Both artificial reefs are located over extensive sand banks, but parts of Bellucia remain on the lower part of the rock. The artificial reefs show differing degree of isolation relative to natural emerged reefs (see Fig. 1). However, there are in the region ample areas of natural reef patches (mainly with base of coralline algae and bryozoans) that make difficult to appraise the importance of the supply of adult and larval fishes by natural reefs. The two natural reefs, Escalvada and Rasas islands, are granitic and are located five km from each other. Escalvada is a single island and Rasas are actually composed by two small islands separated by a shallow and narrow strait. Depth at the interface between reef and unconsolidated substrate varies between 9 and 25 m depending on the island and side of the island.

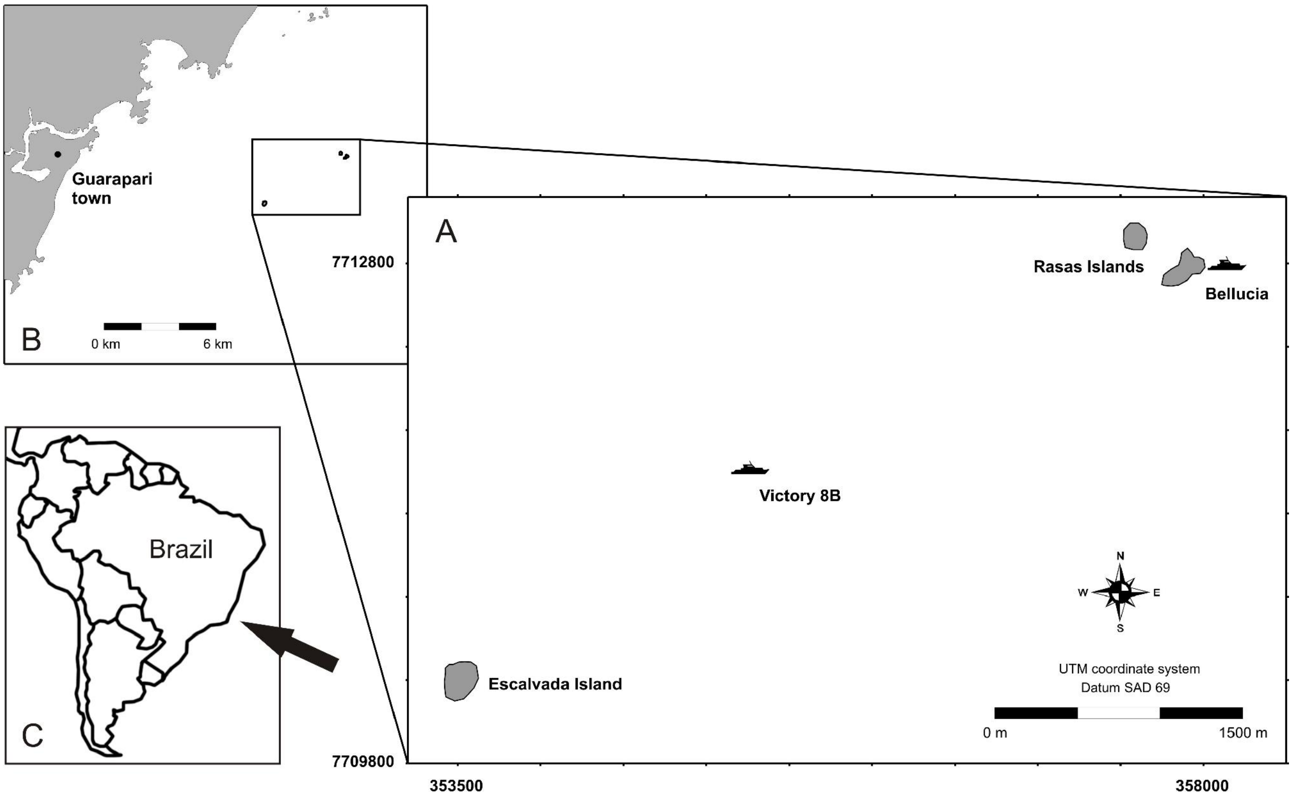

Figure 1: Study area (A), showing its insertion in the Guarapari town (B) and in the Brazilian coast (C).

Reef fish assemblage trophic structures

The reef fish assemblages were assessed through underwater visual census (20 x 2 m belt-transects sample unit) between January and March 2008. This period was chosen because only during austral summer visibility is sufficient to permit accurate visual observations at the study site. Each census was divided in two steps. In the first step, the diver, after selecting one random starting point, swam unrolling a tape and counting the more mobile species (generally those of greater size and of demersal or pelagic habit). In the second step, the diver came back to the initial point rolling the tape and counting the more cryptic species (generally that of smaller size and benthic habit). This method is largely used on the Brazilian coast because it is suitable in low visibility, keeps sample unit within a defined habitat and is comparatively accurate for estimating density of cryptobenthic species (Floeter et al., 2004; Floeter et al., 2006; Floeter et al., 2007). In each census was registered the number of individuals of each species and estimated their total length in 10 cm size classes (the smallest fishes were classified into two 5 cm-classes). An abundance scale was established to reduce the probability of error in enumerating individuals in schools. Schools up to 20 individuals were enumerated; larger schools were classified as containing 30, 50, 100, 200, 500, 1000 or 2000 individuals. The number of samples in natural reefs (113 at Escalvada and 126 at Rasas) was higher than in artificial reefs (35 on the Bellucia and 46 on the Victory) due to the large difference in total area between theses sites. In order to warrant that all environments existing in the reefs were being sampled, the censuses were stratified in three or four sectors. Around islands, census were distributed among north, south, east and west sides, the Rasas samples being additionally divided between the two islands. On shipwrecks, censuses were performed on stern, bow and superstructure; Victory´s superstructure and stern were considerated separate sectors, despite being together, due to a number of characteristics, mainly depth. In each sector, censuses were also distributed among subsectors. Thus, in all islands, censuses were further stratified according to the depth gradient in three strata, including surface (3 m minimum depth), middle rocky shore (about half-way between surface and interface) and interface. On stern and bow of shipwrecks, censuses were performed on the main deck and cargo hold and at the interface (as in natural reefs). No further subdivision was applied for the superstructure of the Victory and censuses were performed on upper decks horizontal surfaces. The single census performed on the remains of Bellucia’s superstructure, due to small size and low depth gradient, was grouped with deck censuses of the stern sector.

The censuses were performed by two divers (TS and HTP). To avoid bias caused by difference in observer expertise, the field procedure was standardized during pre-sampling training. During it, the two divers realized visual censuses swimming side by side to guarantee that the same reef fish community had been available to both. No obvious discrepancy in number of species, individuals and fish number per size class were detected between divers (no test was performed due to low number of values) and differences in estimates (mainly for schools) were debated after the dive to reach a consensus. Subsequently to training, sampling was done with divers realizing census concurrently in the same sectors and subsectors to avoid systematic bias.

Fish number and size data were transformed to biomass data through length-weight relationship equations (Froese & Pauly, 2008) using size center-of-class. Throughout the study, references to abundance actually refer to biomass (in g m^{-2}). When no specific equation was available, mean genus or family equations were applied. Species were grouped into eight trophic guilds following Ferreira et al. (2004) [roving herbivores (ROH), territorial herbivores (TEH), omnivores (OMN), carnivores (CAR), piscivores (PIS), sessile invertebrate feeders (SIF), mobile invertebrate feeders (MIF) and planktivores (PLK)], based on literature available for the main diet of adults (e.g. Randall, 1967) and on published works about the trophic structure of Brazilian reef fish communities (Floeter & Gasparini, 2000; Gasparini & Floeter, 2001; Ferreira et al., 2004; Floeter et al., 2004; Floeter et al., 2007). Although feeding plasticity, as well as ontogenetic shifts, make difficult grouping fish into independent feeding guilds (Floeter et al., 2004), this approach is useful to assess the general patterns of trophic organization and evaluate how biotic and abiotic characteristics of the habitat can determine the community structure.

The guilds are described in details in Ferreira et al. (2004) but, in synthesis, ROH are generally large fishes that include detritus, turf algae and macroalgae in their diet; TEH are small herbivores that mainly consume turf algae farmed within vigorously defended territories; MIF feed primarily on mobile invertebrates associated to both hard and soft bottoms; SIF feed on hard substrate-associated sessile invertebrates such as sponges, cnidarians, ascidians, hydrozoans and bryozoans; OMN feed on a mix of animal and plant material; PLK feed primarily on macro- and micro-zooplankton; CAR feed on both mobile invertebrates and fishes; and PIS feed mainly on live fishes.

Substrate characteristics

In order to evaluate the influence of substrate upon the trophic structure of the reef fish assemblages (and thus to turn possible the discussion on the effect of substrate nature and age), benthic composition and substrate rugosity were determined. Study sites were stratified similarly to fish censuses. Benthic composition was determined through the photoquadrat method (photos showed an area of 27.2 x 20.4 cm) and the rugosity was determined through the chain-and-tape method (1 m long chain with 3.3 cm links). Transects were 10 m long and data collected consisted of five photos and one measure of rugosity per transect.

In the whole, 48 transects were performed at each natural reef and 15 on each artificial reef. The photoquadrats were analysed in the Coral Point Count with Excel extensions software, CPCe V3.5 (Kohler & Gill, 2006). In each photoquadrat were distributed 20 random points and the biotic (functional groups) or abiotic categories below these points were registered. The biotic categories were “Crusting coralline algae”, “Branching coralline algae”, “Non-coralline algae”, “Stony corals”, “Firecorals”, “Anemones”, “Gorgonians”, “*Carijoa riisei*”, “Hydroids”, “Bryozoans”, “Zoanthids”, “Sponges”, “Ascidians”, “Bivalves”, “Barnacles” and “Crinoids”. The abiotic categories were “Sedimentation” (fluid mud deposited due to high precipitation rates, covering live and/or dead organisms), “Unconsolidated substrate” (i.e., mud, sand or gravel deposits, indiscriminately) and “Pavement” (bare rock or metal). Mobile animals and unidentified sessile animals were quantified but not shown. The relative abundance of each category was averaged among all five photoquadrats of the same transect. The rugosity index was calculated as the ratio of contoured vs. straight distance (10 m) between two points.

Statistical analyses

Differences in trophic structure between artificial and natural reefs were tested by analysis of variance (ANOVA, $\alpha = 0.05$). Guild biomass was included in models as the dependent variable and reef nature (two levels: natural and artificial) and reef site (four levels: Escalvada, Rasas, Victory and Bellucia) as independent variables (reef site was nested within reef nature). In order to reduce heteroscedasticity among factor levels, raw data were log-transformed ($\log_{10} x + 1$) before analysis. SIMPER analyses were applied to examine the contributions of fish species (within each guild) and benthic categories to the average dissimilarity (Bray-Curtis) between artificial and natural reefs. Only the most influent species or categories that, added up, cause 90 % of the total dissimilarity were considered to be significant. To explore the variation in trophic structure among reefs, non-metric multi-dimensional scaling (nMDS), using the Bray-Curtis similarity index, was applied on square root-transformed data. To this, the censuses were grouped into subsectors "interface", "middle" and "surface" for natural reefs and "interface", "deck" and "superstructure" (as before, the single Bellucia superstructure census was grouped with deck censuses) for the artificial reefs. The consistence of visually-defined groups in nMDS was tested through analysis of similarities (ANOSIM). In order to synthesize the influence of substrate variables (rugosity and benthic cover) over the trophic structure, a canonical correspondence analysis (CCA) was done. Data were grouped as in SIMPER and nMDS analyses, standardized ($x' = [(x - \text{mean}) / SD] + 2$) and square-root transformed prior to examination.

Results

Trophic structure of reef fish assemblages

The trophic structure of the reef fish assemblages varied distinctively between natural and artificial reefs (Fig. 2) and between artificial reefs (Fig. 3), but differences were small between natural reefs (Fig. 4). Biomass of all guilds but SIF differed between natural and artificial reefs and biomass of all guilds but TEH differed between artificial reefs. In contrast, only OMN and PIS differed between natural reefs. In general, when artificial and natural reefs are combined, the most abundant guilds were MIF (199.0 g m^{-2}, 48.0 % of total biomass), OMN (95.1 g m^{-2}, 22.9 %) and ROH (57.4 g m^{-2}, 13.9 %). In total, 130 *taxa* were observed on artificial and natural reefs (64 on the Victory, 68 on the Bellucia, 91 at Escalvada and 99 at Rasas). One hundred and fourteen *taxa* were observed during censuses on natural reefs (including 41 restricted to those reefs) and 89 were observed during artificial reefs censuses (16 exclusive). The most speciose guilds (natural and artificial reefs combined) were MIF and CAR, with 40 and 27 *taxa*, respectively (Table 1).

Overall, the mean biomass (all guilds combined) was more than three times greater on artificial (873.4 g m^{-2}) than on natural reefs (259.2 g m^{-2}). On artificial reefs, the most abundant guilds were MIF (616.2 g m^{-2}, 70.6 % of total biomass) and OMN (164.8 g m^{-2}, 18.9 %), while on natural reefs they were ROH (72.8 g m^{-2}, 28.1 %), OMN (71.4 g m^{-2}, 27.6 %) and MIF (57.6 g m^{-2}, 22.2 %) (Fig. 2). The guilds ROH, TEH and CAR were significantly more abundant and contributed more to the total biomass on natural reefs and MIF, OMN, PLK and PIS were more abundant on artificial reefs, although the three latter proportionally contributed more to the total biomass of natural than artificial reefs due the enormous biomass of MIF on the latter (Fig. 2).

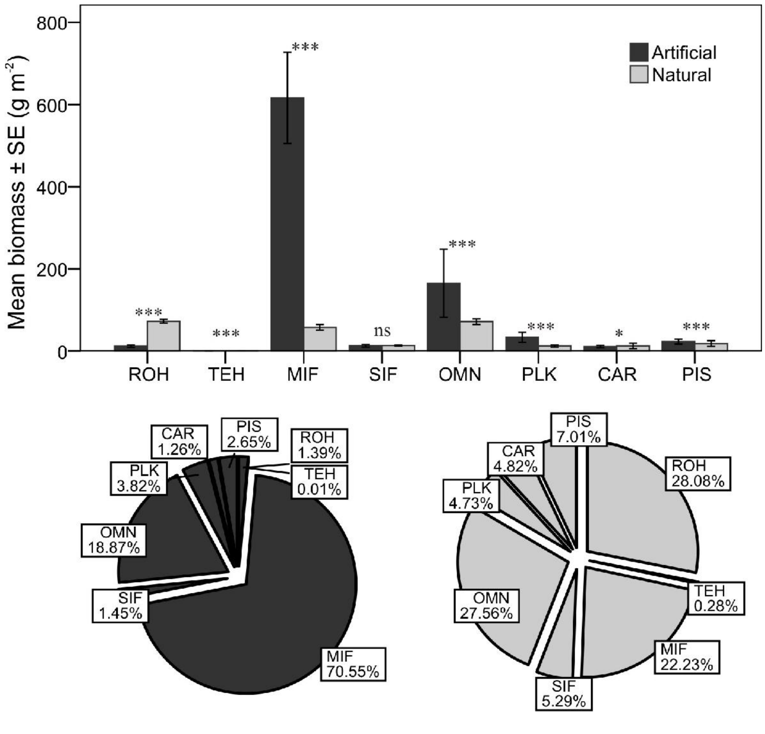

Figure 2: Trophic structure of reef fish assemblages on natural and artificial reefs, south-eastern Brazil. See methodology for details on guilds acronyms. The ANOVA results are shown above the guild columns (*** indicate $p \leq 0.001$, * $p \leq 0.05$ and ns $p > 0.05$).

The mean biomass (all guilds combined) was more than four times higher on the Bellucia (1,531.7 g m^{-2}) than on the Victory (372.5 g m^{-2}). On the former, the most abundant guilds were MIF (1,043.3 g m^{-2}, 68.1 %) and OMN (372.2 g m^{-2}, 24.3 %) while on the latter they were MIF (291.2 g m^{-2}, 78.2 %) and PIS (38.3 g m^{-2}, 10.3 %) (Fig. 3). The guilds ROH, MIF, SIF, OMN, PLK and CAR were significantly more abundant on the Bellucia (however, MIF, SIF and PLK contributed more to the total biomass on the Victory) and PIS were more abundant and contributed more to the total biomass on the Victory (Fig. 3).

Between Escalvada and Rasas, the mean biomass (all guilds combined) was very similar (295.5 g m^{-2} and 226.7 g m^{-2}, respectively). At Escalvada, the most abundant guilds were OMN (100.0 g m^{-2}, 30.8 %), ROH (68.8 g m^{-2}, 23.3 %) and MIF (66.9 g m^{-2}, 22.6 %), while on Rasas they were ROH (76.3 g m^{-2}, 33.7 %), OMN (53.9 g m^{-2}, 23.8 %) and MIF (49.3 g m^{-2}, 21.7 %) (Fig. 4). The guilds OMN and PIS were significantly more abundant and contributed more to the total biomass at Escalvada (Fig. 4).

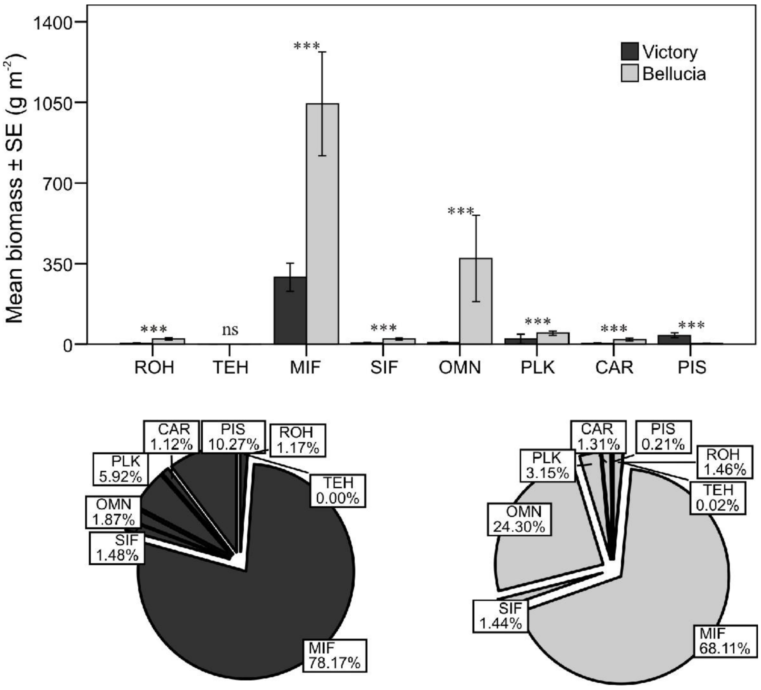

Figure 3: Trophic structure of reef fish assemblages on artificial reefs (Victory and Bellucia), south-eastern Brazil. See methodology for details on guilds acronyms. The ANOVA results are shown above the guild columns (*** indicate $p \leq 0.001$ and ns $p > 0.05$).

Species responsible for ROV dissimilarity between artificial and natural reefs (SIMPER analyses, 90 % of total dissimilarity) were the surgeonfishes *Acanthurus bahianus* (with a 42 %-contribution to total dissimilarity) and *Acanthurus chirurgus* (29 %) and the parrotfishes *Sparisoma axillare* (13 %) and *Sparisoma frondosum* (7 %) (Table 1). All these species were more abundant at natural reefs although *S. frondosum* was more abundant on the Bellucia than on any other reef.

Within the TEH, the species that caused major dissimilarity between artificial and natural reefs were the damselfishes *Stegastes pictus* (44 %) and *Stegastes fuscus* (20 %) (Table 1). The latter was only observed on natural reefs while the former was also abundant on the Bellucia.

Artificial and natural reefs differed in MIF biomass mainly by the grunts *Heamulon aurolineatum* (61 %), *Haemulon plumieri* (6 %), *Haemulon steindachneri* (3 %), *Anisotremus virginicus* (4 %) and *Anisotremus surinamensis* (2 %), the wrasses *Bodianus rufus* (6 %) and *Halichoeres poeyi* (3 %), the squirrelfish *Holocentrus adscensionis* (6 %) and the goatfish *Pseudupeneus maculatus* (2 %) (Table 1). Only three of these species, *H. aurolineatum*, *A. surinamensis* and *H. steindachneri*, showed higher biomass on artificial reefs. Albeit a speciose guild, a single MIF species (*H. aurolineatum*) encompassed 93.5 % of the total guild biomass on artificial reefs. On the contrary, on natural reefs 78.2 % of the guild biomass was distributed among five species (*H. aurolineatum*, *H. plumieri*, *B. rufus*, *H. adscensionis* and *A. virginicus*). *Haemulon aurolineatum* remained the most abundant species overall on both reef types but its biomass was distinctively higher (576.0 g m^{-2} and 65.9 % of total fish biomass) on artificial than on natural reefs (14.0 g m^{-2} and 5.4 % of fish biomass). Mean biomass of *H. aurolineatum* was also varied between artificial reefs (974.0 g m^{-2} and 273.2 g m^{-2} on the Bellucia and Victory, respectively, i.e. 63.6 % and 73.3 % of total fish biomass). Two *Haemulon* species (*H. plumieri* and *H. steindachneri*), *H. adscensionis* and *P. maculatus* were more abundant on the Bellucia than on the Victory.

The angelfishes *Holacanthus tricolor* (45 %) and *Holacanthus ciliaris* (20 %) with the butterflyfishes *Chaetodon striatus* (16 %) and *Chaetodon sedentarius* (9 %) were responsible for SIF-dissimilarity between artificial and natural reefs (Table 1). *Holacanthus ciliaris* and *C. sedentarius* were more abundant on artificial reefs. The species more abundant at natural reefs, *C. striatus* and *H. tricolor,* were also more abundant on the Bellucia than on the Victory.

The *taxa* that accounted for most PLK dissimilarity between artificial and natural reefs were the nocturnal squirrelfish *Myripristis jacobus* (33 %) plus the wrasse *Clepticus brasiliensis* (22 %), the damselfish *Chromis multilineata* (19 %), the creolefish *Cephalopholis furcifer* (11 %) and the scad *Decapterus* spp. (6 %) (Table 1). While *C. multilineata* and *C. furcifer* were characteristic of natural reefs, *C. brasiliensis*, *M. jacobus* (both particularly abundant on the Bellucia) and *Decapterus* spp. were more abundant on artificial reefs. Actually, *Decapterus* spp. was only observed on artificial reefs, occasionally and in large schools.

Omnivores that differed between artificial and natural reefs were the pinfish *Diplodus argenteus* (48 %), the damselfish *Abudefduf saxatilis* (12 %), the angelfishes *Pomacanthus paru* (11 %) and *Pomacanthus arcuatus* (9 %), the filefish *Cantherhines pullus* (7 %) and the spadefish

Chaetodipterus faber (6 %) (Table 1). *Chaetodipterus faber* (only observed on the Bellucia, occasionally and in large schools) and *P. arcuatus* were more abundant on artificial reefs and the other species on natural reefs. *Diplodus argenteus* and *P. paru* were more abundant on the Bellucia than on the Victory and *A. saxatilis* and *D. argenteus* were more abundant at Escalvada than at Rasas.

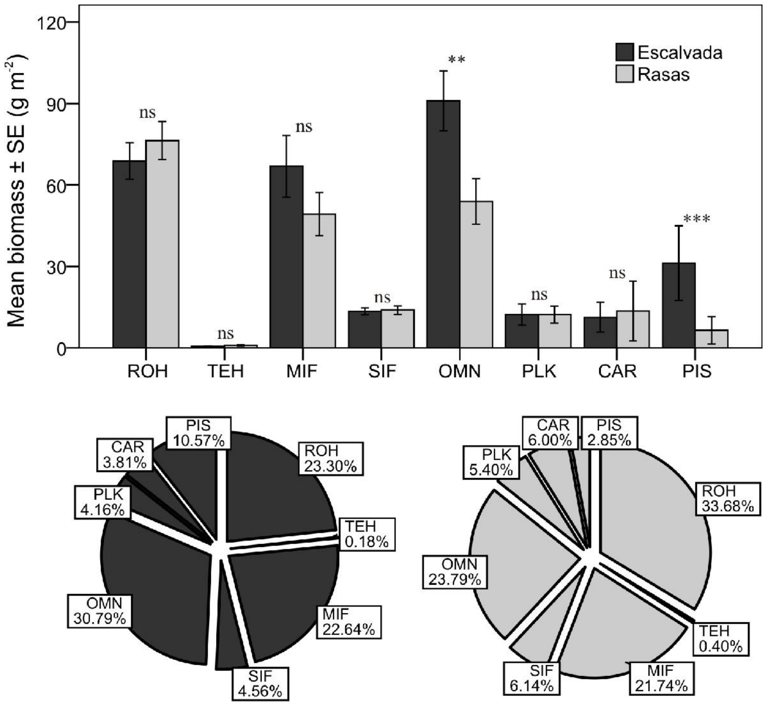

Figure 4: Trophic structure of reef fish assemblages on natural reefs (Escalvada and Rasas islands), south-eastern Brazil. See methodology for details on guilds acronyms. The ANOVA results are shown above the guild columns (*** indicate $p \leq 0.001$, ** $p \leq 0.01$ and ns $p > 0.05$).

The main carnivore species differing between artificial and natural reefs were the croaker *Odontoscion dentex* (19 %), the coney *Cephalopholis fulva* (17 %) and the soapfish *Rypticus saponaceus* (9 %). Other 12 species (*Scorpaena plumieri*, *Lutjanus jocu*, *Lutjanus analis*, *Pagrus pagrus*, *Ocyurus chrysurus*, *Malacanthus plumieri*, *Gymnothorax moringa*, *Labrisomus nuchipinnis*, *Dasyatis centroura*, *Ogcocephalus vespertilio*, *Lutjanus synagris* and *Paralichthys brasiliensis*) were responsible for the remaining dissimilarity (90 %) (Table 1). *G. moringa*, *O. dentex*, *R. saponaceus* and *S. plumieri* were more abundant on artificial reefs and *L. jocu*, *L. analis*, *L. synagris* and *O. vespertilio* were only observed there. The other species were more abundant on natural reefs (with *L. nuchipinnis*, *M. plumieri*, *P. pagrus* and *P. brasiliensis* only encountered there).

Fishes that contributed to the dissimilarity in PIS between artificial and natural reefs were the jack *Caranx crysos* (43 %) together with the groupers *Mycteroperca acutirostris* (14 %), *Mycteroperca interstitialis* (10 %) and *Mycteroperca bonaci* (8 %), the trumpetfish *Aulostomus strigosus* (14 %) and the lizardfish *Synodus synodus* (5 %) (Table 1). The jack and the trumpetfish were more abundant on natural reefs. The jack was also very abundant on the Victory but was not recorded on the Bellucia.

Artificial and natural reefs relationships

Grouping analyses (nMDS and cluster) showed the formation of three groups (Fig. 5), one composed by all natural reef subsectors, one by shallow artificial reef subsectors (deck and interface of Bellucia plus superstructure of Victory) and one by deep artificial reef subsectors (deck and interface of Victory). The natural reef group was significantly different from the deep artificial reef group (ANOSIM, R = 0.958, p = 0.036) and from the shallow artificial reef group (ANOSIM, R = 0.994, p = 0.012). However, no differences was found between the two artificial reefs groups (ANOSIM, R = 0.917, p = ns). The main difference in trophic structure among these groups is related to MIF and OMN biomasses. The MIF guild was more abundant in the shallow artificial group (959.4 g m^{-2}) than in the deep artificial group (165.1 g m^{-2}) and in the natural group (57.5 g m^{-2}). Omnivorous fishes showed a similar pattern of biomass distribution (286.5 g m^{-2}, 4.8 g m^{-2} e 71.4 g m^{-2}, at shallow artificial, deep artificial and natural groups, respectively), differing only between deep artificial and natural groups (MIF was more abundant on deep artificial and OMN on natural). Clearly, the high biomass of MIF (1,206.9 g m^{-2} on Bellucia’s interface, 946.6 g m^{-2} on Bellucia’s deck and 692.5 g m^{-2} on Victory’s superstructure) was responsible for the association of shallow artificial subsectors.

Substrate characteristics

Rugosity index was high on artificial than on natural reefs (Table 2). There, pre-existent re-entrances into the structure (such as hatchways, door and hold openings) and external ironware (such as stairs and handrails), in association to corrosion and crushing of metallic walls, turned the surface highly rugged and irregular. In fact, the older artificial reef (Bellucia) was the most rugose

Table 1: Reef fish assemblages (arranged by guilds) on natural and artificial reefs, south-eastern Brazil. See methodology for details on guild acronyms. Mean biomass in g m^{-2}. The species causing up to 90 % of the total dissimilarity between artificial and natural reefs, as detected by SIMPER analysis for each guild, are boldfaced.

Species	Guild	Artificial reefs (mean biomass ± SD)			Natural reefs (mean biomass ± SD)		
		Victory n = 46	Bellucia n = 35	Total	Escalvada n = 113	Rasas n = 126	Total
Acanthurus bahianus	**ROH**	**0.42 ± 1.60**	**2.72 ± 4.54**	**1.41 ± 3.39**	**30.18 ± 26.32**	**28.37 ± 35.17**	**29.22 ± 31.25**
Acanthurus chirurgus	**ROH**	**1.94 ± 7.48**	**10.77 ± 14.22**	**5.75 ± 11.69**	**18.32 ± 28.14**	**21.55 ± 43.15**	**20.02 ± 36.78**
Acanthurus coeruleus	ROH	1.96 ± 7.98	-	1.11 ± 6.06	0.40 ± 4.24	0.54 ± 4.54	0.47 ± 4.39
Cryptotomus roseus	ROH	-	-	-	0.37 ± 2.71	0.26 ± 1.53	0.31 ± 2.16
Kyphosus spp.	ROH	-	-	-	10.98 ± 50.8	2.81 ± 20.95	6.67 ± 38.23
Scarus trispinosus	ROH	-	0.67 ± 3.96	0.29 ± 2.60	-	-	-
Scarus zelindae	ROH	-	0.67 ± 3.96	0.29 ± 2.60	-	-	-
Sparisoma amplum	ROH	-	-	-	0.17 ± 1.79	0.01 ± 0.13	0.09 ± 1.23
Sparisoma axillare	**ROH**	**0.01 ± 0.06**	**2.71 ± 11.42**	**1.18 ± 7.56**	**7.75 ± 27.76**	**18.74 ± 40.85**	**13.54 ± 35.63**
Sparisoma frondosum	**ROH**	**0.03 ± 0.22**	**4.79 ± 12.21**	**2.09 ± 8.31**	**0.59 ± 3.21**	**4.06 ± 12.92**	**2.42 ± 9.78**
Sparisoma radians	ROH	-	-	-	-	0.01 ± 0.13	0.01 ± 0.09
Sparisoma spp. (juv)	ROH	0.19 ± 0.03	0.01 ± <0.01	0.19 ± 0.02	1.45 ± 0.08	0.29 ± 0.01	1.74 ± 0.05
Sparisoma tuiupiranga	ROH	-	0.04 ± 0.25	0.02 ± 0.16	0.07 ± 0.36	-	0.03 ± 0.25
Microspathodon chrysurus	TEH	-	-	-	-	0.02 ± 0.22	0.01 ± 0.16
Stegastes fuscus	**TEH**	**-**	**-**	**-**	**0.23 ± 0.96**	**0.58 ± 2.05**	**0.41 ± 1.63**
Stegastes pictus	**TEH**	**0.01 ± 0.05**	**0.26 ± 0.42**	**0.12 ± 0.30**	**0.28 ± 0.67**	**0.27 ± 0.57**	**0.27 ± 0.62**
Stegastes variabilis	TEH	<0.01 ± <0.01	-	<0.01 ± <0.01	0.02 ± 0.09	0.04 ± 0.12	0.03 ± 0.11
Amblycirrhitus pinos	MIF	-	0.02 ± 0.04	0.01 ± 0.03	0.04 ± 0.14	0.19 ± 0.78	0.12 ± 0.58
Anisotremus moricandi	MIF	-	1.97 ± 7.56	0.85 ± 5.03	0.90 ± 3.50	0.63 ± 2.62	0.76 ± 3.06
Anisotremus surinamensis	**MIF**	**2.52 ± 7.90**	**-**	**1.43 ± 6.06**	**1.33 ± 10.17**	**0.04 ± 0.45**	**0.65 ± 7.01**
Anisotremus virginicus	**MIF**	**4.25 ± 12.51**	**4.72 ± 9.52**	**4.45 ± 11.25**	**2.99 ± 11.34**	**7.41 ± 25.08**	**5.32 ± 19.89**
Balistes vetula	MIF	-	-	-	-	0.12 ± 0.70	0.06 ± 0.51
Bodianus pulchellus	MIF	1.77 ± 3.63	3.65 ± 9.18	2.58 ± 6.64	0.07 ± 0.74	0.03 ± 0.21	0.05 ± 0.53
Bodianus rufus	**MIF**	**2.96 ± 7.56**	**3.76 ± 7.74**	**3.31 ± 7.60**	**7.84 ± 17.08**	**8.83 ± 14.95**	**8.36 ± 15.97**
Calamus spp.	MIF	-	-	-	0.79 ± 6.00	0.16 ± 1.6	0.46 ± 4.28
Coryphopterus dicrus	MIF	0.03 ± 0.10	0.01 ± 0.03	0.02 ± 0.08	0.01 ± 0.02	<0.01 ± 0.01	<0.01 ± 0.01
Coryphopterus glaucofraenum	MIF	<0.01 ± <0.01	-	<0.01 ± <0.01	<0.01 ± <0.01	<0.01 ± <0.01	<0.01 ± <0.01
Dactylopterus volitans	MIF	-	-	-	1.92 ± 20.36	-	0.91 ± 14.00
Diodon hystrix	MIF	1.29 ± 6.14	3.30 ± 15.22	2.16 ± 10.99	1.58 ± 8.75	0.90 ± 7.11	1.22 ± 7.92
Doratonotus megalepis	MIF	-	-	-	-	<0.01 ± <0.01	<0.01 ± <0.01
Elacatinus figaro	MIF	-	<0.01 ± <0.01	<0.01 ± <0.01	<0.01 ± <0.01	<0.01 ± <0.01	<0.01 ± <0.01
Emblemariopsis signifera	MIF	-	-	-	-	<0.01 ± <0.01	<0.01 ± <0.01
Equetus lanceolatus	MIF	-	-	-	-	<0.01 ± <0.01	<0.01 ± <0.01
Eucinostomus argenteus	MIF	-	-	-	-	0.01 ± 0.1	<0.01 ± 0.07
Gramma brasiliensis	MIF	<0.01 ± 0.01	0.01 ± 0.03	0.01 ± 0.02	0.01 ± 0.07	<0.01 ± 0.02	0.01 ± 0.05
Haemulon aurolineatum	**MIF**	**273.22 ± 408.29**	**974.00 ± 1,337.07**	**576.03 ± 987.72**	**23.14 ± 98.15**	**5.74 ± 31.98**	**13.97 ± 71.74**
Haemulon parra	MIF	-	2.59 ± 9.52	1.12 ± 6.34	-	0.05 ± 0.57	0.03 ± 0.41
Haemulon plumieri	**MIF**	**-**	**17.00 ± 24.99**	**7.35 ± 18.36**	**8.39 ± 24.69**	**10.46 ± 49.48**	**9.48 ± 39.67**
Haemulon steindachneri	**MIF**	**1.97 ± 5.74**	**12.51 ± 64.02**	**6.52 ± 42.28**	**5.32 ± 37.07**	**1.70 ± 9.17**	**3.41 ± 26.35**
Halichoeres brasiliensis	MIF	0.41 ± 1.28	0.55 ± 0.94	0.47 ± 1.14	0.52 ± 2.42	0.71 ± 2.52	0.62 ± 2.47
Halichoeres dimidiatus	MIF	-	0.18 ± 0.55	0.08 ± 0.37	-	0.53 ± 2.07	0.28 ± 1.52
Halichoeres penrosei	MIF	0.28 ± 1.88	-	0.16 ± 1.42	0.02 ± 0.18	0.30 ± 1.29	0.17 ± 0.96
Halichoeres poeyi	**MIF**	**0.78 ± 1.05**	**0.90 ± 1.00**	**0.83 ± 1.02**	**0.70 ± 1.42**	**1.30 ± 2.31**	**1.02 ± 1.96**
Halichoeres sazimai	MIF	0.12 ± 0.47	-	0.07 ± 0.36	-	-	-
Holocentrus adscensionis	**MIF**	**1.24 ± 3.16**	**14.39 ± 22.35**	**6.92 ± 16.15**	**7.43 ± 15.05**	**8.39 ± 27.74**	**7.93 ± 22.60**
***Hypleurochilus* spp.**	**MIF**	**-**	**<0.01 ± <0.01**	**<0.01 ± <0.01**	**<0.01 ± <0.01**	**<0.01 ± 0.01**	**<0.01 ± 0.01**

Table 1: Cont.

Species	Guild	Artificial reefs (mean biomass ± SD)			Natural reefs (mean biomass ± SD)		
		Victory n = 46	Bellucia n = 35	Total	Escalvada n = 113	Rasas n = 126	Total
Malacoctenus aff. *triangulatus*	MIF	0.01 ± 0.02	0.01 ± 0.01	0.01 ± 0.02	0.01 ± 0.01	0.01 ± 0.02	0.01 ± 0.01
Malacoctenus delalandei	MIF	<0.01 ± <0.01	-	<0.01 ± <0.01	<0.01 ± 0.01	<0.01 ± <0.01	<0.01 ± 0.01
Mulloidichthys martinicus	MIF	0.11 ± 0.75	0.70 ± 2.71	0.36 ± 1.88	0.38 ± 2.90	0.11 ± 0.91	0.24 ± 2.10
Opistognathus whitehursti	MIF	-	-	-	<0.01 ± <0.01	-	<0.01 ± <0.01
Callionymus bairdi	MIF	-	-	-	-	<0.01 ± <0.01	<0.01 ± <0.01
Pareques acuminatus	MIF	0.03 ± 0.19	2.65 ± 6.07	1.16 ± 4.17	0.46 ± 2.19	0.04 ± 0.29	0.24 ± 1.53
Pseudupeneus maculatus	**MIF**	**0.03 ± 0.20**	**0.26 ± 1.09**	**0.13 ± 0.73**	**2.99 ± 7.76**	**1.53 ± 5.85**	**2.22 ± 6.85**
Serranus atrobranchus	MIF	0.01 ± 0.04	-	0.01 ± 0.03	-	-	-
Serranus baldwini	MIF	0.01 ± 0.06	0.10 ± 0.13	0.05 ± 0.11	0.05 ± 0.13	0.08 ± 0.18	0.06 ± 0.16
Serranus flaviventris	MIF	0.18 ± 0.26	0.01 ± 0.04	0.11 ± 0.21	<0.01 ± <0.01	-	<0.01 ± <0.01
Sphoeroides spengleri	MIF	-	-	-	0.02 ± 0.18	0.02 ± 0.07	0.02 ± 0.13
Canthigaster figueiredoi	SIF	0.10 ± 0.19	0.30 ± 0.50	0.19 ± 0.37	0.22 ± 0.58	0.29 ± 0.68	0.26 ± 0.63
Chaetodon sedentarius	**SIF**	**0.66 ± 1.00**	**0.65 ± 1.84**	**0.65 ± 1.41**	**0.18 ± 0.88**	**0.05 ± 0.26**	**0.11 ± 0.64**
Chaetodon striatus	**SIF**	**0.01 ± 0.04**	**1.09 ± 2.12**	**0.48 ± 1.48**	**2.25 ± 3.06**	**1.62 ± 2.79**	**1.92 ± 2.93**
Chilomycterus reticulatus	SIF	-	2.46 ± 14.57	1.06 ± 9.58	-	-	-
Chilomycterus spinosus	SIF	0.30 ± 2.03	-	0.17 ± 1.53	-	0.64 ± 4.06	0.34 ± 2.96
Holacanthus ciliaris	**SIF**	**4.39 ± 12.74**	**6.46 ± 15.52**	**5.28 ± 13.95**	**1.60 ± 6.17**	**2.82 ± 7.80**	**2.24 ± 7.09**
Holacanthus tricolor	**SIF**	**0.05 ± 0.36**	**11.13 ± 22.62**	**4.84 ± 15.75**	**9.22 ± 11.63**	**8.49 ± 14.22**	**8.84 ± 13.04**
Apogon americanus	PLK	-	-	-	<0.01 ± 0.02	-	<0.01 ± 0.01
Cephalopholis furcifer	**PLK**	**<0.01 ± 0.02**	**3.43 ± 6.75**	**1.48 ± 4.72**	**0.36 ± 2.56**	**4.19 ± 21.92**	**2.38 ± 16.09**
Chromis flavicauda	PLK	-	-	-	<0.01 ± 0.02	0.02 ± 0.14	0.01 ± 0.1
Chromis jubauna	PLK	<0.01 ± <0.01	0.03 ± 0.11	0.01 ± 0.07	-	-	-
Chromis multilineata	**PLK**	**0.15 ± 0.71**	**0.80 ± 1.46**	**0.43 ± 1.14**	**6.72 ± 34.40**	**1.81 ± 8.05**	**4.13 ± 24.43**
Clepticus brasiliensis	**PLK**	**-**	**19.12 ± 50.05**	**8.26 ± 33.99**	**1.57 ± 9.52**	**4.18 ± 17.11**	**2.95 ± 14.08**
Clupeidae	PLK	20.89 ± 141.25	-	11.86 ± 106.45	-	-	-
***Decapterus* spp.**	**PLK**	**0.96 ± 2.97**	**0.32 ± 1.89**	**0.68 ± 2.57**	**-**	**-**	**-**
Myripristis jacobus	**PLK**	**-**	**23.57 ± 35.66**	**10.18 ± 26.05**	**3.51 ± 11.37**	**1.67 ± 7.70**	**2.54 ± 9.63**
Opistognathus aff. *aurifrons*	PLK	-	0.01 ± 0.07	0.01 ± 0.04	0.01 ± 0.09	<0.01 ± 0.01	0.01 ± 0.07
Pempheris schomburgki	PLK	-	0.92 ± 3.06	0.40 ± 2.05	0.01 ± 0.11	-	0.01 ± 0.08
Pseudocaranx dentex	PLK	-	-	-	-	0.03 ± 0.38	0.02 ± 0.27
Ptereleotris randalli	PLK	0.05 ± 0.34	-	0.03 ± 0.26	0.10 ± 0.66	0.02 ± 0.13	0.06 ± 0.46
Thalassoma noronhanum	PLK	-	-	-	-	0.32 ± 1.22	0.17 ± 0.90
Abudefduf saxatilis	**OMN**	**-**	**0.11 ± 0.42**	**0.05 ± 0.28**	**15.34 ± 67.09**	**5.01 ± 10.36**	**9.89 ± 46.92**
Acanthostracion polygonia	OMN	0.15 ± 1.03	0.55 ± 3.24	0.32 ± 2.26	0.55 ± 2.76	0.60 ± 3.05	0.58 ± 2.91
Acanthostracion quadricornis	OMN	0.52 ± 3.55	-	0.30 ± 2.68	0.07 ± 0.63	0.02 ± 0.18	0.04 ± 0.45
Cantherhines macrocerus	OMN	-	-	-	1.59 ± 6.39	0.51 ± 2.51	1.02 ± 4.78
Cantherhines pullus	**OMN**	**0.12 ± 0.78**	**1.37 ± 3.36**	**0.66 ± 2.35**	**1.01 ± 2.50**	**1.47 ± 3.07**	**1.25 ± 2.82**
Centropyge aurantonota	OMN	-	-	-	-	<0.01 ± <0.01	<0.01 ± <0.01
Chaetodipterus faber	**OMN**	**-**	**335.50 ± 1,090.51**	**144.97 ± 730.33**	**-**	**-**	**-**
Diplodus argenteus	**OMN**	**1.09 ± 4.48**	**24.70 ± 45.13**	**11.29 ± 31.86**	**64.60 ± 93.18**	**36.92 ± 89.58**	**50.01 ± 92.15**
Gnatholepis thompsoni	OMN	<0.01 ± <0.01	-	<0.01 ± <0.01	-	-	-
Hypsoblennius invemar	OMN	-	-	-	<0.01 ± <0.01	<0.01 ± <0.01	<0.01 ± <0.01
Parablennius marmoreus	OMN	0.03 ± 0.05	0.01 ± 0.03	0.02 ± 0.04	0.01 ± 0.01	0.01 ± 0.02	0.01 ± 0.01
Parablennius pilicornis	OMN	-	-	-	<0.01 ± <0.01	<0.01 ± 0.01	<0.01 ± 0.01
Pomacanthus arcuatus	**OMN**	**4.30 ± 13.22**	**6.70 ± 25.31**	**5.34 ± 19.29**	**1.17 ± 6.13**	**2.87 ± 11.95**	**2.06 ± 9.66**
Pomacanthus paru	**OMN**	**0.74 ± 5.02**	**3.26 ± 9.78**	**1.83 ± 7.51**	**6.64 ± 26.52**	**6.52 ± 18.50**	**6.58 ± 22.60**
Stephanolepis hispidus	OMN	-	-	-	<0.01 ± <0.01	<0.01 ± <0.01	<0.01 ± <0.01
Alphestes afer	CAR	-	-	-	-	0.13 ± 1.48	0.07 ± 1.08
Bothus lunatus	CAR	-	-	-	-	0.01 ± 0.12	0.01 ± 0.09
Bothus ocellatus	CAR	-	-	-	0.01 ± 0.11	-	<0.01 ± 0.07
Cephalopholis fulva	CAR	0.02 ± 0.06	1.20 ± 3.81	0.53 ± 2.55	1.34 ± 6.16	1.31 ± 5.03	1.32 ± 5.58
Dasyatis centroura	CAR	-	4.59 ± 27.17	1.98 ± 17.86	-	11.03 ± 123.86	5.82 ± 89.93

Table 1: Cont.

Species	Guild	Artificial reefs (mean biomass ± SD)			Natural reefs (mean biomass ± SD)		
		Victory n = 46	Bellucia n = 35	Total	Escalvada n = 113	Rasas n = 126	Total
Diplectrum radiale	CAR	0.12 ± 0.61	-	0.07 ± 0.46	-	-	-
Elops saurus	CAR	-	-	-	5.33 ± 56.63	-	2.52 ± 38.94
Fistularia tabacaria	CAR	-	-	-	0.60 ± 4.27	-	0.29 ± 2.94
Gymnothorax funebris	CAR	0.04 ± 0.26	-	0.02 ± 0.20	0.02 ± 0.17	-	0.01 ± 0.11
Gymnothorax miliaris	CAR	-	-	-	-	<0.01 ± 0.02	<0.01 ± 0.02
Gymnothorax moringa	**CAR**	**0.03 ± 0.20**	**0.12 ± 0.39**	**0.07 ± 0.30**	**0.06 ± 0.28**	**0.02 ± 0.17**	**0.04 ± 0.23**
Gymnothorax vicinus	CAR	-	0.07 ± 0.30	0.03 ± 0.20	-	0.09 ± 0.68	0.05 ± 0.50
Labrisomus nuchipinnis	**CAR**	**-**	**-**	**-**	**0.14 ± 0.71**	**0.04 ± 0.22**	**0.08 ± 0.51**
Lutjanus alexandrei	CAR	-	-	-	-	0.05 ± 0.54	0.03 ± 0.39
Lutjanus analis	**CAR**	**2.94 ± 12.57**	**-**	**1.67 ± 9.54**	**-**	**-**	**-**
Lutjanus jocu	**CAR**	**-**	**3.87 ± 9.26**	**1.67 ± 6.33**	**-**	**-**	**-**
Lutjanus synagris	**CAR**	**0.29 ± 1.99**	**-**	**0.17 ± 1.50**	**-**	**-**	**-**
Malacanthus plumieri	**CAR**	**-**	**-**	**-**	**0.08 ± 0.41**	**0.17 ± 0.81**	**0.13 ± 0.65**
Ocyurus chrysurus	**CAR**	**0.03 ± 0.18**	**-**	**0.02 ± 0.13**	**0.36 ± 3.03**	**0.08 ± 0.67**	**0.21 ± 2.14**
Odontoscion dentex	**CAR**	**-**	**8.43 ± 16.44**	**3.64 ± 11.51**	**0.41 ± 2.52**	**0.22 ± 1.30**	**0.31 ± 1.97**
Ogcocephalus vespertilio	**CAR**	**-**	**0.42 ± 1.74**	**0.18 ± 1.15**	**-**	**-**	**-**
Pagrus pagrus	**CAR**	**-**	**-**	**-**	**1.47 ± 11.11**	**0.05 ± 0.52**	**0.72 ± 7.66**
Paralichthys brasiliensis	**CAR**	**-**	**-**	**-**	**0.73 ± 5.75**	**-**	**0.35 ± 3.96**
Rypticus saponaceus	**CAR**	**0.68 ± 2.71**	**-**	**0.39 ± 2.06**	**0.19 ± 1.59**	**0.38 ± 1.85**	**0.29 ± 1.73**
Scorpaena brasiliensis	CAR	-	-	-	0.10 ± 0.76	-	0.05 ± 0.53
Scorpaena isthmensis	CAR	-	-	-	0.01 ± 0.16	-	0.01 ± 0.11
Scorpaena plumieri	**CAR**	**-**	**1.32 ± 4.24**	**0.57 ± 2.84**	**0.39 ± 2.32**	**0.03 ± 0.25**	**0.20 ± 1.61**
Aulostomus strigosus	**PIS**	**-**	**1.12 ± 4.78**	**0.48 ± 3.17**	**1.48 ± 6.06**	**0.40 ± 2.04**	**0.91 ± 4.44**
Caranx crysos	**PIS**	**26.08 ± 66.11**	**-**	**14.81 ± 51.26**	**28.89 ± 145.60**	**5.65 ± 56.14**	**16.64 ± 108.48**
Caranx hippos	PIS	-	-	-	-	0.12 ± 1.37	0.06 ± 0.99
Caranx latus	PIS	-	-	-	0.12 ± 1.29	-	0.06 ± 0.89
Caranx ruber	PIS	-	-	-	-	0.01 ± 0.06	<0.01 ± 0.04
Mycteroperca acutirostris	**PIS**	**5.19 ± 12.50**	**0.96 ± 5.68**	**3.36 ± 10.30**	**-**	**0.12 ± 1.40**	**0.07 ± 1.01**
Mycteroperca bonaci	**PIS**	**1.28 ± 5.14**	**0.44 ± 2.59**	**0.92 ± 4.23**	**0.63 ± 3.98**	**-**	**0.30 ± 2.75**
Mycteroperca interstitialis	**PIS**	**5.20 ± 17.68**	**-**	**2.96 ± 13.51**	**-**	**-**	**-**
Synodus intermedius	PIS	0.53 ± 1.80	0.05 ± 0.20	0.32 ± 1.37	0.06 ± 0.38	0.08 ± 0.44	0.07 ± 0.42
Synodus synodus	**PIS**	**-**	**0.69 ± 3.49**	**0.30 ± 2.30**	**0.04 ± 0.31**	**0.08 ± 0.49**	**0.06 ± 0.42**
Total		**372.53 ± 467.69**	**1,531.67 ± 1,729.89**	**873.40 ± 1314.80**	**295.48 ± 304.34**	**226.68 ± 226.15**	**259.21 ± 267.65**

site, showing that wreck rugosity tends to grow with time. Rugosity was very similar between the two natural reefs (Table 2).

Among biotic and abiotic substrate categories, those differentiating artificial from natural reefs (SIMPER analyses, 90 % of the total dissimilarity) were “Unconsolidated substrate” (19 % contribution to total dissimilarity), “Branching coralline algae” (18 %), “Sedimentation” (13 %), “Bryozoans” (9 %), “Sponges” (9 %), “Crusting coralline algae” (8 %), “Non-coralline algae” (6 %), “*Carijoa riisei*” (5 %) and “Hydroids” (4%). As expected, due differences in depth, all algae categories were more abundant on natural reefs (Table 2). There, algae cover reached 45 % of total cover (with branching coralline algae reaching almost 24 %), while on artificial reefs only 5 % of the surface was covered by algae. “Bryozoans”, “*Carijoa riisei*” and “Hydroids” were more abundant on artificial reefs (Table 2). Although sponges can actually cause 9 % of the total dissimilarity between artificial and natural reefs, their abundance was very similar on artificial reefs (20.15 % of total cover) and on natural reefs (20.30 %). “Sedimentation” covered a greater portion of the substrate at artificial than at natural reefs (18 and 4 %, respectively). “Unconsolidated substrate” was more common at artificial reefs, reflecting their high ratio between reef perimeter and area.

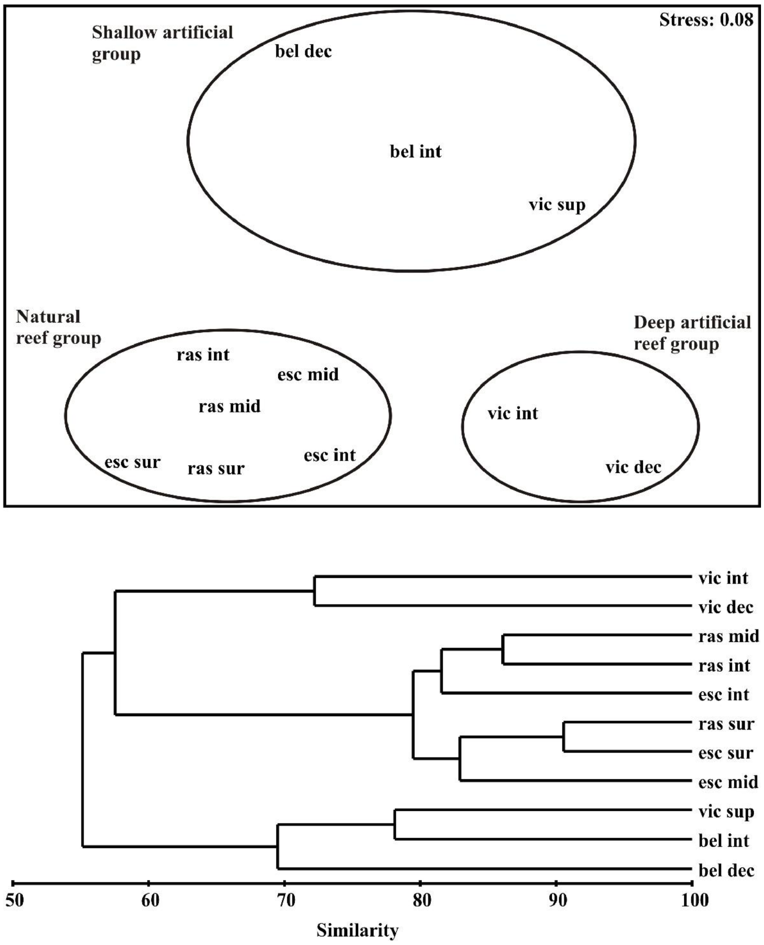

Figure 5: nMDS (top) and cluster analysis (bottom) of the trophic structure of reef fish assemblages on natural and artificial reefs, south-eastern Brazil. The plane resulting from nMDS and the dendrogram from clustering use the same legends: esc = Escalvada, ras = Rasas, vic = Victory, bel = Bellucia, int = interface, mid = middle rock shore, sur = surface, dec = deck and sup = superstructure (see text for details).

Substrate influence over the trophic structure

The two main axes in the CCA analysis explain 63.6 % of the variance in the reef fish trophic structure. With exception of CAR and OMN, all guilds appear to be related with the substrate variables (Fig. 6). PLK and MIF were positively related with “Rugosity index”, “*Carijoa riisei*”, “Hydroids”, “Bryozoans” and “Sedimentation”, which were all more conspicuous on artificial reefs. Both herbivores guilds (ROH and TEH) were positively related with the algae categories (“Branching coralline algae”, “Crusting coralline algae” and “Non-coralline algae”) and SIF were positively related with “Sponges”. PIS were negatively related with “Sponges” because of their higher abundance on the Victory, where sponges were less common.

Discussion

Differences between artificial and natural reefs

Albeit the trophic structure of the reef fish assemblages was strongly distinct between natural and artificial reefs, the greatest difference is related to a single guild, the MIF. This was the most abundant guild on artificial reefs and only the third most abundant on natural ones. Within the MIF, the tomtate *Haemulon aurolineatum* determined the distribution pattern observed. Although this was the more abundant species in both artificial and natural reefs, its biomass was forty times higher on artificial ones. As other grunts, the tomtate is a reef-associated fish that rests over hard bottoms during day-time and migrates to adjacent soft bottoms at night, where it forages over infaunal invertebrates (Ogden & Ehrlich, 1977; Sedberry, 1985; Burke, 1995; Nagelkerken et al., 2000). So, food availability can be pointed out as a key factor driving the strong tomtate biomass difference because the proportion between reef and adjacent soft bottoms (where this species mainly feeds) is much greater for artificial reefs as these are located on the fringe or in extensive sand banks and possesses much smaller area than natural reefs. Thus, considering that the maximum foraging distance from the center of the reef and that the food quantity and quality are the same for both reef types, foraging area per unit resting area is much higher for artificial structures (Fig. 7), leading to a greater carrying capacity (Monte-Luna et al., 2004). However, the distance that the fish can roam for foraging at night can actually differ between artificial and natural reefs as a function of the reef size and needs further investigations. There are strong evidences that during the study period tomtate recruited more at artificial than natural reefs (Capítulo 3). The temporal persistence of this difference in recruitment could be important to explain the major divergences between artificial and natural reefs.

Table 2: Rugosity index and benthic cover (%) of natural and artificial reefs, south-eastern Brazil. The categories causing up to 90 % of the total dissimilarity between artificial and natural reefs (rugosity not included), as detected by SIMPER analysis, are boldfaced.

	Artificial reefs (mean ± SD)			**Natural reefs (mean ± SD)**		
	Victory n = 15	**Bellucia n = 15**	**Total**	**Escalvada n = 45**	**Rasas n = 45**	**Total**
Rugosity index	1.32 ± 0.22	1.51 ± 0.22	1.41 ± 0.23	1.20 ± 0.11	1.22 ± 0.10	1.21 ± 0.11
Crusting coralline algae	**0.73 ± 1.58**	**3.75 ± 2.43**	**2.24 ± 2.53**	**9.19 ± 5.59**	**14.63 ± 14.01**	**11.91 ± 10.96**
Branching coralline algae	**0.34 ± 0.74**	**2.82 ± 2.52**	**1.58 ± 2.22**	**22.11 ± 17.42**	**25.65 ± 15.41**	**23.88 ± 16.46**
Non-coralline algae	**1.81 ± 2.63**	**1.41 ± 1.47**	**1.61 ± 2.10**	**9.96 ± 10.57**	**7.58 ± 6.32**	**8.77 ± 8.74**
Stony corals	-	1.13 ± 2.50	0.57 ± 1.83	0.63 ± 1.62	0.17 ± 0.49	0.40 ± 1.21
Firecorals	-	-	-	0.65 ± 1.96	3.97 ± 8.79	2.31 ± 6.55
Anemones	0.07 ± 0.26	-	0.03 ± 0.18	-	-	-
Gorgonians	0.33 ± 0.82	-	0.17 ± 0.59	2.67 ± 4.69	1.45 ± 2.53	2.06 ± 3.80
Carijoa riisei	**4.68 ± 5.21**	**7.79 ± 6.32**	**6.23 ± 5.91**	**0.04 ± 0.20**	**0.08 ± 0.28**	**0.06 ± 0.25**
Hydroids	**6.70 ± 4.71**	**4.63 ± 4.64**	**5.67 ± 4.71**	**1.83 ± 1.82**	**2.02 ± 2.33**	**1.92 ± 2.08**
Bryozoans	**16.37 ± 12.53**	**12.04 ± 5.89**	**14.20 ± 9.87**	**6.09 ± 7.55**	**2.95 ± 3.40**	**4.52 ± 6.03**
Zoanthids	0.07 ± 0.26	0.07 ± 0.26	0.07 ± 0.25	-	0.71 ± 3.33	0.35 ± 2.37
Sponges	**15.28 ± 10.43**	**25.02 ± 8.84**	**20.15 ± 10.71**	**19.54 ± 8.87**	**21.06 ± 9.93**	**20.30 ± 9.40**
Ascidians	5.09 ± 5.54	0.07 ± 0.27	2.58 ± 4.62	0.98 ± 1.98	0.25 ± 0.64	0.61 ± 1.51
Bivalves	-	-	-	0.02 ± 0.14	0.02 ± 0.14	0.02 ± 0.14
Barnacles	0.07 ± 0.27	0.07 ± 0.26	0.07 ± 0.26	0.05 ± 0.23	-	0.02 ± 0.16
Crinoids	0.88 ± 1.51	-	0.44 ± 1.14	0.13 ± 0.64	0.23 ± 0.93	0.18 ± 0.80
Sedimentation	**20.69 ± 23.15**	**15.76 ± 11.49**	**18.23 ± 18.13**	**5.39 ± 7.47**	**2.21 ± 4.72**	**3.80 ± 6.42**
Unconsolidated substrate	**25.29 ± 30.62**	**25.24 ± 18.86**	**25.26 ± 24.99**	**18.85 ± 20.84**	**15.19 ± 15.48**	**17.02 ± 18.35**
Pavement	1.33 ± 4.89	-	0.67 ± 3.47	0.02 ± 0.15	0.29 ± 1.24	0.16 ± 0.89

A number of depth-related differences between artificial and natural reefs were expected because the formers are, overall, deeper than the latter. The guilds most affected would be essentially herbivorous as algae cover and productivity tend to diminish as depth augments and light availability declines. Correspondingly, total algae cover and ROV and TEH abundances were much higher on natural than on artificial reefs. Light availability to photosynthetic organisms also varies inversely to the concentration (or deposition) of suspended sediment. Resuspension was not measured but a muddy layer was encountered covering a large portion of the horizontal surfaces of artificial reefs. This layer is probably alimented by material normally deposited onto the plane surface of the surrounding sandbanks from where it would be easily, if intermittently, re-suspended by waves and current. Beyond the increase in water turbidity during resuspensive events (pers. obs.), the deposited layers would induce smothering effects on benthos (Rogers, 1990).

The SIF are adapted to consume low-caloric food sources, mainly benthic invertebrates associated to hard substrates (sponges, cnidarians and ascidians) (Harmelin-Vivien, 2002; Ferreira et al., 2004; Floeter et al., 2004). This guild was not significantly different between artificial and natural reefs. The main differences (dissimilarity) between artificial and natural reefs were caused by bryozoans, *Carijoa riisei* and hydroids, more abundant on artificial reefs, and sponges. These were the most abundant invertebrate in both artificial and natural reefs, where they had very similar abundance (although actually being responsible for some dissimilarity). *Holacanthus ciliaris* and *H. tricolor were* the two most abundant SIF species (representing more than 80 % of the guild biomass), and have a diet based almost entirely on sponges (Randall, 1967). So, the SIF similarity between artificial and natural reefs is related to sponge abundance. The octocoral *Carijoa riisei*, the invertebrate with the greatest difference between artificial and natural reefs, is not known to be predated by fishes (Souza et al., 2007; Wagner et al., 2007).

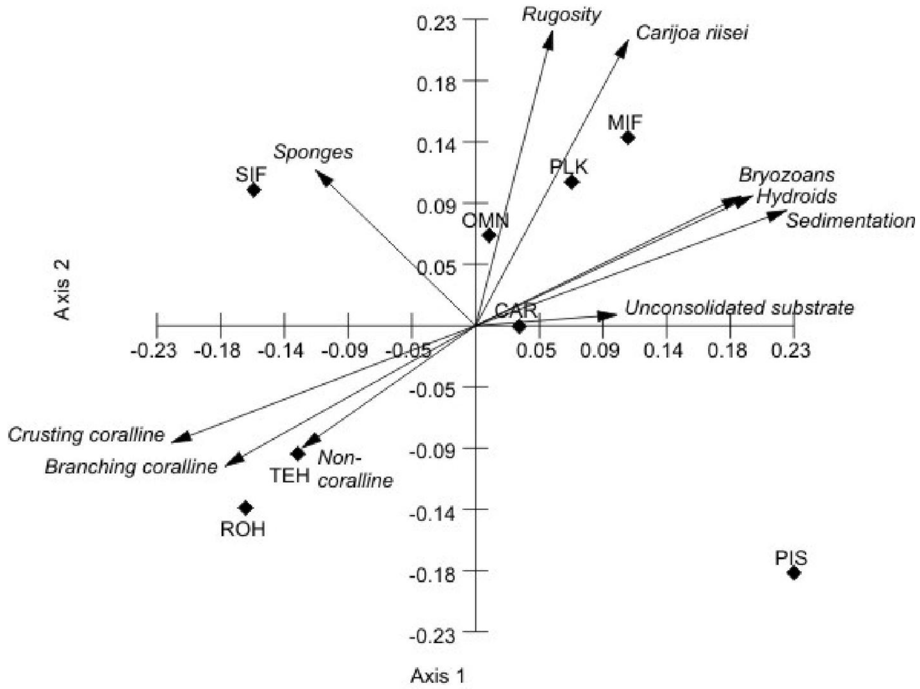

Figure 6: Canonical correspondence analysis (CCA) between the trophic structure of reef fish assemblages and substrate variables (rugosity and benthic cover) on natural and artificial reefs, south-eastern Brazil. The word "algae" was suppressed from the three algal categories labels (crusting, branching and non-coralline).

The OMN have a plastic diet, feeding on a mix of low-nutritional resources (plant material) associated with highly digestible animal protein (Ferreira et al., 2004; Floeter et al., 2004). Although this guild showed much higher biomass on artificial than on natural reefs, the enormous biomass of MIF on wrecks lowered their contribution to the total biomass to below that on natural reefs. The difference between artificial and natural reefs was caused by a single species, *Chaetodipterus faber*, which was observed a few times on the Bellucia swimming in large schools (discussed in the next section). The species *Abudefduf saxatilis*, *Diplodus argenteus*, *Cantherhines pullus* and *Pomacanthus paru* were more abundant on natural reefs, what suggest a preference by algae items in their diet or some other specific need determinant to feeding or reproductive success as shallow depths or adequate substrate for nests (e.g., *A. saxatilis)*. Beside *C. faber*, only *Pomacanthus arcuatus* was more abundant on artificial reefs. *Pomacanthus paru* and *P. arcuatus* have a similar diet, ingesting mainly sponges and algae, and a similar feeding apparatus (Randall, 1967; Hourigan et al., 1989). As one was more abundant on natural reefs and the other on artificial ones, competitive exclusion cannot be excluded. However, Hourigan et al. (1989) found that these species defends intraspecific pair-territories but not interspecific ones, suggesting that food resources are not limiting in this case.

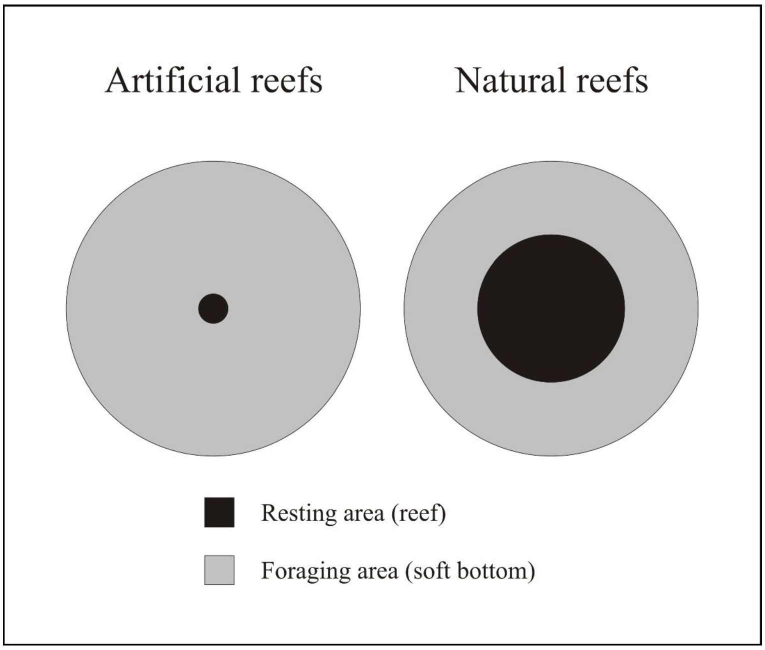

Figure 7: Theoretical model proposed to explain the high biomass of tomtate *Haemulon aurolineatum* at artificial reefs. As the proportion between foraging and resting area are much greater (not to scale in this figure) for artificial reefs and assuming that the foraging area is the limiting factor, the carrying capacity of the artificial reefs are much greater.

The planktivores are a trophic guild influenced by water motion (Clarke et al., 2009) and currents (Thresher, 1983; Clarke et al., 2009), which determine the food availability and feeding performance, and partially influenced by light (Lazzaro, 1987), as many species are selective visual predators. This guild was more abundant on artificial reefs, where the upper water column is free of obstacle as the shipwrecks reach up to 18 or 20 m below the surface. Thus, in the column upper section the currents can flow without interferences, reaching greater speeds. On the contrary, natural reefs have a greater size and, since they are islands, have a significant portion reaching to (and above) the surface, creating an important resistance to the water movements (M. Toffoli, unpubl. thesis). Moreover, water transparency could be higher above artificial reefs as they are at greater depth and because resuspension material stays concentred in the lower water column, which can improve the feeding performance of planktivores.

Carnivores feed on high caloric prey items, both invertebrates and fishes (Ferreira et al., 2004). This guild was slightly more abundant on natural reefs, but this was determined mainly by the sole occurrence of a big roughtail stingray *Dasyatis centroura* and a school of ladyfish *Elops saurus*. Snappers (*Lutjanus analis*, *L. jocu* and *L. synagris*) and the reef croaker *Odontoscion dentex* were particularly abundant on artificial reefs. The higher snapper biomass and higher frequency of occurrence at artificial reefs may result from attraction from natural reefs (Capítulo 3) and the combination of large structures over sandy to muddy (inside the -broken- cargo hold), open and deep grounds. In contrast, reef croaker presence would depend upon structural complexity as the species lives in close association with holes and crevices (discussed in the next section). Interestingly, it was not recorded on the Victory, possibly due to the lack of infractuosity of adequate size or orientation.

Piscivores, together with OMN, were the unique guilds that differed in all comparisons (artificial *vs.* natural, artificial *vs.* artificial and natural *vs.* natural). The groupers (*Mycteroperca acutirostris*, *M. bonaci* and *M. interstitialis*) and the bluestriped lizardfish *Synodus synodus* were the species that have caused PIS to be more abundant on artificial reefs. Like snappers, groupers could actually be attracted from natural reefs (Capítulo 3). Potential preys, such as tomtate, are highly abundant and ample refuges are available and, as predicted by optimal foraging theory (Pyke et al., 1977), these factors are probably determinant in defining their spatial distribution. The most abundant PIS species, *Caranx crysos*, was slightly more abundant on natural reefs, but strong differences between artificial and between natural reefs were detected (discussed in the next section). Despite their higher abundance on artificial reefs, PIS proportionally contributed more to the total biomass of natural reefs. Even so, if large carnivores and piscivores are dislocated from natural to artificial reefs (due to attraction), strong modifications in the structure of the assemblages may be occurring as these key-species are known to control the biomass of lower trophic levels (Steneck & Sala, 2005).

Differences between artificial and between natural reefs

MIF biomass, albeit similar between natural reefs, varied significantly between artificial reefs due to tomtate being more than three times more abundant on the Bellucia than on the Victory. A number of factors can be either tentatively excluded or pointed out as to causing this difference. The proportion between reefal area and adjacent sand bottom can be excluded because there is no strong contrast between reefs (at least compared to the difference in area between artificial and natural reefs). Top-down effects driven by PIS-removing tomtate biomass by predation are, possibly, higher on the Victory, as PIS were more abundant on Victory. On the other hand, tomtate, although mainly foraging on unconsolidated substrate adjacent to reefs in night-time, can also take advantage of planktonic food resources (Randall, 1967; Sedberry, 1985) during day-time (Arena et al., 2007). This is a plausible explanation if taking the higher abundance of PLK on the Bellucia as a suggestion that plankton is more readily available or plentiful there and taking into account that on the Victory, tomtate abundance was much higher on the top (superstructure) than near the bottom (deck and interface). At highest locales on the Victory, abundance reached a value similar to that observed on the Bellucia, suggesting that these fishes aggregate were plankton is more abundant due to current and wave surge (Thresher, 1983; Clarke et al., 2009).

Artificial reefs differed in respect to depth and herbivorous guilds were expected to differ accordingly. While ROV were significantly more abundant on the Bellucia, TEH were not (but *S. pictus* abundance was much higher on the Bellucia). This reflects food constraints because the total algae cover was higher on the Bellucia. However, the blue tang *Acanthurus coeruleus*, was most abundant on the Victory than at any other site while absent from the Bellucia. Total algae cover was higher on the Bellucia but non-coralline algae were more abundant on the Victory. Since the blue tang does not consume detritus together with algae (Dias et al., 2001; Ferreira & Gonçalves, 2006), it can use the fleshy algae available on the lateral walls of the Victory. Besides receiving less siltation than horizontal surfaces, the Victory's vertical walls are vastly larger than equivalent surfaces at the Bellucia. Space use segregation between the three Western South Atlantic surgeonfishes has been evidenced by Dias (2001), in which the blue tang forages on the upper portions of the lateral walls of reefs.

Although similar between natural reefs, SIF biomass varied significantly between artificial reefs with, mainly, higher *H. tricolor* biomass on the Bellucia. Such pattern appears directly related to sponge availability. Natural reefs, for their part, appear to support similar SIF abundances that feed on equivalent sponge covers.

The distributional pattern of omnivore species follows those of sponge, PLK or algae. The most abundant OMN species was the spadefish *C. faber*, which was only recorded on the Bellucia swimming in large schools in the water column. Its diet is based mainly on sponges, reaching more than 30 % of the total ingested, but planktonic food also is important (Randall, 1967). Concomitantly, both sponges and plankton-feeders (a probable indicator of plankton availability) were more abundant on the Bellucia than at any other site. The OMN species more abundant on natural reefs, *A. saxatilis*, *C. pullus*, *D. argenteus* and *P. paru*, were also more abundant on the Bellucia than on the Victory. This pattern coincides with that of total algae abundance and reinforces the hypothesis that algae availability determines the abundance of these species. Between natural reefs, the largest differences are related to *A. saxatilis* and *D. argenteus*, both more abundant at Escalvada than at Rasas. Available data do no allow the establishment of a specific hypothesis as of the reason for this pattern. However, one interestingly behaviour was recurrently observed: while males *A. saxatilis* energetically defend their nests against intruders, small groups of *D. argenteus* follow divers to opportunistically attack nests and feed on eggs when the *A. saxatilis*, intimidated by the close proximity of the diver, momentarily neglects to protect the nest.

The Bellucia is placed on the edge of a rock outcrop that reaches 3 m below the surface. The water above is free to flow, but under rough sea conditions a strong turbulence and surge may develop in the immediate vicinity of the rock (reaching the wreck) as the obstacle obstructs the laminar current flow and modifies the height, length and inclination of waves. In the other hand, the Victory is placed in an even, soft and deep bottom and its presence cannot be detected from the surface (but strong vertical surge may develop; pers. obs.). These characteristics, however, do not appear sufficient to explain the higher PLK biomass on the Bellucia. These are mostly caused by *Clepticus brasiliensis* and *Myripristis jacobus*, species that use the numerous crevices of the Bellucia as either, spawning substrate and diurnal refuge.

The main difference in CAR between artificial reefs is caused by *O. dentex*, a nocturnal fish that during day-time was encountered in high abundance association with caves and crevices on the Bellucia. Interestingly, it was not recorded on the Victory, possibly due to the lack of infractuosity of adequate size or orientation. The dog snapper *L. jocu*, observed only on the Bellucia, is another abundant carnivore seen using crevices as a refuge during day-time. These species and *C. fulva*, *G. moringa*, *O. vespertilio* and *S. plumieri* apparently benefited from the structural complexity of the Bellucia, probably because it enhances their feeding performance.

Piscivores were more abundant on the Victory than on the Bellucia and at Escalvada than at Rasas. Differences were driven by *C. crysos* and, in the case of artificial reefs, the groupers. On artificial reefs, *C. crysos* was only observed on the Victory and on natural ones it was present in higher abundance at Escalvada. At the moment this pattern cannot be explained and may actually have occurred by chance since this is a highly mobile pelagic species that may very well travel between sites. The groupers were more abundant on Victory than in any other site. Considering that tomtate, due to its high availability, probably is their main food source, its abundance cannot be the limiting factor on the Bellucia. As the Victory structure is well preserved at the moment, the large, empty and protected spaces presented by cargo holds (surrounded by large, overhanging or hollow structures) can be attractive to small (this study) and large groupers (Capítulo 5), that can use these ample refuges as a resting place.

Evolution of assemblage structure over artificial reefs

Due to the age effect on structure stabilization (such as promoted by metal corrosion and crumbling) and colonization (either by benthos or fish), it was expected that the trophic structure of the older artificial reef (Bellucia) would have been more similar to that of natural reefs than to that of the younger artificial reef (Victory). Contrary to this, the century-old shipwreck Bellucia was more similar to the shallower portions (superstructure) of the more recent purposely sunk Victory than to, for example, nearby natural reef of Rasas Islands. This pattern was strongly influenced by tomtate abundance, which was spectacularly high on shallow artificial reef subsectors. Adult tomtate do not appear to have a strong affinity with reef substrate *per se* (they use the reef only as a diurnal refuge, staying in schools in the water column), it is probable that their distribution is more determined by factors such as predation avoidance or plankton abundance (discussed earlier) than by substrate characteristics.

The relationships between habitat complexity and fish assemblages has been widely debated in the literature (Risk, 1972; Roberts & Ormond, 1987; Grigg, 1994; Beukers & Jones, 1997; Chabanet et al., 1997; Nemeth, 1998; Öhman & Rajasuriya, 1998; Ferreira et al., 2001; Almany, 2004). The dimensions of the habitat complexity that are known to determine abundance and richness of fishes are the availability of shelter from predators (Beukers & Jones, 1997), nesting sites (Gratwicke & Speight, 2005) and food supply (Nakamura & Sano, 2005), which all tend to be greater at more complex sites as the large quantity and diversity of microhabitats provide more ecological niches. However this was not verified in our reef sites and fish richness was higher on natural reefs although rugosity was lower. The century-old Bellucia surprisingly showed richness much similar to that of the five-year-old Victory. Species accumulation curves of these artificial reefs are overlaid (Fig. 8), much as are overlaid at a much higher level those of Escalvada and Rasas, showing that not even after 100 years a shipwreck can support fish richness similar to that of nearby natural reefs.

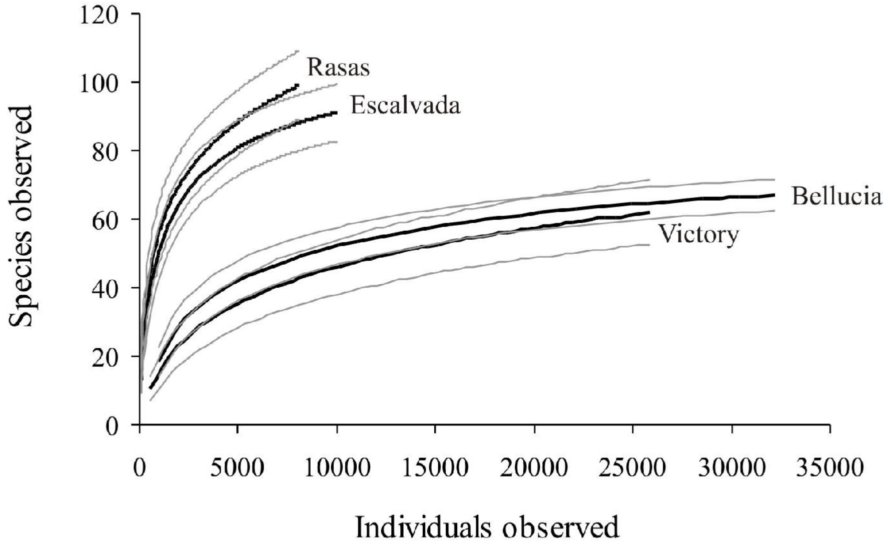

Figure 8: Expected species accumulation curves with 95 % confidence intervals (Colwell et al., 2004) computed using EstimateS (Colwell, 2009). In this plot, the species richness does not differ significantly when the intervals of two or more independent curves are overlaid.

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CAPÍTULO 3

Target fishes in artificial and nearby natural reefs: structural differences among taxa evidence the complexity of the attraction-production issue

Thiony Simon, Hudson Tercio Pinheiro and Jean-Christophe Joyeux

Abstract

Fish community structures on artificial and natural reefs off Guarapari, south-eastern Brazil, were assessed in order to evaluate the potentials of production and attraction that artificial reefs exert over species targeted by local fisheries. Two artificial structures, the shipwrecks Bellucia (an iron freighter sunk in 1903) and Victory 8B (a derelict freighter intentionally sunk in 2003), and two natural reefs, Rasas and Escalvada islands, were included in this study. Two hundred and thirty-nine underwater visual censuses (20 x 2 m belt-transects sample unit) were realized in natural and 81 censuses in artificial reefs between January and April 2008. Four genera (*Caranx*, *Haemulon*, *Lutjanus* and *Mycteroperca*) were focused upon due to their importance to local fisheries. Length frequency, mean biomass and frequency of occurrence were compared between artificial and natural reefs. Production is evidenced by the enormous abundance and presence of recruits of a single grunt species, the tomtate (*Haemulon aurolineatum*), while evidences for attraction are high concentrations of adult top predator demersal fishes (*Mycteroperca* spp. and *Lutjanus* spp.). Results are inconclusive for the pelagic predators *Caranx* spp. These intentional and accidental artificial reefs can actually be causing negative impacts (shifts in predation, competition or nutrient input) on nearby areas, either soft bottoms or natural reefs. Despite being unplanned for fisheries purposes, the artificial reefs are submitted to commercial and recreational fisheries and, due to the strong attraction they exert over large predators, these structures need harvest regulations. Otherwise, lack of management, policy and law enforcement transform artificial reefs in open grounds to fishermen and consequently act as a trap for large and threatened fish species.

Keywords

Conservation • Shipwreck • Impact • Reef fish • Threatened fish • Management

Introduction

Topics in artificial reef research have included a wide number of themes, such as general reviews and theory, fisheries ecology and management, general ecology, design and monitoring, habitat protection and mitigation, sport diving, mariculture, waste disposal and coastal protection and development (Baine, 2001). Although the initial increase in total fish production due to the establishment of an artificial reef has been frequently explained by the rapid colonization and high fish density at these structures (Bohnsack, 1989), many questions involving the attraction-production issue remain in debate (Stone et al., 1979; Lindberg, 1997; Powers et al., 2003). Nowadays, when most of reef fish stocks are overexploited and hence below the carrying capacity of natural habitats, total fish production is probably not limited by habitat availability (Lindberg, 1997). Thus, without well-devised management practices, artificial reefs, and in especial those from poorly planned programs, are most likely to be fishing artefacts than gears for preservation, management or tourism capable of increasing total biomass of exploited or overfished species.

Independently if artificial reefs attract or produce fishes, they impact their surrounding natural environments as they modify a pre-existent ecosystem. Impacts can affect adjacent natural reefs, soft-bottoms and pelagic ecosystems under the form of physical (hydrodynamic and depositional patterns), chemical (dissolution of harmful compounds) or ecological modifications (predation and competition). For example, benthic communities in sediments adjacent to artificial reefs can be affected by a reduction in sediment oxygenation as a function of the accumulation of detritus and their decomposition at reef edge (Wilding, 2006), by modification in grain size (Davis et al., 1982; Ambrose & Anderson, 1990) and by forage by reef-associated organisms (Davis et al., 1982). As the real benefits of artificial reefs are questionable while their impacts are not, these structures should be used with caution and with an extensive pre- and post-implantation monitoring.

The use of artificial reefs, for diverse purposes, has been increasing along the Brazilian coast in the last years, followed by an increase in artificial reef research (Brotto & Araujo, 2001; Godoy & Coutinho, 2002; Godoy et al., 2002; Zalmon et al., 2002; Cunningham & Saul, 2004; Jardeweski & Almeida, 2005; Brotto et al., 2006; Conceição & Pereira, 2006; Krohling et al., 2006; Brotto et al., 2007; Brotto & Zalmon, 2008; Krohling & Zalmon, 2008). However, the impacts that these structures can be causing on nearby natural environments have not been assessed yet. The present work aims at evaluating if target fishes (those of local fisheries importance) on artificial reefs in south-eastern Brazil are produced there or attracted from natural reefs. Additionally, some impacts are discussed and attention is called towards the risks presented by poorly planned artificial reefs.

Material and methods

Study area

This work was carried out at two artificial reefs (Bellucia and Victory 8B shipwrecks) and two natural rocky reefs (Rasas and Escalvada islands), located 10 km off Guarapari, south-eastern Brazil (see the Fig. 1. of the "Capítulo 1"). The Bellucia sunk in 1903 after colliding with a submerged rock adjacent to the Rasas Islands. Also metallic, the Victory 8B vessel was intentionally deployed as artificial reef in 2003 in a deep sandy area. The local environmental agency was responsible for the initiative, but the project can be considered to have failed in respect to several key procedures: a) structure preparation (although thoroughly cleaned of machinery, furniture, oil, wiring, etc., anticorrosive and antifouling paints were left on place, difficulting definitive incrustation); b) ecologically-appropriate site selection (near natural reefs); and c) environmental monitoring (absence of pre-monitoring; post-monitoring started two years after implantation; fish recruitment and attraction have not evaluated by monitoring). The Bellucia is about 300 m from Rasas while the Victory 8B is relatively isolated from natural emersed reefs (about 2 km from Escalvada and 3 km from Rasas), although a number of uncharted, low-relief deep reefs are much closer (500-1000 m). Maximum depths (interface structure-unconsolidated substratum) are 35 m for Victory 8B, 27 m for Bellucia and 25 m for both islands. The Victory 8B is 17 m tall (i.e. rises up to 18 m of the surface) while the Bellucia's tallest remains stand about 5 m above the unconsolidated substrate (shallower parts are 20 m below the surface).

Data acquisition and analysis

Reef fish communities of artificial and natural reefs were assessed by two observers (TS and HTP) through replicated underwater visual census (UVC; 20 x 2 m belt-transects sample unit) from January to April 2008. In the artificial reefs the censuses were performed in all horizontal surfaces (from bow to stern), including the interface between reef and unconsolidated substrate, and in the natural ones those were distributed around the islands and among the vertical gradient (from near surface to the interface). Two hundred and thirty-nine censuses were realized in natural reefs and 81 censuses in artificial ones. The difference in sample size reflects the strong difference in area size between natural and artificial reefs. Fish were counted by species and length classes (0-5, 6-10, 11-20, 21-30 cm TL, and so on). Size of large schools (more than 20 individuals) was estimated in abundance classes (30, 50, 100, 200, 500, 1000 and 2000 individuals). Each census was performed in two steps: on the way out (unrolling the 20 m tape), the diver counts the larger and more mobile species and on the way back (rolling the tape) the smaller and more cryptic species. Abundance data (ind. m^{-2}) were transformed to biomass data (g m^{-2}) using length-weight relationship equations (Froese & Pauly, 2008) on the centre of each length class prior to descriptive and statistical analysis. See “Capítulo 2” for more detailed descriptions of the study sites and sample design.

Four target fish genera were focused upon due to their importance to local fisheries to test if they are been produced in the artificial reefs or attracted from nearby natural reefs. Jacks (*Caranx* spp.) are mainly fished by trolling in the upper water column by small boats, highly valued snappers (*Lutjanus* spp.) and groupers (*Mycteroperca* spp.) are fished by hook-and-line and spear while grunts (*Haemulon* spp.), mainly *H. aurolineatum*, are intensively fished with traps and hook-and-line to be used as live bait in tuna fisheries. *Caranx ruber, C. hippos, C. latus* and *L. alexandrei* were only recorded on natural reefs, *L. analis, L. jocu, L. synagris* and *M. interstitialis* were only recorded at artificial reefs and *C. crysos, M. acutirostris, M. bonaci, H. aurolineatum, H. parra, H. plumieri* and *H. steindachneri* were found over both types of substrate. The length frequencies of the four genera were compared between artificial and natural reefs to evaluate the presence of recruits and small individuals. Additionally, mean biomass and frequency of occurrence were used as indicators of attraction or production. Mann–Whitney U tests were used to determine whether significant differences in mean biomass existed between artificial and natural reefs. Differences in length frequency and frequency of occurrence were tested through chi-square test, the latter using the Harber correction (Zar, 1999); low-frequency classes (≤ 3 ind.) were added to an adjacent one.

Results

Length frequencies of the target reef fish genera (Fig. 1) were only significantly different between artificial and natural reefs for *Haemulon* spp. (χ^2; $p < 0{,}001$). Only for *Haemulon* spp. were detected recruits (TL <5 cm) and small juveniles (6-10 cm TL), on both artificial and natural reefs (Table 1; Fig. 1). On artificial reefs, recruits were of *H. aurolineatum* and *H. steindachneri* and small juveniles were of *H. aurolineatum* and *H. plumieri*, while on natural reefs recruits were of *H. plumieri* and small juveniles were of *H. aurolineatum* and *H. plumieri*. The tomtate *Haemulon* *aurolineatum* showed the greater number of recruits and small juveniles, but the formers were only present on artificial reefs (Table 1). Also, although tomtate was the most abundant species at both artificial and natural reefs, its biomass was more than 40 times higher on artificial structures. There, the species formed schools of tens of thousands and reached a mean biomass of 576 g m^{-2} (Fig. 2).

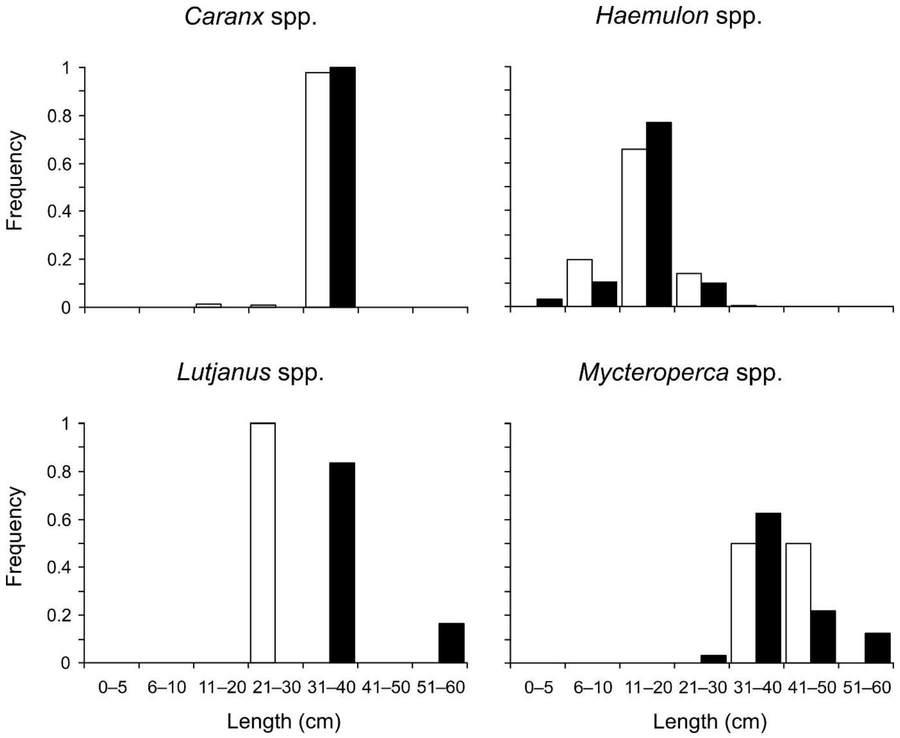

Figure 1: Length frequency (in number) of selected fish genera on natural (open bars) and artificial (filled bars) reefs off Guarapari, Brazil.

The biomass of grunts, snappers and groupers (U test; all $p < 0.001$) were higher on artificial reefs (Fig. 2). Contrarily to other predators, jacks showed higher biomass on natural reefs (U test; $p = 0.003$), but the difference was small in absolute (Fig. 2). Curiously, jacks were not registered in the Bellucia censuses and their Victory 8B biomass (26.1 g m^{-2}) was higher than on natural reefs (16.6 g m^{-2}). Frequency of occurrence of grunts, snappers and groupers (χ^2; all with $p < 0{,}001$) were higher on artificial than on natural reefs. In the other hand, jacks, despite a higher biomass on natural reefs, were more frequent on artificial ones (χ^2; $p < 0{,}001$) (Fig. 2).

The grunts were dominated by *H. aurolineatum* on artificial structures (97 % of genus biomass) and by *H. aurolineatum* (52 %) and *H. plumieri* (35 %) in natural reefs. *Caranx crysos* dominated the jacks biomass on both artificial (100 %) and natural (99 %) reefs. *Mycteroperca acutirostris* (46 %)

and *M. interstitialis* (41 %) were the groupers of higher biomass on artificial reefs while *M. bonaci* (81 %) dominated in natural reefs. Within the snappers, *L. alexandrei* was the only species observed on natural reefs and was only observed there. On artificial reefs, *L. analis* and *L. jocu* showed the largest biomass (48 % for each species) (Fig. 2).

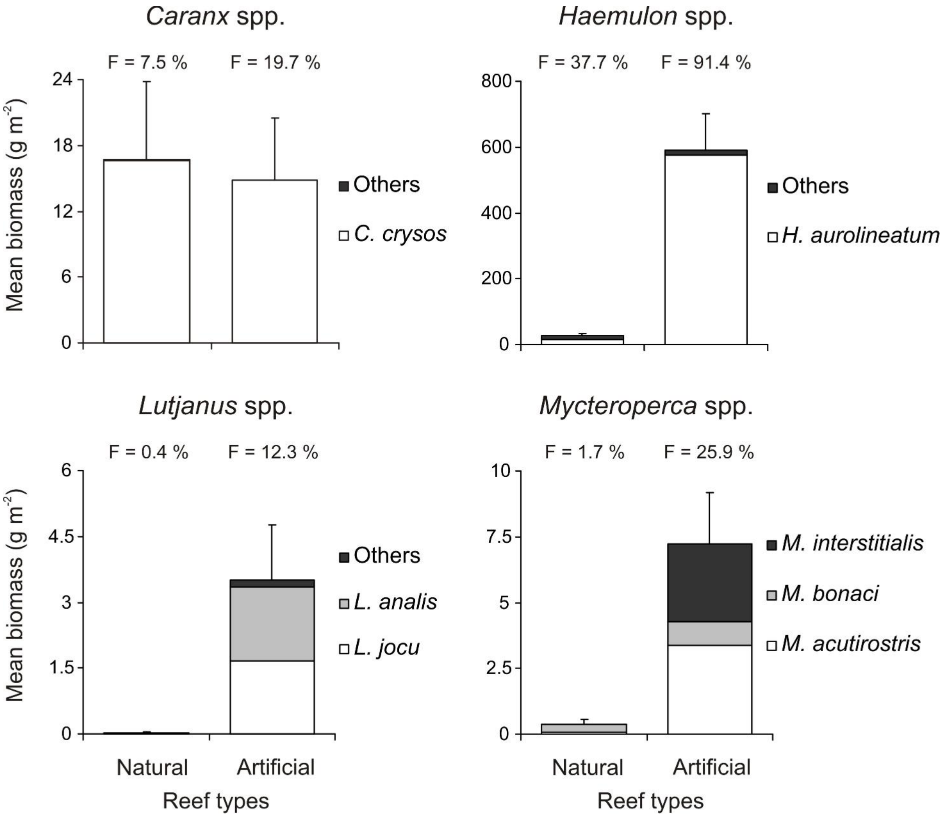

Figure 2: Mean biomass (+ SE) of selected fish genera on natural and artificial reefs off Guarapari, Brazil. The frequency of occurrence (F) on censuses is indicated above the respective bar.

Discussion

Production evidences and their impacts

The ample size range detected for grunts indicated that these species recruit, grow and probably live their all life cycle on artificial and natural reefs. The tomtate, the species with the largest biomass on both artificial and natural reefs (Capítulo 2), was commonly observed as recruit on artificial reefs during the sample period (austral summer). Similar pattern was observed by Jordan et al. (2004), which encountered peaks of recruitment of *Haemulon* spp. in the early summer (boreal hemisphere), mainly on artificial reefs. These are strong evidences that artificial reefs are suitable habitats for grunts, from recruit to adult individuals. In other genera, the absence of recruits is probably due to seasonality or particular requirements to recruitment (nursery areas) not found at sampled sites. For example, Beets and Hixon (1994) encountered both adults and a large pulse of recruits of Nassau grouper (*Epinephelus striatus*) in shallow-water artificial reefs, thus giving evidence that such structures can support groupers at all life stages.

Table 1: Length frequency (number of individuals counted) of all species of the selected fish genera on natural and artificial reefs off Guarapari, Brazil.

	Artificial reefs (total censuses = 81)							**Natural reefs (total censuses = 239)**						
Length class (cm)	**0–5**	**6–10**	**11–20**	**21–30**	**31–40**	**41–50**	**51–60**	**0–5**	**6–10**	**11–20**	**21–30**	**31–40**	**41–50**	**51–60**
Haemulon aurolineatum	1770	5548	41973	5280					1000	3242	332			
Haemulon parra				6	3						1			
Haemulon plumieri		1	23	51	15			2	1	51	272	30		
Haemulon steindachneri	50		1	64	2					15	104			
Caranx crysos					96						3	317		
Caranx hippos												1		
Caranx latus												1		
Caranx ruber										4				
Lutjanus alexandrei											1			
Lutjanus analis					1		2							
Lutjanus jocu					8									
Lutjanus synagris					1									
Mycteroperca acutirostris					7	3	1					1		
Mycteroperca bonaci					3	1						1	2	
Mycteroperca interstitialis				1	10	3	3							

The most important factors responsible for maintaining elevated tomtate recruits density at the studied artificial reefs are high settlement and survival of early juveniles. Vertical reef relief has long been pointed out as a determinant factor for the large differences detected in abundance of fish recruits between artificial and natural reefs because vertical structures can be more attractive to fish settlement and recruitment than moderately sloped bottoms (Rilov & Benayahu, 2000). In an artificial reef experiment, the recruitment of fishes has been shown to be higher in the upper portions of vertical artificial structures than in horizontal ones, probably as a function of the larval distribution in the water column when they approach the shore (Rilov & Benayahu, 2002). Our sites present very distinct vertical reliefs. Depth at natural reefs range 0-25 m over, generally, a gentle to moderately strong slope. On the contrary, artificial reefs range 20-27 m (Bellucia) or 18-35 m (Victory 8B) and are abruptly vertical for 2-5 m (Bellucia) or 5-17 m (Victory 8B). In a study aiming at comparing *Haemulon* spp. recruitment, Jordan et al. (2004) found that in natural reefs these recruits and juveniles were more abundant in shallower areas while the contrary was observed on artificial reefs. Although no final conclusion for this pattern could be achieved, nearshore natural environments are probably not, as previously proposed, obligatory nursery areas. Supposedly, deep artificial reefs offer conditions not encountered in deep natural reefs involving post-settlement ecological process such as predation, competition and food quality and quantity. In the present study, the differences in depth range and slope between artificial and natural reefs can actually cause the differences in tomtate recruitment patterns, but this hypothesis need of a temporal assessment. The high survival of early juveniles can be guaranteed by the availability of refuge from predators (Sherman et al., 2002). However, a meta-analysis by Jordan et al. (2004) evidenced that recruits of *Haemulon* spp. presented, in Florida, higher density at shallow and less complex natural reefs than at deeper and more complex ones, showing that refuges are not the unique determinant to survival. As the studied artificial reefs have higher rugosity than the natural reefs (Capítulo 2), the artificial structures can offer refuges in larger quantity, increasing the survival of the juveniles that recruit there.

Man-made structures are known to strongly modify nearby infaunal communities due to habitat modification (as in sediment grain size) and foraging by reef-associated predators (Davis et al., 1982; Ambrose & Anderson, 1990). The tomtate, as other grunts (Ogden & Ehrlich, 1977; Burke, 1995; Nagelkerken et al., 2000), is a reef-associated fish that rests over hard bottoms during day-time and migrates to adjacent soft bottoms at night where it forages over infaunal invertebrates. Thus, the enormous tomtate density at artificial reefs represents an important impact for the benthic communities of adjacent unconsolidated substrate not experimented before structure implantation.

Attraction evidences and their impacts

The great abundance and frequency of small grunts (mainly the tomtate) on artificial reefs, in some cases associated with the availability of ample re-entrances to be used as refuge, are potential attraction factors to large predators such as jacks, snappers or groupers (Bohnsack & Sutherland, 1985). In fact, the near absence of snappers and groupers on natural reefs is a good indication that high occurrence and biomass on artificial reefs result from attraction. Also, the possibility that they are being more intensively removed from natural than artificial reefs by spearfishing is not remote. However, if artificial reefs are deeper and are less accessible to apneists, both reef types are within reach of SCUBA and surface-supplied air diving, the latter being much (and illegally) used by professional fishermen for lobster, octopus and reef fishes. On the other hand, the concentration of adult groupers and snappers on artificial reefs and the arrival of two Goliath groupers *Epinephelus itajara* (total length estimated in 100 and 170 cm) on the Victory 8B soon after the sampling period (pers. obs.) evidence the attraction potential of artificial structures to large predators. Actually, since the deployment of the Victory 8B, various groupers of large size (*Epinephelus nigritus* and *E. itajara*) have been related by divers over the years, to disappear some time later due to capture or natural relocation. The apparent absence on the Bellucia of *Caranx* spp., a highly-mobile, upper-water-column genus, may have resulted from behavioural preference (due to closeness from Rasas) or census limitations as UVC is not always very efficient to register such type of fishes. On the Victory 8B, *C. crysos* is commonly seen attacking schools of tomtate (pers. obs.), showing that they also can be attracted there due to food availability. Additionally, *Caranx latus*, not registered in the Victory 8B censuses, was observed after the sample period trying to predate *Decapterus macarellus* schools (Capítulo 5).

Food availability, one of the main constraints to optimal foraging of predators (Pyke et al., 1977), is not a limiting factor on artificial reefs, at least for some species. Thus, high prey concentration in a restricted area would attract snappers and groupers from natural reefs (as discussed above) because these predators encounter food on artificial reefs at lower energy costs of search. The present study does not aspire at resolving the complex problem of the attraction-production issue (see Lindberg, 1997). However, if artificial reefs are collaborating to the remotion of large predator fishes from natural reefs, they would alter important ecological process, such as predation and competition, and alter diversity and abundance of prey species (cascading effects) by either permitting prey survival in areas they abandoned or increasing prey extraction near newly settled areas. Loss of functional roles can lead to decreased ecological stability and ecosystems can become both less resilient to natural disturbances and less resistant to invasion by exotic species (Stallings, 2009).

Despite strong evidences for grunt production on artificial reefs, attraction of individuals that, eventually, encounter them during foraging migrations is possible. This would cause a diminution of the flow of nutrients and organic matter from adjacent to natural reefal areas because grunt feed on unconsolidated environments during night-time and defecate on the reef while resting during day-time (Meyer & Schultz, 1985).

Necessity of management policies

The attraction-production dilemma has been extensively debated for a long time (Bohnsack, 1989; Grossman et al., 1997; Pickering & Whitmarsh, 1997; Wilson et al., 2001; Osenberg et al., 2002; Powers et al., 2003; Brickhill et al., 2005). Many of these studies consider this issue as a dichotomic problem albeit production and attraction probably only are the extremes of a gradient (Bohnsack, 1989). Thus, off Guarapari as elsewhere, artificial reefs will at the same time favorize an increase in biomass for some fishes (such as grunts) and attract others (such as snappers and groupers) from nearby areas. This is not to say that grunts are not attracted from natural reefs or snappers and groupers produced on artificial structures (such features are not detectable from our data).

Albeit the artificial reefs studied were not effectively planned for fisheries purposes, they undoubtedly offer suitable habitats to a number of target fishes. In such habitats, these fishes can find food in abundance and this would, hypothetically, benefit reproductive output and spillover of eggs and larvae. The Victory 8B, besides being used for spearfishing, is also subjected to trolling and to heavy professional tomtate captures. Thus, even when unplanned for fisheries, artificial structures strongly need protection or regulation to limit undesirable impacts to reefal and infaunal adjacent communities. In fact, lack of management, policy use and law enforcement can transform such behaviourally-attractive structures into traps, increasing the threat to already overfished stocks.

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CAPÍTULO 4

Length-weight relationships for some cryptobenthic reef fishes off Guarapari, southeastern Brazil[*]

Victor Camilato, Thiony Simon, Hudson T. Pinheiro, Caio R. Pimentel and Jean-Christophe Joyeux

Summary

The present work provides length-weight relationships for eight species of cryptobenthic reef fishes captured at natural and artificial environments on the southeastern Brazilian coast.

Introduction

Length-weight relationships (LWR) are fundamental to estimate the biomass of fishes in researches that utilize non-destructive methods, many applied in reef ecosystems. However, few data exist about small and cryptobenthic species (Balart et al., 2006). Cryptobenthic fishes often are diminutive species with coloration and behavior in close association with the substratum (Depczynski & Bellwood, 2003). In the present work we report the LWR of eight cryptobenthic reef fishes from shallow rocky reefs of the southwestern Atlantic.

Material and methods

The fishes were collected at two natural rocky reefs (Rasas and Escalvada Islands) and two nearby artificial reefs, a shipwreck (Bellucia) and a derelict vessel intentionally deployed to promote recreational diving (Victory 8B). All reefs are located 10 km off Guarapari, southeastern Brazil (20°40’56”S 40°23’10”W). The fishes were captured between January and March 2008 during

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[*] No prelo em *Journal of Applied Ichthyology*

SCUBA diving using hand nets at depths of 6-33 m. After collection, they were fixed in 10% formalin, preserved in 70% ethanol and identified to species level following Greenfield (1988), Cervigón (1993; 1994), Carvalho-Filho (1999) and Humann & Deloach (2002). The total length (TL) was measured at the nearest 0.05 mm and the total wet weight (W) was obtained at 0.0001 g precision after blotting the fish dry on paper towel. Species with few individuals (n = 7-12) were analyzed due to the absence of published LWR for the species or for the Brazilian coast. As for any linear regression, LWR computed from narrow size ranges should not be extrapolated outside that range. The growth model of the type $W = aTL^b$ was adopted, where W is the wet weight in g, TL is the total length in cm, a is a constant, and b is the allometric coefficient (King, 1995; Froese, 2006).

Results and discussion

LWR were estimated from 260 specimens belonging to eight cryptobenthic reef fish species distributed in five families (Table 1). All relationships presented are new, except for that of *Malacoctenus triangulatus* and *Phaeoptyx pigmentaria* that are new for the Brazilian coast.

Despite some recently published works for estuarine or reef fishes of the Brazilian coast (Frota et al., 2004; Vianna et al., 2004; Giarrizzo et al., 2006; Joyeux et al., 2009), LWR for small and cryptobenthic fishes are poorly documented (e.g., Macieira & Joyeux, 2009). We hope that the present work is useful for future research related to trophic ecology and ecosystem modeling and that it calls attention for the need to increase investigations of the cryptobenthic reef fishes from the Brazilian coast.

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Table 1: Length-weight relationships for eight cryptobenthic reef fishes of the southeastern Brazilian coast. The number of individuals (n), minimum and maximum total length (cm) and weight (g), *a* and *b* parameters for the equation ln(W) = ln(*a*) + *b*ln(TL) with respective 95% confidence limits and the coefficient of determination (r^2) are shown.

Family **Species**	**n**	**Total Length (cm)**		**Weight (g)**		***a* (95% CL)**	***b* (95% CL)**	r^2
		min	**max**	**min**	**max**			
Apogonidae								
Apogon americanus Castelnau, 1855	9	2.44	9.71	0.137	14.7	0.0055 (0.0038 to 0.0081)	3.46 (3.24 to 3.67)	0.995
Phaeoptyx pigmentaria (Poey, 1860)	7	2.44	6.54	0.125	2.85	0.0071 (0.0041 to 0.0125)	3.17 (2.80 to 3.54)	0.990
Blenniidae								
Parablennius marmoreus (Poey, 1876)	47	2.21	5.78	0.0685	1.80	0.0043 (0.0036 to 0.0050)	3.52 (3.39 to 3.64)	0.986
Gobiidae								
Coryphopterus dicrus Böhlke & Robins, 1960	84	1.14	4.94	0.0067	1.26	0.0053 (0.0048 to 0.0058)	3.45 (3.36 to 3.54)	0.985
Lythrypnus phorellus Böhlke & Robins, 1960	44	0.87	2.05	0.0047	0.0818	0.0076 (0.0069 to 0.0084)	3.08 (2.88 to 3.29)	0.955
Labrisomidae								
Malacoctenus triangulatus Springer, 1959	47	1.99	5.06	0.0465	1.28	0.0045 (0.0034 to 0.0061)	3.43 (3.21 to 3.65)	0.956
Starksia brasiliensis (Gilbert, 1900)	12	1.48	3.49	0.0248	0.399	0.0071 (0.0060 to 0.0083)	3.15 (2.97 to 3.32)	0.994
Tripterygiidae								
Enneanectes altivelis Rosenblatt, 1960	10	1.35	2.70	0.0225	0.192	0.0085 (0.0066 to 0.0111)	3.18 (2.83 to 3.52)	0.983

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CAPÍTULO 5

Protection in the giant: Goliath grouper (*Epinephelus itajara*) as a refuge for mackerel scad (*Decapterus macarellus*)[*]

Raphael M. Macieira, Thiony Simon, Caio R. Pimentel and Jean-Christophe Joyeux

Summary

Here we report the use of *Epinephelus itajara* by *Decapterus macarellus* as a protection from *Caranx latus* predation attacks.

Keywords

Predation • Predator avoidance • Schooling behaviour • Risk assessment

In fishes, peaceful associations between species such as cleaning (Francini-Filho & Sazima, 2008; Gasparini et al., 2008) or following (Sazima et al., 2007; Félix & Hackradt, 2008) are well known but others remain elusive due to their transient nature. As with crypsis, camouflage, schooling (Steele & Anderson, 2006) or mimicry (e.g. Caley & Schluter, 2003), the association of one species to another for protection is one of many behavioural adaptations related to the avoidance of predation. Predation is a strong selective pressure that is considered important for the development of several morphological and behavioural characteristics of animals during both evolutionary and ecological times. Thus, decision making by prey appears to reflect an adaptative equilibrium between predation avoidance costs and vital needs (e.g. feeding and reproduction) (Lima & Dill, 1990). Here, we describe how a prey, the mackerel scad *Decapterus macarellus* (Cuvier, 1833), uses a potential predator, the Goliath grouper *Epinephelus itajara* (Lichtenstein, 1822), for

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[*] No prelo em *Marine Biodiversity Records*

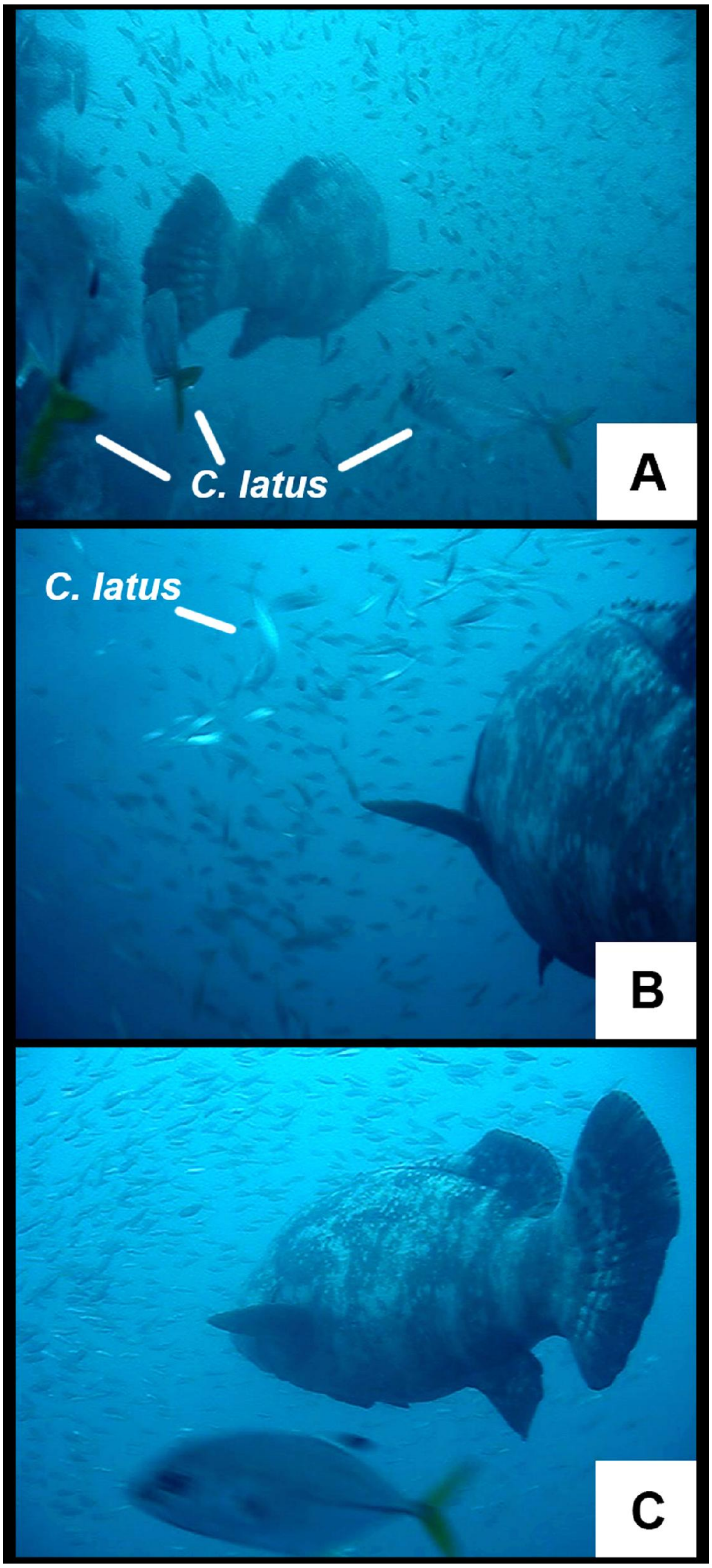

Figure 1: Sequence of anti-predatory behaviour: (A) *Caranx latus* approximating the *Decapterus macarellus* school, (B) *C. latus* attacking the *D. macarellus* school and the school assumes a denser formation while enclosing *Epinephelus itajara* and (C) *E. itajara* being followed by the *D. macarellus* school after the attack.

protection during predation attacks by still another species, the horse-eye jack *Caranx latus* Agassiz, 1831.

The observation was made during SCUBA fieldwork at the artificial reef Victory 8B, Guarapari, south-eastern Brazil (20º40'S, 40º21'W), at 25 m depth. About 10 horse-eye jacks (30 cm total length) approximated and tried to attack a 300-individual mackerel scad school (c. 10 cm TL). The school assumed a denser formation and tightly surrounded one large (170 cm TL) Goliath grouper. Thereafter, the school followed the grouper into the water column away from the vessel until the whole group got out of view (Fig. 1).

The Goliath grouper is a carnivorous teleost which diet includes about 13 % fish (Randall, 1967) and is, thus, a potential predator of both scads and jacks. Risk assessment by mackerel scad school obviously led to the decision that the grouper offered a lower danger of predation than the jacks while offering some protection against them. However, there is no evidence that the grouper actually presents a risk to either jack or scad. Even so, the present observation suggests that one behavioural decision made by a prey under risk of predation can be to seek shelter near another predator that offers a lesser danger.

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