

Marcos Rogério Rosa

Reef communities of the Saint Peter and Saint Paul's Archipelago across an
euphotic-mesophotic depth gradient (0-90 m)

Thesis submitted to the Oceanographic Institute of the
University of São Paulo, in partial fulfillment of the
requirements for the degree of Doctor of Sciences in
Biological Oceanography.

Orientador Prof. Dr. Ronaldo Bastos Francini-Filho

Coorientador Prof. Dr. Paulo Yukio Gomes Sumida

São Paulo

2014

University of São Paulo
Oceanographic Institute

Reef communities of the Saint Peter and Saint Paul's Archipelago across an
euphotic-mesophotic depth gradient (0-90 m)

Marcos Rogério Rosa

Thesis submitted to the Oceanographic Institute of the University of São Paulo, in
partial fulfillment of the requirements for the degree of Doctor of Sciences in
Biological Oceanography.

Certified in __/__/____

Prof(a). Dr(a).

Grade

Agradecimentos

Agradeço primeiramente a Deus por me dar forças para seguir nessa caminhada da vida

A minha família, em especial a minha esposa Josiane C. B. S. Rosa pelo amor, companheirismo e enorme paciência.

Ao professor Ronaldo Bastos Francini-Filho pela orientação, confiança e estímulo a sempre fazer o melhor. Muito obrigado!

Ao professor Paulo Yukio Gomes Sumida pela orientação, oportunidade de trabalho em seu laboratório, inúmeras experiências passadas e momentos tão agradáveis.

A Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) pela concessão da bolsa de doutorado e ao Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq (Edital CNPq n° 26/2009 e 39/2012) pelo financiamento concedido.

A Laís Silva Rodrigues, Aline Alves, Guilherme Henrique Pereira-Filho, Ericka Coni, Camilo Moitinho Ferreira, Diego Valverde Medeiros, José de Anchieta Nunes, Daniel Sartor, Maurício Villela, Zaira Matheus, Alice Groissman, Ana Paula Moreira, Gilberto Menezes Amado-Filho e Fabiano Lopes Thompson pelo apoio nas amostragens, com equipamentos e financeiro.

A APA Fernando de Noronha/Rocas/São Pedro e São Paulo/ICMBio pelas permissões concedidas.

A tripulação do Transmar I e Transmar III, bem como a Secretaria de Comissão Interministerial para os Recursos do Mar (SECIRM) pelo suporte logístico.

Aos colegas de laboratório por todo companheirismo.

Aos amigos do Instituto Oceanográfico da USP – Riguel Feltrin Contente, Camila Contente, Jana del Favero, Eudriano Costa, Claudia Namiki, Wellington “Frango”, Tulia Martinez, Renata Porcaro, Maria de Lourdes Zani-Teixeira, Betina Galerane, “Jaum” Manoel Alfaro, Mauricio Shimabukuro, Arthur Guth, Juliana Genistretti, Carol “De los Angeles” Araujo, Michelle Quesada, Sandra Bromberg, Cao, Jasão Dias, Hélio Santos e muitos outros pelo apoio, discussões e diversão ao longo deste período tão importante.

Aos professores June Dias e Mario Katsuragawa pelo carinho e confiança desde minha chegada ao Instituto Oceanográfico.

Aos amigos professores da UNESP – CLP, Otto B. F. Gadig, Denis Abessa, Tania M. Costa, Teodoro Vaske-Junior.

Aos eternos amigos da UNESP – CLP que mesmo distantes sempre estarão presentes em cada nova conquista.

Por fim, a todas as pessoas que fizeram parte de mais esta grande conquista em minha vida. Muito obrigado!

Summary

| | |
|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----|
| Introduction..... | 1 |
| Literature cited | 9 |
| Chapter 1..... | 24 |
| Reef fish assemblages of the remote St. Peter and St. Paul's Archipelago (Mid Atlantic Ridge, Brazil) across an euphotic-mesophotic depth gradient. | 24 |
| 1.1. Abstract..... | 24 |
| 1.2. Introduction | 26 |
| 1.3. Study area | 28 |
| 1.4. Materials and methods..... | 28 |
| 1.4.1. Sampling procedures | 28 |
| 1.4.2. Data analyses..... | 30 |
| 1.5. Results..... | 32 |
| 1.5.1. Structure of reef fish assemblages | 32 |
| 1.5.2. Influence of habitat characteristics on the structure of reef fish assemblages .. | 34 |
| 1.6. Discussion..... | 34 |
| 1.7. Acknowledgments | 41 |
| 1.8. Literature cited | 42 |
| 1.9. Legend for figures..... | 52 |
| Chapter 2..... | 62 |
| Changes in benthic communities across a depth gradient in the remote St. Peter and St. Paul Archipelago (Mid-Atlantic Ridge, Brazil): The influence of biotic and abiotic factors | 62 |
| 2.1. Abstract..... | 62 |
| 2.2. Introduction | 64 |
| 2.3. Methods..... | 67 |
| 2.4. Results | 70 |
| 2.5. Discussion | 73 |
| 2.6. Acknowledgements | 79 |
| 2.7. Literature Cited | 80 |
| 2.8. Table Legends | 89 |
| 2.9. Figure Legends | 95 |
| Chapter 3..... | 102 |

| | |
|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----|
| Bathimetric distribution, abundance, epibiosis, vitality and size of branching black-corals (Cnidaria: Antipatharia) in the mesophotic zone of the remote St. Peter and St. Paul's Archipelago (Mid Atlantic Ridge, Brazil)..... | 102 |
| 3.1. Abstract..... | 102 |
| 3.2. Introduction | 104 |
| 3.3. Materials and methods..... | 106 |
| 3.3.1. Study area..... | 106 |
| 3.3.2. Sampling procedures | 107 |
| 3.3.3. Data analyses..... | 108 |
| 3.4. Results..... | 108 |
| 3.5. Discussion..... | 110 |
| 3.6. Literature cited | 115 |
| 3.7. Legend for figures..... | 125 |
| Chapter 4..... | 131 |
| Ecology of the bearded fireworm <i>Hermodice carunculata</i> (Pallas, 1766) (ANNELIDA: POLYCHAETA: AMPHINOMIDAE) in the remote St. Peter and St. Paul's Archipelago (Mid Atlantic Ridge, Brazil): A specialized mesophotic coral predator? | 131 |
| 4.1. Abstract..... | 131 |
| 4.2. Introduction | 133 |
| 4.3. Materials and methods..... | 135 |
| 4.3.1. Study area..... | 135 |
| 4.3.2. Sampling procedures | 135 |
| 4.3.3. Data analyses..... | 136 |
| 4.4. Results..... | 137 |
| 4.5. Discussion..... | 138 |
| 4.6. References..... | 142 |
| 4.7. Legends for figures | 149 |
| 5. Concluding remarks..... | 154 |

Index of figures

- Figure 1 – 1.** Map showing: A) the location of the St. Peter and St. Paul's Archipelago (SPSPA) and other Brazilian oceanic islands in the South Atlantic Ocean and B) Detail of the SPSPA showing the study area (light grey). 54
- Figure 1 – 2.** Fish abundance (mean + SE) across the depth gradient. ANOVA results: *P < 0.05, **P < 0.01, ***P < 0.001, ns - not significant. Homogeneous groups are identified by equal letters. 55
- Figure 1 – 3.** Non-metric multi-dimensional scaling (MDS) ordination based on similarities (Bray-Curtis) in fish abundance between three distinct depth strata as defined by Analysis of Similarities (ANOSIM) (see Results). 56
- Figure 1 – 4.** Size frequency distribution of fish across the depth gradient. Significant differences in size distribution were determined using pairwise Kolmogorov–Smirnov tests (alpha set at 0.003 after Bonferroni correction). Homogeneous groups within each depth stratum are linked by equal number of signals. 57
- Figure 1 – 5.** Abundance (mean + SE) of fish within different trophic categories across the depth gradient. ANOVA results: *P < 0.05, **P < 0.01, ***P < 0.001, ns - not significant. Homogeneous groups are identified by equal letters. 58
- Figure 1 – 6.** Biomass (mean + SE) of piscivorous fish in three Brazilian locations: the St. Peter and St. Paul's Archipelago (SPSPA), the Trindade/Martim Vaz Insular Group (TMVIG) and the coastal no-take zone of the National Marine Park of Abrolhos (Abrolhos Archipelago plus Parcel dos Abrolhos Reef). ANOVA results: P < 0.001 in all cases. Homogeneous groups are identified by equal letters. 59

Figure 1 – 7. Canonical Correspondence Analysis (CCA) plot showing (A) habitat characteristics and depth strata, and (B) fish species. Abbreviations of species names: genus indicated by tree first letter and specific epithet by the tree following letters (see full names in (Table 1 – 1)). 60

Figure 2 – 1. Maps showing: (A) the location of the St. Peter and St. Paul Archipelago (SPSPA) and other Brazilian oceanic islands in the South Atlantic Ocean; (B) detail of the sampling area (light grey); the arrow indicates the depth gradient sampled; (C) schematic depth profile of photosynthetically active radiation incident in each depth strata. 97

Figure 2 – 2. Panoramic and close-up views of rocky reefs, St. Peter and St. Paul Archipelago. (A) Belmonte Islet with the Scientific Station and the cove; (B) shallow vertical rocky wall covered by *P. caribaeorum* (bottom right) and *C. racemosa* (centre) (13 m depth); (C) algal turf (centre), *Dictyota menstrualis* (brown) and sponges; (D) distinct specimens of *S. wellsi* (green), CCA (pink) and sponges (35 m); (E) characteristic mesophotic vertical reefs where the incident light decreases (40 m); (F) colony of black coral *Tanacetipathes* sp. (50 m). 98

Figure 2 – 3. Benthic cover at St. Peter and St. Paul Archipelago: (A) major benthic categories (mean + SE) for both shallow (<30 m depth) (white bar) and mesophotic (>30 m) (black bar) reefs; (B) relative cover of the 26 most abundant taxa across the depth gradient. 99

Figure 2 – 4. Benthic community structure in the remote St. Peter and St. Paul Archipelago. (A) Non-metric multi-dimensional scaling (nMDS) ordination based on benthic cover and Bray-Curtis similarity index. Groups are circled at a 20 % similarity level. (B) Simple linear regression analysis of the three groups of organisms according

| | |
|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----|
| to their light dependence: phototrophic (full circle), non-phototrophic (empty circle) and symbiont organisms (grey triangle). <i>P</i> values are indicated for each regression according to the ANOVA. | 100 |
| Figure 2 – 5. Canonical Correspondence Analysis plot showing (a) predictive variables and depth strata, TERH – territorial herbivorous fish and ROVH – roving herbivorous fish; (b) benthic attributes. See full names of benthic attributes in Table 2. | 101 |
| Figure 3 – 1. Maps showing: (A) the location of the St. Peter and St. Paul Archipelago (SPSPA) and other Brazilian oceanic islands in the South Atlantic Ocean; (B) detail of the sampling area (light grey); the arrow indicates the depth gradient sampled; (C) schematic depth profile of photosynthetically active radiation incident in each depth strata. | 126 |
| Figure 3 – 2. Abundance and distribution of black-corals in depth strata from 0 to 100 m. The occurrence of colonies started at 45 m to over 90 m depth | 127 |
| Figure 3 – 3. a) Relative cover of black-corals (mean + SE) according to depth strata and b) Height of black-corals (cm) (mean + SE) according to depth strata. | 128 |
| Figure 3 – 4. The single black-coral colony sampled in 2003, 2010 and 2013. | 129 |
| Figure 4 – 1. Map showing: A) the location of the St. Peter and St. Paul's Archipelago (SPSPA) and other Brazilian oceanic islands in the South Atlantic Ocean, as well as the coastal area of the Abrolhos Bank and B) Detail of the SPSPA showing the study area (light grey). | 150 |
| Figure 4 – 2. Bearded fireworm abundance (mean + SE) across the depth gradient, with significant differences ($P < 0.001$). Homogeneous groups are identified by the same letters. | 151 |

- Figure 4 – 3.** Bearded fireworm abundance by samples (mean + SE) on euphotic and mesophotic zone, with significant differences recorded at $P < 0.001$ 151
- Figure 4 – 4.** Abundance of black-coral and *Hermodice carunculata* overlaid. Colony of black-coral showed on bars, values are given on left axes and abundance of *Hermodice carunculata* showed on line, values are given on right axes. 152
- Figure 4 – 5.** Principal Component Analysis (PCA) with *H. carunculata* (HCAR) and (A) the six distinct depth strata, and (B) the benthic cover with the organism selected based on significance in the correlation analysis. 153

Index of tables

- Table 1 – 1.** Reef fish species recorded in the St. Peter and St. Paul’s Archipelago and their respective trophic groups. N – Total number of individuals recorded, FO – frequency of occurrence in samples. Species arranged according to total N. Bold denotes species retained for quantitative analyses (see text). 61
- Table 2 – 1.** Group/Taxa found per depth stratum in the SPSPA. * represents turf-forming algae that were classified as: ^a corticated with hollow thallus, ^b filamentous uniseriate and pluriseriate with extensive prostate filaments, ^c siphonous with thin separate filaments, ^d smaller-sized corticated, ^e smaller-sized filamentous pluriseriate, ^f filamentous uniseriate and pluriseriate with erect thallus and ^g blade-like with one or few layers of cells (according Balata et al., 2011). ⁺ indicates new records for the SPSPA. (x) presence and (-) absence. 89
- Table 2 – 2.** Mean and standard deviation of the 26 most abundant benthic organisms in the St. Peter and St. Paul Archipelago according to depth strata. * indicates significant between-strata differences (ANOVA). Letters indicate homogeneous groups according to the Student-Newman-Keuls a posteriori test. 92
- Table 2 – 3.** Summary of ANOSIM and SIMPER results. Similarities between samples of the same depth are presented in bold on the diagonal. Dissimilarities are shown above the diagonal, and ANOSIM results appear below the diagonal. n.s. – not significant... 94
- Table 3 – 1.** Number of colonies (mean ± SE), density (mean ± SE), length (mean ± SE) and relative cover (mean ± SE) of black-corals between 40 and 90 m depth. 130

Abstract

This thesis focuses on the investigation of reef communities of the Saint Peter and Saint Paul's Archipelago (SPSPA) across an euphotic/mesophotic depth gradient. Sampling was performed on shallow and mesophotic areas (0 to 90 m depth) using SCUBA and a Remotely Operated Vehicle (ROV). The present work is composed of four chapters: Chapter 1 deals with the quantitative assessment of reef fish communities, which were divided in three distinct communities associated with different depth strata. Clear shifts in habitat use and in size-frequency distributions were recorded for some species. Abundance of black-corals and depth were the most important factors affecting the structure of fish communities, with a clear association of fish with branching black-corals in the mesophotic zone. Chapter 2 presents the first detailed qualitative assessment of benthic communities of the SPSPA. The influence of biotic and abiotic variables shaping the structure of the benthic communities was evaluated. A total of 77 benthic taxa belonging to six major functional groups were recorded. Macroalgae was the richest group (41 infrageneric taxa), with 17 new records for the SPSPA. Turf algae were the most abundant group on both shallow and mesophotic reefs. Two distinct communities were detected: a shallow one composed primarily by the zoanthid *Palythoa caribaeorum* (Duchassaing and Michelotti, 1861), the fleshy alga *Caulerpa racemosa* (Forsskål) J. Agardh, crustose coralline algae (CCA) and *Bryopsis* spp., and another deeper community dominated by CCA, bryozoans and scleractinian corals. Abiotic variables were the most important predictors of benthic community structure. Chapter 3 brings information on abundance, distribution size and associated fauna (epibionts) of black-corals. Although two species of black-corals, *Tanacetipathes hirta* (Gray, 1857) and *T. thamnea* (Warner, 1981), are known to occur in the SPSPA, they are undistinguishable underwater. Epibiosis, mainly by zoanthids and entanglement by fishing monofilament were important factors negatively affecting the health of black-coral colonies. Black-corals were intensively used as refuge by reef fish, especially by the endemic oblique butterflyfish *Prognathodes obliquus* (Chaetodontidae). A single black-coral colony repeatedly visited and monitored for ten years showed a decrease in vitality since the first observation, mainly related to fouling by algal detritus and entanglement by fishing monofilaments. Chapter 4 discusses the ecology (abundance, distribution and habitat preferences) of the fireworm *Hermodice carunculata*, a major predator on mesophotic zone of SPSPA. A total of 278 individuals of bearded fireworm were observed, with significant difference in abundance between euphotic and mesophotic zones. A direct association of *H. carunculata* with black-corals (*Tanacetipathes* spp.), the scleractinian *Madracis decactis* and depth was found. A final session with concluding remarks wraps up information on the ecology of Mesophotic Reef Ecosystems highlighting their possible importance for the stability and persistence of reef fish and benthic communities of the SPSPA, which are under threat of overfishing and climate change, thus requiring urgent protective measures.

Keywords: Benthic community, black-corals, endemic reef fish, *Hermodice carunculata*, mesophotic reef ecosystems and *Prognathodes obliquus*.

Resumo

O tema central desta tese é estudar a ecologia de comunidades recifais ao longo do gradiente de profundidade no Arquipélago São Pedro e São Paulo (ASPSP), com ênfase nos Ecossistemas Recifais Mesofóticos (ERMs). As amostragens foram realizadas da superfície até a zona mesofótica (0 a 90 m de profundidade), utilizando SCUBA e Veículos Submersíveis de Operação Remota (VSORs). Esta tese é composta por quatro capítulos. No Capítulo 1 foi realizada uma avaliação quantitativa das comunidades de peixes, as quais formaram três comunidades distintas associadas aos diferentes estratos de profundidade e ao uso de diferentes habitats de acordo com mudanças ontogenéticas (tamanho do corpo). Corais-negros e profundidade foram os fatores mais importantes na estruturação das comunidades de peixes, com uso intenso dos corais-negros por peixes na zona mesofótica. O Capítulo 2 apresenta a primeira avaliação qualitativa das comunidades bentônicas do ASPSP, além de uma avaliação da influência de variáveis bióticas e abióticas na estruturação das comunidades. Foram registrados 77 táxons bentônicos pertencentes a seis grupos. Macroalgas foi o grupo mais rico (41 táxons), com 17 novos registros para o ASPSP. Algas formadoras de tufos (*turf*) constituíram o grupo mais abundante em ambos os ambientes, eufótico e mesofótico. Foram observadas duas comunidades distintas: uma superficial composta principalmente pelo zoantídeo *Palythoa caribaeorum*, a pela alga *Caulerpa racemosa carnuda*, algas calcárias incrustantes (CCA) e *Bryopsis* spp, e outra mais profunda dominada por CCA, briozoários e corais escleractíneos. As variáveis abióticas, particularmente profundidade e luz, foram mais importantes na estrutura da comunidade bentônica. O Capítulo 3 traz informações sobre a abundância, distribuição, tamanho e vitalidade de corais-negros. Duas espécies de corais-negros, *Tanacetipathes hirta* (Gray, 1857) e *T. thamnea* (Warner, 1981), foram identificadas. Epibiose por zoantídeos e estrangulamento por monofilamentos afetaram negativamente as colônias de coral negro, uma delas monitorada durante dez anos. Esta última apresentou uma diminuição da vitalidade devido principalmente à presença de algas e estrangulamento por monofilamento. Corais-negros formam um grupo-chave na zona mesofótica do ASPSP, sendo intensamente utilizados como habitat por diversos peixes recifais, principalmente espécies endêmicas (e.g., o peixe-borboleta *Prognathodes obliquus*). O Capítulo 4 aborda a ecologia do principal predador de invertebrados bentônicos na zona mesofótica do ASPSP, o verme-de-fogo *Hermodice carunculata*, descrevendo sua abundância e distribuição batimétrica e discutindo seu potencial em impactar as comunidades bentônicas, especialmente os corais escleractínios e os corais-negros na zona mesofótica do ASPSP. Observou-se um total de 278 indivíduos, com diferença significativa na abundância entre as zonas eufótica e mesofótica. Foi encontrada uma associação direta entre *H. carunculata* e 1) corais-negros (*Tanacetipathes* spp), 2) o coral escleractíneo *Madracis decactis* e 3) profundidade. Sugere-se aqui que os ecossistemas mesofóticos são essenciais para a estabilidade para as comunidades recifais eufóticas do ASPSP, tornando urgente a necessidade de novos estudos, principalmente com foco no potencial impacto da pesca e mudanças climáticas.

Palavras chave: Comunidade bentônica, corais negros, ecossistemas de recifes mesofóticos, *Hermodice carunculata*, peixes recifais endêmicos e *Prognathodes obliquus*.

Introduction

Despite their biological and socio-economic importance, reefs around the world are highly threatened by global change (e.g. ocean warming and acidification) and human activities, such as pollution, sedimentation and overfishing (Bellwood *et al.*, 2004; Wilkinson, 2008; Bellwood *et al.*, 2012, Chan and Connolly, 2013). These impacts are directly affecting the integrity of reef communities, particularly compromising their ability to recover after major disturbances, such as mass mortalities of benthic organisms (Guidetti *et al.* 2003; García-Charton *et al.* 2004; Balata *et al.* 2007).

Given this context, much has been discussed about theories and concepts related to reef ecosystems, with the importance of the "Mesophotic Reef Ecosystems" (MREs) receiving more attention only in recent years (Hinderstein *et al.*, 2010 Pugliese *et al.*, 2010). The MREs are characterized by the presence of light-dependent organisms (e.g. corals and crustose calcareous algae) and associated communities that are typically found at depths ranging from 30 to 40 m, but sometimes extending to over 150 m. Besides dominance by some light-dependent species of corals and algae, MREs are also characterized by high abundance of filter-feeders, mainly sponges (Hinderstein *et al.*, 2010; Kahng *et al.*, 2010), and are still largely unknown due to the logistical difficulties of conducting studies in depth greater than 30 m (Hinderstein *et al.*, 2010; Lesser *et al.*, 2009). MREs are considered as extensions of the adjacent shallow reefs, with organisms showing specific adaptations (e.g. optimal photosynthetic activity at depth) that results in unique communities (Khang and Kelley, 2007; Slattery *et al.*, 2011).

The first *in situ* mesophotic reef studies were carried out in the 1960's and 1970's, using SCUBA (Goreau and Wells, 1967; Goreau and Goreau, 1973; Goreau and Land, 1974; Lang 1974), despite the limitations of this diving technique below 30 m depth

(Bak *et al.*, 2005; Kahng and Maragos, 2006; Kahng and Kelley, 2007; Hinderstein *et al.*, 2010). Detailed descriptions showing the vertical zonation of reef communities were carried out only during the 1980's in the western Atlantic (Frike and Meischner, 1985; Reed, 1985; Ohlhorst and Liddell, 1988; Hanisak and Blair, 1988) and Indo-Pacific (Colin 1986, Colin *et al.*, 1986; Thresher and Colin, 1986). The emergence of new technologies in the 2000's, such as technical diving with gas mixtures (TRIMIX), rebreathers and underwater vehicles (remotely operated, autonomous and manned), opened whole new possibilities for the study of MREs (Menza *et al.*, 2007; Pugliese *et al.*, 2009; Gleason *et al.*, 2010; Kahng *et al.*, 2010; Garcia-Sais, 2010; Hinderstein *et al.*, 2010). Even though technology has improved our understanding of MREs, these ecosystems are still poorly understood.

Environmental stresses that may affect reefs in depths shallower than 30 m (natural or human-induced) generally do not reach the MREs, leading these latter to be considered as refuges for the shallow reef biota (Bongaerts *et al.*, 2010; Lesser *et al.*, 2009). For instance, corals living on their lower depth limit of distribution are more protected from bleaching (i.e. loss of symbiotic zooxanthellae) and disease triggered by increased sea surface temperature and sea pollution than those nearer the surface (Hinderstein *et al.*, 2010; Gori *et al.*, 2011; Bridge and Guinotte, 2012; Kelmo and Attrill, 2013). The refuge role of MREs are mainly related to their potential as sources of larvae and juveniles for the replenishment of degraded shallow reef areas (Bongaerts *et al.*, 2010; Slattery *et al.*, 2011). In spite of this importance, the ecological processes and the magnitude of biotic connections between shallow and deep reefs are still largely unknown (Slattery *et al.*, 2011; Kahng *et al.*, 2014). Thus, increasing knowledge about MREs may provide clues for the conservation of the entire reef ecosystems, both euphotic and mesophotic (Reigl and Piller, 2003; Bongaerts *et al.*, 2010).

Besides representing an important source of propagules for shallow reefs, MREs may also contribute for the replenishment of fish communities in coastal areas (Reigl and Piller, 2003; Francini-Filho and Moura, 2008; Bongaerts *et al.*, 2010.). This is particularly true for reef fish from families Serranidae and Lutjanidae, which generally aggregate seasonally in MREs to spawn (Domier *et al.*, 2002; Domier and Sadovy, 2005). Studies on the occurrence and functioning of MREs are still incipient (Hinderstein *et al.*, 2010; Khang *et al.*, 2014) and virtually absent for the South Atlantic Ocean (but see Feitoza *et al.* 2005; Pereira-Filho *et al.* 2011; Moura *et al.* 2013).

MREs are characterized by the dominance of light-dependent organisms, particularly scleractinian corals and calcareous algae, down to 60 m depth. In depths greater than 60 m, the community is dominated by filter-feeders such as sponges, gorgonians (Octocorallia) and black-corals (Antipatharia) (Lang 1974; Liddel and Ohlhrst, 1988; Bongaerts *et al.*, 2010; Slattery *et al.*, 2011; Kahng *et al.*, 2014). Gorgonians and black-corals are key organisms in MREs, since they have relatively large sizes and branching morphologies. This creates a 3-dimensional, structurally more complex habitat that serves as substrate for epibiont organisms, as well as feeding grounds and refuge for the mobile fauna (Grigg, 1965; Kahng and Grigg, 2005; Bo *et al.*, 2008; 2009; 2013; Tsounis *et al.*, 2010). Black-corals are important for a range of organisms that live associated with them, such as arthropods, annelids, echinoderms, mollusks, sponges, cnidarians and fish (Boland & Parrish 2005; Wagner and Tonnen, 2012), which may lead to unique coevolutionary strategies (Bo *et al.*, 2009; 2011).

The health of reefs, whether euphotic or mesophotic, depends on biotic and abiotic factors, with carnivorous (piscivores and invertivores) playing essential roles in shaping reef communities (Hixon, 1991; Heithaus and Dill, 2006; Heithaus *et al.*, 2008). Large carnivores, such as sharks, influence the equilibrium between herbivores and the benthic

community (Dulvy *et al.*, 2003; Heithaus *et al.*, 2008). However, the exploitation of oceans by humans has led to a global decline of approximately 90% of the predators, with the consequent collapse of local and regional populations of more than 50 species of predatory fish (Jackson *et al.*, 2001; Dulvy *et al.*, 2003; Myers and Worm, 2003; Baum and Myers, 2004).

The overexploitation of top marine carnivores results in a catastrophic effect called "trophic cascade" (Pace *et al.*, 1999). The removal of large carnivores results in an increase of prey populations (*e.g.*, herbivores), ultimately influencing the base of the food chain (Pinnegar *et al.* 2000; Shurin *et al.*, 2002; Mumby *et al.*, 2006) and driving marine communities to disruption (Duffy, 2003; Shears and Babcock, 2002). The trophic cascade is amplified in less diverse ecosystems such as rocky reefs (Roberts 1995; Pace *et al.*, 1999; McClanahan *et al.*, 2002). Therefore, it is essential to look throughout the fish communities and consider the whole reef, taking an ecosystem approach and integrating the biology of populations and communities, physical factors and their interactions in order to better understand the effects of the loss of biodiversity on reef ecosystem functioning (Roberts, 1995).

Brazilian reef environments are considered as priority areas for biodiversity conservation in the Atlantic Ocean, mainly owing to their small size (ca. 5% of reefs in the Atlantic), high endemism levels (25 and 50% for corals and fish, respectively) and escalating threats (Moura, 2000). Despite their importance, the number of studies on Brazilian reefs is still small when compared to other regions such as the Caribbean and Indo-Pacific, with a significant increase in the last 20 years (*e.g.*, Rosa & Moura, 1997; Leão and Kikuchi, 2005; Leão *et al.*, 2003; Luiz-Junior *et al.*, 2008; Floeter *et al.*, 2008; Castro *et al.*, 2010; Francini-Filho *et al.*, 2013).

The amount of information available for the Brazilian oceanic islands is even more restricted, with some works on fish communities of the Fernando de Noronha Archipelago, Trindade and Martin Vaz Island Group and Rocas Atoll (Rosa and Moura 1997; Floeter *et al.*, 2008; Krajewski, *et al.* 2011; Pinheiro *et al.* 2011; Batista *et al.*, 2012; Pereira-Filho *et al.*, 2012), as well as works about benthic communities of the Rocas Atoll and the Trindade and Martin Vaz Island Group (Paiva *et al.*, 2007; Pereira-Filho *et al.*, 2012).

The first *in situ* work about Brazilian MREs was made by Feitoza *et al.* (2005), which described semi-quantitatively the reef fish communities of the Paraíba State (Northeastern of Brazil). More recently, Pereira-Filho *et al.* (2011) used an ROV and TRIMIX diving to study MRES of the Trindade and Martin Vaz Island Group. Finally, Moura *et al.* (2013) while mapping the Abrolhos shelf using a side-scan sonar, showed the occurrence and extended of MREs in the region.

The Saint Peter and Saint Paul Archipelago (SPSPA) is a small group of rocky islands located in the central equatorial Atlantic Ocean, about 1010 km from the city of Natal, Brazil (Edwards and Lubbock, 1983). It is composed by five major islands (Belmonte, Challenger, Northeast, Islet and South Islet Cabral) and numerous small rocks (Campos *et al.*, 2005). It lies within the Environmental Protection Area (APA) Fernando de Noronha - Rocas - St. Peter and St. Paul, created by Federal Decree No. 92755, of June 5, 1986, which covers an area of 79,706 ha and encompasses the Fernando de Noronha Archipelago, the Rocas Atoll and the SPSPA (IBAMA, 2005). In 1998, the Brazilian Government launched the Pro-Arquipélago Program and, as a consequence, a scientific station was deployed in the SPSPA, given Brazil the rights and duties over 450,000 km² of Exclusive Economic Zone around the SPSPA (an area equivalent to about 15% of the entire Brazilian EEZ or 6% of the national territory;

Souza, 2006; Vianna *et al.*, 2009). The Pro-Arquipélago Program enabled research to be conducted systematically in the SPSPA (*e.g.*, Campos *et al.*, 2005; Monteiro *et al.*, 2006; Hazin *et al.*, 2008; Motoki, 2009; Vaske–Junior *et al.*, 2009). The geographic isolation of the SPSPA makes it less susceptible to impacts that are common in Brazilian coastal reefs, such as pollution and sedimentation (Gibson and Atkinson 2003; Schiel *et al.* 2006). The bottom profile of the archipelago starts with a gentle slope down to 20-30 m depth, followed by a nearly vertical wall extending to about 600 m (Edwards and Lubbock, 1983; Thompson, 1981), thus providing unique opportunities for comparative analysis between shallow and mesophotic reef ecosystems. The archipelago has been well studied since the creation of the scientific station, with several studies focusing on fish (Feitoza *et al.* 2003, Ferreira *et al.* 2010; Vaske *et al.*, 2005; 2006; 2010), mobile invertebrates (Manning and Chace, 1990; Gianuca and Vooren, 2007; Fonteles-Filho, 2006), microbiology (Moreira *et al.* 2013) and benthic communities (Vieira *et al.* 2012; Amaral *et al.* 2010) with its shallow fauna well known.

The SPSPA has been suffering with impacts from fishing activities since the 1950's, with the record of Japanese vessels authorized by the Brazilian Government fishing there. However, it was not until the 1970's that Brazilian vessels began to explore the archipelago, with continuous fishing operations starting in 1988 (Vaske-Junior *et al.*, 2006; 2010; Luiz and Edwards, 2011). Fishing is carried out from anchor point, close to the SPSPA, to a few kilometers away (Vaske *et al.*, 2006; 2010). Fishing gears include longlines and handlines, targeting large pelagic fish such as the yellowfin–tuna (*Thunnus thynnus*), mackerel (*Acanthocybium solandri*) and kingfish (*Elagatis bipinnulata*) (Vaske *et al.*, 2006), as well as trap fisheries targeting the lobsters *Panulirus argus* and *Panulirus echinatus* (Pinheiro, *et al.* 2003; Sankarankutty *et al.*, 2001; Fonteles-Filho, 2006). Shark catches were commonly reported until the 1970's,

but are rare nowadays, with occurring of oceanic species only (Vaske *et al.*, 2006; 2010; Luiz and Edwards, 2011). Overfishing is suggested as the cause of the local extinction of the Galápagos shark *Carcharhinus galapagensis* in the SPSPA (Luiz and Edwards, 2011).

The aim of this thesis is to perform a qualitative and quantitative assessment of reef communities (special focus on fish and benthic communities, black-corals and the locally abundant fireworm *Hermodice carunculata*), across an euphotic-mesophotic gradient (0-90 m depth). The possible role of MREs of the SPSPA as refuges for the shallow biota is discussed. The specific objectives of this thesis grouped by chapter are as follows: Chapter 1: 1) Provide the first quantitative assessment of reef fish assemblages of the SPSPA across an euphotic-mesophotic gradient (0-90 m), 2) describe the composition (body size and trophic structure) and the relative influence of habitat characteristics, such as depth, benthic cover and complexity, 3) Compare the biomass of piscivorous fish of the SPSPA with other Brazilian oceanic islands and marine systems to evaluate its conservation status and evaluate the possible role of the mesophotic zone of the SPSPA as a refuge for reef fish based on the abundance and distribution of fish species across the depth gradient. Chapter 2:1) Present the first detailed quantitative assessment of the benthic communities of shallow and mesophotic reefs of the SPSPA and evaluated the influence of biotic (i.e., the abundance of fish trophic levels) and abiotic variables (i.e., benthic complexity, depth and photossintetically active radiation - PAR) in the structure of benthic communities. Chapter 3:1) Perform the first study on the ecology of black-corals from Brazilian waters, 2) evaluate the distribution, abundance, size, vitality and fauna associated with black-corals, in order to evaluate possible threats and their ecological roles (e.g. providing refuge for reef fish). Chapter 4. 1) Report the bathymetric distribution and

abundance of the bearded fireworm *Hermodice carunculata*, 2) Evaluate its relationship with benthic cover and depth and 3) Discuss the potential of this fireworm to impact the mesophotic zone of SPSPA, mainly as a coral predator or as a coral disease vector.

Literature cited

- Amaral, F. M. D.; Hudson, M. M.; Silveira, F. L.; Migotto, A. E.; Pinto, S. M.; Longo, L. L. 2002. Cnidarians of Saint Peter and St. Paul Archipelago, Northeast Brazil. Proc. 9th Int. Coral Reef Symp., v. 1, p. 567-572
- Bak, R. P. M.; Nieuwland, G.; Meesters, E. H. 2005. Coral reef crisis in deep and shallow reefs: 30 years of constancy and change in reefs of Curacao and Bonaire. Coral Reefs, v. 24, p. 475-479.
- Balata, D.; Piazzini, L.; Benedetti-Cecchi, L. 2007. Sediment disturbance and loss of beta diversity on subtidal rocky reefs. Ecology, v. 88, p. 2455–2461.
- Batista, H.; Veras, D.; Oliveira, P.; Oliveira, D.; Tolotti, M.; Marins, Y.; Zill, J.; Pereira, R.; Hazin, F.; Silva, M. 2012. New records of reef fishes (Teleostei: Perciformes) in the Rocas Atoll Biological Reserve, off northeastern Brazil. Check List, v. 8, n. 3, p. 584-588.
- Baum, J. K.; Myers, R. A. 2004. Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. Ecology Letters, v. 7, p. 135–145.
- Bellwood, D. R.; Hughes, T. P.; Folke, C.; Nystrom, M. 2004. Confronting the Coral Reef Crisis. Nature, v. 429, p. 827-833.
- Bellwood D. R., A. H. Baird, M. Depczynski, A. Gonzalez-Cabello, A. S. Hoey, C. D. Lefevre, Tanner, J. k. 2012. Coral recovery may not herald the return of fishes on damaged coral reefs. Oecologia, v. 170, p. 567-573.

- Bo, M.; Tazioli, S.; Spanò, N.; Bavestrello, G. 2008. *Antipathella subpinnata* (Antipatharia, Myriopathidae) in Italian seas. *Italian Journal of Zoology*, v. 75, p. 185–195.
- Bo, M.; Bavestrello, G.; Canese, S.; Ginsti, M.; Salvati, E.; Angiolillo, M.; Greco, S. 2009. Characteristics of a black coral meadow in the twilight zone of the central Mediterranean Sea. *Marine Ecology Progress Series*, v. 397, p. 53–61.
- Bo, M.; Bertolino, M.; Borghini, M.; Castellano, M.; Harriague, A. C.; Di Camillo, C. G.; 2011. Characteristics of the mesophotic megabenthic assemblages of the Vercelli seamount (North Tyrrhenian Sea). *PloS one*, v. 6, n. 2, p. 16357.
- Bo, M., Cerrano, C.; Canese, S.; Salvati, E.; Angiolillo, M.; Santangelo, G.; Bavestrello, G. 2013. The coral assemblages of an off-shore deep Mediterranean rocky bank (NW Sicily, Italy). *Marine Ecology*, p. 1-11.
- Boland, R. C.; Parrish, F. A. 2005. A description of fish assemblages in the black coral beds off Lahaina, Maui, Hawai'i. *Pacific Science*, v. 59, p. 411–420.
- Bongaerts, P.; Ridgeway, T.; Sampayo, E. M.; Hoegh-Guldberg, O. 2010. Assessing the 'deep reef refugia' hypothesis: focus on Caribbean reefs. *Coral Reefs*, v. 29, p. 309-327.
- Bridge T, Guinotte J. 2012. Mesophotic coral reef ecosystems in the Great Barrier Reef world heritage area: their potential distribution and possible role as refugia from disturbance. Townsville: Great Barrier Reef Marine Park Authority; 2012. pp. 1–57.
- Campos, T. F. C.; Virgens, N. J.; Srivastava, N.K.; Petta, R. A.; Harmann, L. A.; Moraes, J. F. S.; Mendes, L.; Silveira, S. R. M. 2005. Arquipélago de São Pedro e

São Paulo e São Paulo, soerguimento tectônico de rochas infracrustais no Oceano Atlântico. Sítios Geológicos e Paleontológicos do Brasil, SIGEP 002, UNB. 12 p.

Castro, C. B.; Medeiros, M. S.; Loiola, L. L. 2010. Octocorallia (Cnidaria: Anthozoa) from Brazilian reefs. *Journal of Natural History*, v. 44, p. 763-827.

Chan, N. C. S.; Connolly, S. R. 2013. Sensitivity of coral calcification to ocean acidification: a meta-analysis. *Global Change Biology*, v. 19, n. 1, p. 282-290.

Colin, P. L. 1974. Observation and collection of deep reef fishes off the coasts of Jamaica and Honduras. *Marine Biology*, v. 24, n. 1, p. 29-38.

Domeier, M, L., Colin, P.L., Donaldson, T.J., Heyman, W.D., Pet, J.S., Russell, M., Sadovy, Y., Samoily, M.A., Smith, A., Yeeting, B.M. & Smith, S. 2002. Transforming coral reef conservation: reef fish spawning aggregations component. Spawning Aggregation Working Group Report, The Nature Conservancy, Hawaii, April 22, 2002. 85 pp

Duffy, J. E. 2003. Biodiversity loss, trophic skew and ecosystem functioning. *Ecology Letters*, v. 6, p. 680–687.

Dulvy, N. K.; Sadovy, Y.; Reynolds, J. D. 2003. Extinction vulnerability in marine populations. *Fish and Fishery*, v. 4, p. 25–64.

Edwards, A.; Lubbock, R. 1983a. Marine zoogeography of St. Paul's Rocks. *Journal Biogeography*, v. 10, p. 65-72.

Edwards, A. & Lubbock, R. 1983b. The ecology of Saint Paul's Rocks (Equatorial Atlantic). *Journal Zoology*, v. 200, p. 51-69.

- Feitoza, B. M.; Rocha, L. A.; Luiz, O. J.; Floeter, S. R.; Gasparini, J. L. 2003. Reef fishes of St. Paul's Rocks: new records and notes on biology and zoogeography. *Aquatic Journal Ichthyology and Aquatic Biology*, v. 7, p. 61-82.
- Feitoza, B. M. ; Rosa, R. S. ; Rocha-Filho, L. A. 2005. Ecology and zoogeography of deep-reef fishes in northeastern Brazil. *Bulletin of Marine Science, Miami*, v. 76, n.3, p. 725-742.
- Ferreira, C. E. L.; Luiz-Jr, O. J.; Feitoza, B.; Ferreira, C. G. W.; Gasparini, J. L.; Noguchi, R. C.; Godoy, E. A.; Joyeux, J. C.; Rangel, C. A.; Rocha, L. A.; Floeter, S. R.; Carvalho-Filho, A. 2009. Peixes recifais: síntese do atual conhecimento. In: Viana DL, Hazin FHV, Souza MAC (Eds.). *O Arquipélago de São Pedro e São Paulo: 10 anos de estação científica*. Brasília: SECIRM, 2009, pp. 244-340.
- Floeter, S. R.; Rocha, L.A.; Robertson, D. R.; Joyeux, J. C.; Smith-Vaniz, W.; Wirtz, P.; Edwards, A. J.; Barreiros, J. P.; Ferreira, C.E.L.; Gasparini, J. L.; Brito, A.; Falcon, J. M.; Bowen, B. W.; Bernardi, G. 2008. Atlantic reef fish biogeography and evolution. *Journal of Biogeography*, v. 35, p. 22-47.
- Fontaneles-Filho, A. A. Síntese sobre distribuição, abundância, potencial pesqueiro e biologia lagosta-vermelha *Panulirus argus* (Latreille) e a lagosta-verde *Panulirus laevicauda* (Latreille) do Nordeste do Brasil. Relatório Técnico, Relatório de Avaliação do Potencial Sustentável de Recursos Vivos na Zona Econômica Exclusiva MMA –REVIZEE Análise/Refinamento dos Dados Pretéritos Sobre Prospecção Pesqueira.
(<http://www.mma.gov.br/port/sqa/projeto/revizee/textos.html>). Acesso em: 10
Abri l, 2006.

- Francini-Filho, R. B.; Moura, R. L. 2008. Dynamics of fish assemblages on coral reefs subjected to different management regimes in the Abrolhos Bank, eastern Brazil. *Aquatic Conservation*, v. 18, p. 1166-1179.
- Francini-Filho, R. B.; Coni, E. O. C.; Meirelles, P. M.; Amado-Filho, G. M.; Thompson, F. L.; Pereira-Filho, G. H.; Bastos, A. C.; Abrantes, D. P.; Ferreira, C. M.; Gibran, F. Z.; Guth, A. Z.; Sumida, P. Y. G.; Oliveira, N. L.; Kaufman, L.; Mente-Vera, Carolina, V.; Moura, R. L. 2013. Dynamics of Coral Reef Benthic Assemblages of the Abrolhos Bank, Eastern Brazil: Inferences on Natural and Anthropogenic Drivers. *Plos One*, v. 8, p. e54260.
- Fricke, H.; Meischner, D. 1985. Depth limits of Bermudan scleractinian corals: a submersible survey. *Uar. Biol.* 88:175-187.
- García-Charton, J. A.; Pérez-Ruzafa, Á.; Sánchez-Jerez, P.; Bayle-Sempere, J. T.; Reñones, O.; Moreno, D. 2004. Multi-scale spatial heterogeneity, habitat structure, and the effect of marine reserves on Western Mediterranean rocky reef fish assemblages. *Marine Biology*, v. 144, n. 1, p. 161-182.
- Garcia-Sais, J. R. 2010. Reef habitats and associated sessile-benthic and fish assemblages across a euphotic-mesophotic depth gradient in Isla Desecheo, Puerto Rico. *Coral Reefs* v. 29, p. 277-288.
- Gianuca, D.; Vooren, C. M. 2007. Abundance and behavior of the sally lightfoot crab *Grapsus grapsus* in the colony of the brown booby (*Sula leucogaster*) in the São Pedro and São Paulo Archipelago. *Investigaciones Marinas, Valparaíso*, v.35, n.22, p. 121-125.

- Gibson, R. N.; Atkinson, R. J. A. 2003. The effects of sedimentation on rocky coast assemblages. *Oceanography and Marine Biology*, v. 41, p. 161-236.
- Gleason, A. C. R.; Gracias, N.; Lirman D.; Gintert, B. E.; Smith, T. B.; Dick, M.; Reid R. P. 2010. Landscape video mosaic from a mesophotic coral reef. *Coral Reefs* 29, 253–253.
- Goreau, T. F. & Goreau N. I. 1973. The ecology of Jamaican coral reefs. II Geomorphology, zonation and sedimentary phases. *Bulletin Marine Science*, v. 23, p. 399-464.
- Goreau, T.F. & Land L. S. 1974. Fore-reef morphology and depositional processes, North Jamaica. *Bulletin Marine Science*, v. 23, p. 77-85.
- Gori, A.; Rossi, S.; Linares, C.; Berganzo, E.; Orejas, C.; Dale, M. R. T.; Gili, J. M. 2011. Size and spatial structure in deep versus shallow populations of the Mediterranean gorgonian *Eunicellasingularis* (Cap de Creus, northwestern Mediterranean Sea). *Coral Reefs*, v. 31, n. 3, p. 823-837.
- Grigg, R. W. 1965. Ecological studies of black coral in Hawaii. *Pacific Science*, v. 19, p. 244-260.
- Guidetti, P.; Frascchetti, S.; Terlizzi, A.; Boero, F. 2003. Distribution patterns of sea urchins and barrens in shallow Mediterranean rocky reefs impacted by the illegal fishery of the rock-boring mollusc *Lithophaga lithophaga*. *Marine Biology*, v. 143, n. 6, p. 1135-1142.
- Hazin, F. H. V.; Vaske-Junior, T.; Oliveira, P. G. V.; Macena, B.; Carvalho, F. 2008. Occurrences of whale shark (*Rhincodon typus*, Smith, 1828) in the Saint Peter and Saint Paul Archipelago, Brazil. *Brazilian Journal of Biology*, v. 68, p. 631-637.

- Hanisak, M. D.; Blair, S. M. 1988. Deep-water macroalgal communities with emphasis on Florida and the Bahamas. – In: AGEKIAN, C.R. (ed.): Biogeochemical Cycling and Fluxes Between the Deep Euphotic Zone and Other Oceanic Realms: 61-83. National Undersea Research Program, Research Report 88-1.
- Heithaus, M. R.; Dill, L. M. 2006. Does tiger shark predation risk influence foraging habitat use by bottlenose dolphins at multiple spatial scales? *Oikos*, v. 114, p. 257–264.
- Heithaus, M. R.; Frid, A.; Wirsing, A. J.; Worm, B. 2008. Predicting ecological consequences of marine top predator declines. *Trends in Ecology and Evolution*, v. 23, p. 202–210.
- Hinderstein, L. M.; Marr, J. C. A.; Martinez, F. A.; Dowgiallo, M. J.; Puglise, K. A.; Pyle, R. L.; Zawada, D. G.; Appeldoorn, R. 2010. Introduction to mesophotic coral ecosystems: Characterization, ecology, and management. *Coral Reefs*, v. 29, p. 247-251.
- Hixon, M. A. 1991. Predation as a Process Structuring Coral Reef Fish Communities. In: *The Ecology of Fishes on Coral Reefs*. P. Sale (ed). Academic Press, Inc., San Diego, CA. p. 475-508.
- Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis, Programa das Nações Unidas para o Desenvolvimento and Tetraplan (IBAMA, PNUD and Tetraplan) (2005) Plano de Manejo APA Fernando de Noronha- Roca- São Pedro e São Paulo, Fernando de Noronha: IBAMA.

- Jackson, J. B. C.; Kirby, M. X.; Bergoer, W. H. A.; Botsford, L. W.; Bourque, B. J. et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science*, v. 293, p. 629–637.
- Kahng, S. E.; Grigg, R. W. 2005. Impact of an alien octocoral (*Carijoa riisei*) on black corals in Hawaii. *Coral Reefs*, v. 24, n. 4, p. 556-562.
- Kahng, S. E.; Spalding, H. L.; Brokovich, E.; Wagner, D.; Weil, E.; Hinderstein, L.; Toonen, R. J. 2010. Community ecology of mesophotic coral reef ecosystems. *Coral Reefs*, v. 29, p. 255-275
- Kahng, S. E.; Copus, J. M.; Wagner, D. 2014. Recent advances in the ecology of mesophotic coral ecosystems (MCEs). *Environmental Sustainability*, v. 7, p. 72–81.
- Kelmo, F.; Attrill, M. J. 2013. Severe Impact and Subsequent Recovery of a Coral Assemblage following the 1997–8 El Niño Event: A 17-Year Study from Bahia, Brazil. *PLoS ONE*, v. 8, n. 5, p. e65073.
- Krajewski, J. P.; Floeter, S. R. 2011. Reef fish community structure of the Fernando de Noronha Archipelago (Equatorial Western Atlantic): the influence of exposure and benthic composition. *Environmental Biology Fish*, v. 92, p. 25-40.
- Lang, J. C. 1974. Biological zonation at the base of a reef. *American Science*, v. 62, p. 272-281.
- Leão, Z. M. A. N.; Kikuchi, R. K. P.; Testa, T. 2003. Corals and coral reefs of Brazil. In *Latin American Coral Reefs* ed. Cortes, J. Amsterdam: Elsevier Science. pp. 9–52.

- Leão, Z. M.; Kikuchi, R. K. 2005. A relic coral fauna threatened by global changes and human activities, Eastern Brazil. *Marine Pollution Bulletin*, v. 51, p. 599–611.
- Lesser, M. P.; Slattery, M.; Leichter, J. J. 2009. Ecology of mesophotic coral reefs. *Journal of Experimental Marine Biology and Ecology*, v. 375, n. 1, p. 1-8.
- Luiz-Junior, O. J.; Carvalho-Filho, A.; Ferreira, C. E. L, Floeter, S. R.; Gasparini, J. L.; Sazima, I. 2008. The reef fish assemblage of the Laje de Santos Marine State Park, Southwestern Atlantic: annotated checklist with comments on abundance, distribution, trophic structure, mutualistic associations, and conservation. *Zootaxa*, v. 1807, p. 01-25.
- Luiz, O. J.; Edwards, A. J. 2011. Extinction of a shark population in the Archipelago of Saint Paul's Rocks (equatorial Atlantic) inferred from the historical record. *Biology Conservation*, v. 144, n. 12, p. 2873-2881.
- Manning, R. B.; Chace JR., F. A. Decapod and stomatopod Crustacea from Ascension Island, South Atlantic Ocean. *Smithsonian Contributions to Zoology*. v. 503, p. 1-91. Washington, 1990.
- McClanahan, T. R.; Polunin, N. V. C.; Done, T. J. 2002. Ecological states and the resilience of coral reefs. *Conservation Ecology*, v. 6, p. 18.
- Menza, C.; Kendall, M.; Rogers, C.; Miller, J. 2007. A deep reef in deep trouble. *Continental Shelf Research*, v. 27, p. 2224-2230.
- Monteiro, M. S.; Vaske-Junior, T.; Barbosa, T. M.; Alves, M. D. O. 2006. Predation by a shortfin mako shark *Isurus oxyrinchus*, Rafinesque, 1810, on a calf of pantropical spotted dolphin, *Stenella attenuata*, in Central Atlantic.. *The Latin American Journal of Aquatic Mammals*, v. 5, p. 141-144.

- Motoki, A.; Sichel, S. E.; Campos, T. F. C.; Srivastava, N. K.; Soares, R. S. 2009. Taxa de soerguimento atual do Arquipélago de São Pedro e São Paulo, Oceano Atlântico Equatorial. *Revista Escola de Minas*, v. 62, n. 3, p. 331-342.
- Moura, R. L. 2002. Brazilian reefs as priority areas for biodiversity conservation in the Atlantic Ocean. *Proceedings of the 9th International Coral Reef Symposium*, v. 2, p. 917–920.
- Moura, R. L.; Secchin, N. A.; Amado-Filho, G. M.; Francini-Filho, R. B.; Freitas, M. O.; Minte-Vera, C. V.; Teixeira, J. B.; Thompson, F. L.; Dutra, G. F.; Sumida, P. Y. G.; Guth, A. Z.; Lopes, R. M.; Bastos, A. C. 2013. Spatial patterns of benthic megahabitats and conservation planning in the Abrolhos Bank. *Continental Shelf Research*, v. 70, p. 109–117.
- Mumby, P. J.; Dahlgren, C. P.; Harborne, A. R.; Kappel, C. V.; Micheli, F.; Brumbaugh, D. R.; Holmes, K.E.; Mendes, J. M.; Broad, K.; Sanchirico, J. N.; Buch, K.; Box, S.; Stoffle, R. W.; Gill, A. B. 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. *Science*, v. 311, p. 98-101.
- Myers, R. A.; Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. *Nature*, v. 423, p. 280–283.
- Liddell, W. D.; Ohlhorst, S.L. 1988. Hard substrata community patterns, 1-120111, North Jamaica. *Palaios* 3.
- Pace, M. L.; Cole, J. J.; Carpenter, S. R.; Kitchell, J. F. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution*, v. 14, p. 483–488.

- Paiva, P. C.; Young, P. S.; Echeveria, C. A. 2007. The Rocas Atoll, Brazil: a preliminary survey of the crustacea and Polychaete fauna. *Arquivos do Museu Nacional*, v. 65, p. 241-250.
- Pereira-Filho, G. H.; Amado-Filho, G. M.; Guimarães, S. M. P. B.; Moura, R. L.; Sumida, P. Y. G.; Abrantes, D. P.; Bahia, R. G.; Guth, A. Z.; Jorge, R. R.; Francini Filho, R. B. 2011. Reef fish and benthic assemblages of the Trindade and Martin Vaz island group, southwestern Atlantic. *Brazilian Journal Oceanography* v. 59, p. 201-212.
- Pereira-Filho, G.; Amado-Filho, G.; Moura, R. L.; Bastos, A.; Guimarães, S.; Salgado, L. T.; Francini-Filho, R. B.; Bahia, R.; Abrantes, D.; Guth, A.; Brasileiro, P. 2012. Extensive rhodolith beds cover the summits of Southwestern Atlantic Ocean seamounts. *Journal of Coastal Research*, v. 28, p. 261-269.
- Pinheiro, A. P.; Freire, F. A. M.; Lins Oliveira, J. E. 2013. Population biology of *Panulirus echinatus* Smith, 1869 (Decapoda: Palinuridae) from São Pedro e São Paulo Archipelago, Northeastern Brazil. *Nauplius*, v. 11, n. 1, p. 27-35.
- Pinheiro, H. T.; Ferreira, C. E. L.; Joyeux, J. C.; Santos, R. G.; Horta, P. A. 2011. Reef fish structure and distribution in a south-western Atlantic Ocean tropical island. *Journal Fish Biological*, v. 79, n. 7, p. 1984-2006.
- Pinnegar, J. K.; Polunin, N. V. C.; Francour, P.; Badalamenti, F.; Chemello, R.; Harmelin-Vivien, M. L. et al. 2000. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. *Environmental Conservation*, v. 27, p. 179–200.

- Puglise, K. A.; Hinderstein, L. M.; Marr, J. C. A.; Dowgiallo, M. J.; Martinez, F. A. 2009 Mesophotic coral ecosystems research strategy: International workshop to prioritize research and management needs for Mesophotic Coral Ecosystems. Jupiter, Florida, 12–15 July 2008. Silver Spring, MD: NOAA National Centers for Coastal Ocean Science, Center for Sponsored Coastal Ocean Research, and Office of Ocean Exploration and Research, NOAA Undersea Research Program. NOAA Technical Memorandum NOS NCCOS 98 and OAR OER 2. p 24.
- Reed, J. K. 1985. Deepest distribution of Atlantic hermatypic corals discovered in the Bahamas. *Proc 5th Int Coral Reef Symp.*, v. 6, p. 249–254.
- Riegl, B.; Piller, W. E. 2003. Possible refugia for reefs in times of environmental stress. *International Journal of Earth Sciences* 92, 520–531.
- Roberts, C. M. 1995. Effects of fishing on the ecosystem structure of coral reefs. *Conservation Biology*, v. 9, p. 988–995.
- Rosa, R. S.; Moura, R. L. 1997. Visual assessment of reef fish community structure in the Atol das Rocas Biological Reserve, off north-eastern Brazil. *Proc. 8th Int. Coral Reef Symp.* v. 1, p. 983-986.
- Sadovy, Y.; Domeier, M. 2005. Are aggregation fisheries sustainable: reef fish fisheries as a case study. *Coral Reefs*, v. 24, n. 2, p. 254-262.
- Sankarankutty, C.; Oliveira, J. E. L.; Ferreira, A. C. 2001. On a large specimen of *Panulirus argus* (Latreille, 1804) (Crustacea: Decapoda: Palinuridae) from Archipelago of São Paulo and São Pedro, Brazil. *Nauplius*, v. 9, n. 1, p. 67-68. 2001.

- Schiel, D. R.; Wood, S. A.; Dunmore, R. A. 2006. Sediment on rocky intertidal reefs: effects on early post-settlement stages of habitat-forming seaweeds. *Journal of Experimental Marine Biology and Ecology*, v. 331, n. 2, p. 158–172.
- Shears, N. T. & Babcock, R. C. 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia*, v. 132, p. 131–142.
- Shurin, J. B.; Borer, E. T.; Seabloom, E. W.; Anderson, K.; Blanchette, C. A.; Broitman, B. et al. 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters*, v. 5, p. 785–791.
- Slattery, M.; Lesser, M. P.; Brazeau, D.; Stokes, M. D.; Leichter, J. J. 2011. Connectivity and stability of mesophotic coral reefs. *Journal of Experimental Marine Biology and Ecology*, v. 408, p. 32-41.
- Souza, J. E. B. 2006. O arquipélago de São Pedro e São Paulo. Rio de Janeiro, *Revista do Clube Naval*, v. 115-340, p. 70-72.
- Thresher, R. E. and P. L. Colin, 1986. Trophic structure, diversity and abundance of fishes of the deep reef (30-300 m) at Enewetak, Marshall Islands. *Bull. Mar. Sci.*, v. 38, n. 1, p. 253-272.
- Thompson, G. 1981. St. Peter and St. Paul's Rocks (Equatorial Atlantic) and the surrounding sea floor. Woods Hole Oceanogr Inst Tech Rept WHOI-81-98.
- Tsounis, G.; Rossi, S.; Grigg, R.; Santangelo, G.; Bramanti, L; Gili, J. 2010. The Exploitation and Conservation of Precious Corals. *Oceanography and Marine Biology*, v. 48, p. 161-212.

- Vaske Jr., T.; Lessa, R. P.; Ribeiro, A. C. B.; Nóbrega, M. F.; Pereira, A. A.; Andrade, C. D. P. 2006. The commercial fishery of pelagic fishes off the Saint Peter and Saint Paul Archipelago, Brazil. *Tropical Oceanography*, v. 34, p. 31–41.
- Vaske-Junior, T.; Lessa, R. P.; Gadig, O. B. F. 2009. Feeding habits of the blue shark (*Prionace glauca*) off the coast of Brazil. *Biota Neotropica*, v. 9, p. 1-7.
- Vaske-Jr., T.; Nóbrega, M. F.; Lessa, R. P.; Hazin, F. H. V.; Santana, F. M.; Ribeiro, A. C. B.; Pereira, A. A.; Andrade, C. D. P. 2010. Pesca. In: Vaske Jr., T., et al. (Eds.), *Arquipélago de São Pedro e São Paulo: histórico e recursos naturais*. NAVE/LABOMAR – UFC, Fortaleza, pp. 181–188.
- Vaske Jr., T., Nóbrega, M.F., Lessa, R.P., Hazin, F.H.V., Santana, F.M., Ribeiro, A.C.B., Pereira, A.A., Andrade, C.D.P., 2010. Pesca. In: Vaske Jr., T., et al. (Eds.), *Arquipélago de São Pedro e São Paulo: histórico e recursos naturais*. NAVE/LABOMAR – UFC, Fortaleza, pp. 181–188.
- Viana *et al.*, 2009. *O Arquipélago de São Pedro e São Paulo: 10 anos de Estação Científica/ Orgs. Danielle de Lima Viana... [et al.]*. -- Brasília, DF: SECIRM, 2009. 348 p.
- Vieira, L. M.; Farrapeira, C. M. R.; Amaral, F. M. D.; Lira, S. M. A. 2012. Bryozoan biodiversity in Saint Peter and St. Paul Archipelago, Brazil. *Cahiers de Biologie Marine*, v. 53, p. 159-167.
- Wagner, D.; Luck, D. G.; Toonen, R. J. 2012. The biology and ecology of black corals (Cnidaria: Anthozoa: Hexacorallia: Antipatharia). *Adv Mar Biol.*, v. 2012, p. 63:67-132.

Wilkinson, C. (ed.) 2008. Status of Coral Reefs of the World 2008. Australian Institute of Marine Science, Townsville, Australia.

Chapter 1

This chapter was submitted for publication in *Marine Ecology*. The leading author is Marcos Rogerio Rosa. Gabriela G. Magalhães, Aline C. Alves, Laís S. Rodrigues, Diego V. Medeiros, Paulo Y. G. Sumida, Rodrigo L. Moura, Ricardo S. Rosa, Beatrice D. Ferreira, Fabiano L. Thompson, Guilherme H. Pereira-Filho, Gilberto M. Amado-Filho and Ronaldo B. F. Francini-Filho are coauthors.

Reef fish assemblages of the remote St. Peter and St. Paul's Archipelago (Mid Atlantic Ridge, Brazil) across an euphotic-mesophotic depth gradient.

1.1. Abstract

The first quantitative assessment of reef fish assemblages of the remote St. Peter and St. Paul's Archipelago (SPSPA), Mid Atlantic Ridge, Brazil, is provided here. Sampling was performed up to 90 m depth using SCUBA and a Remotely Operated Vehicle. Distinct fish assemblages associated with the 0-10, 10-50 and 50-90 m depth strata were identified. Abundance of roving herbivores, territorial herbivores and invertebrate feeders decreased with depth, while abundance of piscivores showed the opposite trend. Planktivores were most abundant at intermediate depths. Black-corals and depth were the most important factors affecting fish assemblages' structure, with a clear association of *Chromis enchrysur*, *Prognathodes obliquus* and juveniles of *Bodianus insularis* with branching black-corals in the mesophotic zone. The species-poor fish assemblages of the SPSPA are characterized by the absence/rareness of several species that are common in other Brazilian oceanic islands, such as surgeonfishes (Acanthuridae), parrotfishes (Labridae), snappers (Lutjanidae) and groupers (Epinephelidae), possibly

due to historical (*e.g.*, isolation) and ecological factors (*e.g.*, lack of suitable habitats). The relatively high biomass of mesopredator reef fish (particularly *Caranx lugubris*) in the SPSPA in comparison with other Atlantic and Pacific reef systems, support the hypothesis of mesopredator release following the demise of the Galapagos shark, *Carcharhinus galapagensis*, due to overfishing. The mesophotic zone of the SPSPA may work as a refuge for several species with broad depth distributions, while shallow water specialists may be more susceptible to extinction following global disturbances. The area has no fishery regulations and there is a clear need of implementation of conservation measures.

Keywords: black-corals, *Bodianus insularis*, mesophotic reefs, oceanic islands, *Prognathodes obliquus* and *Stegastes sanctipauli*.

1.2. Introduction

It is now widely recognized that human impacts in the marine environment (*e.g.*, overfishing and pollution) extend well beyond coastal habitats, including remote areas such as the deep sea and isolated oceanic islands (Roberts 2002, Sandin *et al.* 2008a). Shallow rocky and coralline reefs are threatened worldwide by local impacts (mainly pollution, overfishing and sedimentation) and global changes (mainly increased sea surface temperature and acidification) (Bellwood *et al.* 2004, Sala *et al.* 2012).

Mesophotic Reef Ecosystems (MREs) occur in tropical and subtropical regions in depths ranging between 30-150 m. They are considered as extensions of shallow reef communities and may greatly increase availability of suitable habitats for reef organisms (Lesser *et al.* 2009, Hinderstein *et al.* 2010, Harris *et al.* 2013). Although MREs are not immune (Bak *et al.* 2005, Menza *et al.* 2007, Lesser & Slattery 2011), they may be less susceptible to local and global disturbances than shallow reefs, thus possibly functioning as refuges and potential sources of propagules for the biota in shallow threatened reefs (the so called “deep reef refugia” hypothesis; cf. Lesser *et al.* 2009, Bongaerts *et al.* 2010). Despite their importance, MREs remain poorly studied due mainly to logistical challenges, with major gaps in knowledge on community composition, depth range of taxa and other basic biological and ecological aspects (Lesser *et al.* 2009, Khang *et al.* 2010).

Isolated oceanic islands have high endemism levels concentrated in small areas, being recognized as priority areas for biodiversity conservation (Allen 2008, Floeter *et al.* 2008). Although quantitative information on the structure of reef fish assemblages is available for three out of the four Brazilian oceanic islands (Fernando de Noronha Archipelago, Rocas Atoll and the Trindade/Martim Vaz Insular Group) (Rosa & Moura

1997, Minte-Vera *et al.* 2008, Pereira-Filho *et al.* 2011, Pinheiro *et al.* 2011, Krajewski & Floeter 2011), there is only qualitative information for the St. Peter and St. Paul's Archipelago (SPSPA), one of the smallest and most isolated tropical oceanic island in the world (Edwards & Lubbock 1983a, b, Feitoza *et al.* 2003). The SPSPA harbors four recognized endemic reef fish species (*Choranthias salmopunctatus*, *Prognathodes obliquus*, *Enneanectes smithi* and *Stegastes sanctipauli*) (Feitoza *et al.* 2003, Ferreira *et al.* 2009, Anderson & Heemstra 2012) and is an important site for industrial fisheries (Vaske-Jr *et al.* 2006, Hazin *et al.* 2009). Despite its isolation, there is strong evidence of overfishing in the SPSPA (Ferreira *et al.* 2009), which led to the local population extinction of the Galapagos shark *Carcharhinus galapagensis* and sharp decreases in abundance of other shark species (Luiz-Jr & Edwards 2011).

This study provides the first quantitative assessment of reef fish assemblages of the SPSPA. The bottom profile of the archipelago starts with a gentle slope until 20-30 m depth, followed by a nearly vertical wall extending to about 600 m (Thompson 1981), thus offering a unique opportunity to study reef assemblages in a euphotic to mesophotic gradient. Sampling was performed between 0-90 m depth and specific objectives addressed were as follows: 1) describing the composition, body size and trophic structure of reef fish assemblages, 2) evaluating the relative influence of habitat characteristics (depth, benthic cover and complexity) on the structure of fish assemblages, 3) identifying differences/similarities between reef fish assemblages of the SPSPA and other Atlantic and Pacific oceanic reef islands/archipelagos, with emphasis on the hypothesis of mesopredator release in the SPSPA following the demise of the Galapagos shark in the late 90's (Luiz-Jr & Edwards 2011) and 4) evaluate the possible role of the mesophotic zone (30-90 m depth) of the SPSPA as refuge for reef fish based on the abundance and distribution of fish species across the depth gradient.

1.3. Study area

The SPSPA is a small group of five islets and rocks (total emerged area ~15,000 m²) located in the central equatorial Atlantic Ocean, just above the Mid Atlantic Ridge and about 1,000 km off the northeastern Brazilian coast (Figure 1 – 1) (Edwards & Lubbock 1983a, b, Feitoza *et al.* 2003). The SPSPA is influenced by the South Equatorial Current, which flows westward, as well as by the Equatorial Undercurrent, which flows eastward below the surface, in depths between 40-150 m. The area of reefs <100 m depth is about 0.5 km² (Edwards & Lubbock 1983a, b). Shallow rocky reefs of the SPSPA are covered mainly by the zoanthid *Palythoa caribaeorum* and species of algae of the genera *Bryopsis*, *Caulerpa* and *Dictyota*. In depths > 30 m, most common organisms are the scleractinian corals *Madracis decactis* and *Scolymia wellsi*, crustose calcareous algae and bryozoans. Sponges and black-corals of the genus *Tanacetipathes* are relatively abundant in depths > 40 m (Edwards & Lubbock 1983a, b, Feitoza *et al.* 2003).

1.4. Materials and methods

1.4.1. Sampling procedures

Sampling was performed during four expeditions between September 2010 and June 2011, totaling 60 days of fieldwork. Shallow reefs (<30 m depth) were surveyed using SCUBA. Stationary visual census (cf. Minte-Vera *et al.* 2008) and photo-quadrats (cf. Francini-Filho *et al.* 2013) were used to characterize shallow fish and benthic assemblages, respectively. Benthic cover was estimated through the identification of

organisms below 300 randomly distributed points per 0.7 m² quadrat using the Coral Point Count with Excel extensions software (CPCe) (Kohler & Gill 2006).

In the mesophotic zone (30-90 m depth), fish and benthic assemblages were assessed using video footages obtained with a Remote Operated Vehicle (ROV; VideoRay Explorer equipped with a laser scale). Fish abundance was estimated considering approximately the same area (4 m radius) and time (5-min) used in the shallow stationary plots. Relative cover of benthic organisms was quantified from 30 still frames (totaling about 0.7 m²) obtained for each of the 5-min ROV's video sample (i.e. one frame each 10 seconds). The CPCe software was also used, with 10 randomly distributed points used per frame (totaling 300 points per sample unit).

Fish size (total length, TL) was visually estimated for both, stationary plots and video footages, and assigned to one of the following categories: <2, 2-10, 10-20, 20-30, 30-40, >40 cm (cf. Francini-Filho & Moura 2008). The following categories were used in the benthic cover characterizations: bare rock, black-corals, *Caulerpa* spp., crustose calcareous algae, fleshy macroalgae (other than *Caulerpa* spp.), hydrozoans, live scleractinian corals, sediment, turf algae and zoanthids. Benthic complexity was visually estimated for the photo-quadrats and for the ROV video samples by assigning values from 1 to 3, which may be considered a reliable metric considering the gross resolution applied (Wilson *et al.* 2007).

Due to logistical limitations, only one site in the NE coast of the SPSPA was sampled. The NE portion of the archipelago is almost permanently sheltered from the strong waves and currents that act in the other portions of the SPSPA. Despite the lack of site replication, the small area of the SPSPA allowed for the assessment of about 15% of the total perimeter of the archipelago (see Figure 1 – 1), as well as 65% of the

total reef fish species pool known for the area (see Results). A total of 52 5-min ROV video samples, 72 photo-quadrats and 79 stationary visual plots were obtained.

1.4.2. Data analyses

Analyses were performed considering depth strata of 10 m intervals. Samples between 50 and 90 m depth were pooled into a single stratum due to low sample size, thus assuring at least 10 benthic or fish samples per depth stratum. Quantitative analyses were performed for the most abundant species ($> 0.1\%$ of total fish abundance and frequency of occurrence \geq five samples). The 22 species retained for analysis belong to 14 families and represented 97.5% of total fish abundance (Table 2 – 1).

Fish species were classified according to their predominant diet in one of the following trophic categories: roving herbivores, territorial herbivores, invertebrate feeders, omnivores or piscivores (cf. Feitoza et al. 2003, Francini-Filho & Moura 2008, Krajewski & Floeter 2011, Pinheiro *et al.* 2011) (Table 1 – 1).

Analyses were performed using the absolute number of fish individuals recorded per sample. In addition, biomass of mesopredator fish (*Aulostomus strigosus*, Carangidae, Muraenidae, *Rypticus saponaceus* and *Sphyraena barracuda*) was estimated and used to compare shallow fish assemblages of the SPSPA (< 30 m depth) with those from other oceanic Atlantic and Pacific reef systems (considering only similar habitats/depths). Fish counts were converted to biomass using length-weight relationships (Froese & Pauly 2012). Estimates were calculated by multiplying the weight from the midpoint of each size class by the number of fish per size category, and then summing size categories. When length-weight information was not available,

parameters from similarly sized congeners were used (cf. Francini-Filho & Moura 2008).

Size frequency distributions of fish were compared between depth strata using pairwise Kolmogorov-Smirnov tests (Zar 1999). This latter analysis was performed only for fish attaining maximum size ≥ 10 cm TL, as the size resolution used (i.e. 10 cm intervals) did not allow adequate comparisons for relatively small fish. In order to accounting for multiple testing, the Bonferroni correction was applied (Sokal & Rohlf 1995), with alpha set at 0.003 (15 possible pairwise combinations).

One-way analysis of variance (ANOVA) was used to evaluate variations in fish abundance between depth strata and reef systems. In order to attain normality and homocedasticity, fish abundances were converted to $\text{Log}(x+1)$. Student-Newman-Keuls (SNK) multiple comparisons of means were performed as a *post-hoc* test (Zar 1999).

Non-metric multidimensional scaling (MDS) ordination was used to summarize similarities (Bray-Curtis) on the structure of fish assemblages according to depth strata. Analysis of similarities (ANOSIM) was applied to evaluate possible significant differences between groups and the Similar Percentages (SIMPER) analysis was used to identify species mostly contributing to the average similarity within a group, i.e. species typical of each depth stratum (Clarke & Warwick 1994).

Canonical correspondence analysis (CCA) (ter Braak 1996) was used to evaluate the relative influence of habitat characteristics (depth, benthic cover and complexity) on the structure of fish assemblages. A forward selection procedure was used to include only the most important independent variables, i.e. those contributing to increase the explanatory power of the model. Only significant variables, as defined by a Monte Carlo permutation test (999 permutations), were included in the final solution.

1.5. Results

1.5.1. Structure of reef fish assemblages

A total of 35 species belonging to 17 families were recorded (~65% of the reef fish species pool known for the SPSPA) (Feitoza *et al.* 2003, Floeter *et al.* 2008, Ferreira *et al.* 2009) (Table 1 – 1). The top three numerically most abundant species were *Chromis multilineata* (25.4% of total fish abundance), *Melichthys niger* (23.9%) and *Stegastes sanctipauli* (22.0%). Significant differences in abundance between depth strata were recorded for 13 species (Figure 1 – 2). *Aluterus scriptus*, *Cantherhines macrocerus* and *Kyphosus sp.* were recorded exclusively in the shallow zone, while *Prognathodes obliquus*, *Chromis enchrysur* and *Canthidermis sufflamen* were found only in the mesophotic zone. *Halichoeres radiatus*, *Malacoctenus sp.*, *Ophioblennius trinitatis* and *Stegastes sanctipauli* were most abundant in the shallow zone, while *Bodianus insularis* and *Caranx lugubris* were most abundant in the mesophotic zone. The damselfish *Chromis multilineata* showed highest abundance at intermediate depths (20-40 m) (Figure 1 – 2).

The ANOSIM discriminated three fish assemblages associated with the 0-10 m, 10-50 m and 50-90 m depth strata (i.e. no significant differences among samples within each of these strata). However, samples from the 50-90 m depth stratum showed a greater dispersion in the two dimensional diagram than samples from the other strata, with a clear variation according to depth (Figure 1 – 3), suggesting that pooling samples between 50-90 m depth may have masked additional breaks in the structure of fish assemblages. The SIMPER analysis showed that the most typical species of the 0-10 m depth stratum were *S. sanctipauli* and *H. radiatus* (46.6% of cumulative within-group

similarity). *Melichthys niger* and *C. multilineata* characterized the 10-50 m depth stratum (54.5% of cumulative within-group similarity), while *P. obliquus*, *C. enchrysur* and *B. insularis* were typical of the 50-90 m depth stratum (86.2% of cumulative within-group similarity).

A tendency of increased body size with depth was recorded for *H. radiatus* and *Holacanthus ciliaris*, while the opposite pattern was recorded for *B. insularis*. Juveniles of this latter species (<10 cm TL) were recorded almost exclusively below 50 m depth, while relatively large individuals (20-40 cm TL) were most abundant between 10-40 m depth. Individuals < 2 cm TL of *C. multilineata* and *S. sanctipauli*, as well as individuals < 10 cm TL of *Abudefduf saxatilis*, were mostly concentrated in the 0-10 m depth stratum. No clear pattern of change in body size according to depth was recorded for the other species (Figure 1 – 4).

Kolmogorov–Smirnov tests (alpha set at 0.003 after Bonferroni correction). Homogeneous groups within each depth stratum are linked by equal number of signals.

Abundance of roving herbivores, territorial herbivores and invertebrate feeders decreased with depth, while abundance of piscivores showed the opposite pattern. Planktivores were most abundant at intermediate depths (20-40 m). No clear pattern was recorded for omnivores (Figure 1 – 5).

Total biomass of mesopredator fish was $149.2 \pm \text{SE } 48.1 \text{ g.m}^{-2}$. Most abundant mesopredator fish in terms of biomass (>0.5% of total mesopredator biomass) were *C. lugubris* (58.2%), *Caranx latus* (29.2%), *Carangoides crysos* (5.9%), *Sphyrna barracuda* (2.1%), *Rypticus saponaceus* (1.8%), *Muraena pavonina* (1.6%) and *Aulostomus strigosus* (0.7%) (Figure 1 – 6).

1.5.2. Influence of habitat characteristics on the structure of reef fish assemblages

The CCA showed that black-coral cover and depth were, in decreasing order, the main predictors of reef fish assemblage structure. All other independent variables were not significant according to the Monte Carlo test. The first two axes explained nearly 100% of the relationship between habitat characteristics and the structure of fish assemblages. There was a clear gradient of samples following the depth gradient. *Bodianus insularis*, *C. lugubris*, *C. enchrysur* and *P. obliquus* were associated with mesophotic habitats dominated by black-corals. All other species were associated with the shallow zone of the SPSPA (Figure 1 – 7).

1.6. Discussion

The small and isolated Saint Peter and Saint Paul's Archipelago encompasses an impoverished reef fish fauna in comparison with other Atlantic oceanic islands and the Brazilian coast (Floeter *et al.* 2008). Fish assemblages of the SPSPA are marked by the absence/rarity of large piscivorous fish from families Lutjanidae (snappers) and Epinephelidae (groupers), as well as roving herbivores from family Acanthuridae and Labridae (Scarinae and Sparisomatinae), which are relatively common in the other three larger Brazilian oceanic islands (Rosa & Moura 1997, Krajewski & Floeter 2011, Pereira-Filho *et al.* 2011, Pinheiro *et al.* 2011). *Holocentrus adscensionis* is another important reef piscivore (Carr & Hixon 1995, Beets 1997) that is common elsewhere in Brazil (Rosa & Moura 1997, Francini-Filho & Moura 2008, Krajewski & Floeter 2011, Pereira-Filho *et al.* 2011, Pinheiro *et al.* 2011), but rare in the SPSPA. Only a few individuals of the dog snapper *Lutjanus jocu*, the coney *Cephalopholis fulva* and the squirrelfish *H. adscensionis* were sighted during the present surveys, but not recorded

during quantitative sampling. *Lutjanus jocu* and *C. fulva* were classified as rare, while *H. adscensionis* was considered occasional in the SPSPA by Feitoza *et al.* (2003). The absence/rarity of such predators may be explained by historical (*e.g.*, isolation) and ecological factors (*e.g.*, small area and lack of suitable habitats) (Floeter *et al.*, 2008, Moura *et al.*, 2011).

The multivariate techniques employed here suggest major breaks in the structure of reef fish assemblages of the SPSPA in the 10 m and 50 m isobaths. However, the relatively high dispersion of samples from the 50-90 m depth stratum in the MDS diagram suggests that pooling samples between 50-90 m depth may have masked additional breaks in the structure of fish assemblages in depths greater than 50 m. Interestingly, only two vectors (relative cover of black-corals and depth) explained most of the variation in reef fish assemblages' structure, with a tendency of greater influence of depth < 50 m depth and a greater influence of blackcoral cover > 50 m depth (see Fig. 7). The influence of depth in reef fish assemblages is a well-known pattern and may be explained by changes in light, temperature and water motion (*e.g.* McGehee 1994, Brocovich *et al.* 2008, Pereira-Filho *et al.* 2011, Fitzpatrick *et al.* 2012).

The influence of depth may be more pronounced for nearly vertical reef profiles, such as the one sampled here, than for gentle slopes. Colonies of black-corals from the genus *Tanacetipathes* recorded here were relatively large (up to 1.5 m in height) and with branching morphologies, thus greatly increasing substrate complexity. The tridimensional habitat provided by black-corals was clearly used as shelter by *C. enchrysur*, *P. obliquus* and juveniles of *B. insularis* in the mesophotic zone. *Prognathodes obliquus*, which is endemic to the SPSPA, was also recorded grazing over black-coral colonies [see Boland & Parrish (2005) for similar observations on *Forcipiger flavissimus* in Hawaii]. Reef fish species recorded within black-corals in the

mesophotic zone in Hawaii include *Aulostomus chinensis*, *Canthigaster jactator*, *Centropyge potteri*, *Dascyllus albisella*, *Forcipiger flavissimus* and *Oxycirrhites typus*, this latter being considered a nearly obligate black-coral dweller (Boland & Parrish 2005). These results highlight the key roles played by black-corals in the mesophotic zone, as well as the need for additional studies focusing on different aspects of the association between reef fish and branching black-corals.

Ontogenetic shifts in habitat use often occur in reef fish in ways to maximize foraging, reproduction and/or protection against predation (Dahlgren & Eggleston 2000). Ontogenetic trends in the euphotic to mesophotic gradient were previously recorded for reef fish, with juveniles generally concentrated at shallower depths (Colin 1974). In the SPSPA juveniles of *H. radiatus* and *H. ciliaris* were generally sighted seeking refuge around boulders within the inlet. In the Gulf of California, juveniles of *Halichoeres dispilus* were most abundant at shallower depths, where refuge availability was higher, while adults concentrated in mesophotic black-coral dominated habitats to forage (Aburto-Oropeza & Balart 2001). Smaller individuals of *A. saxatilis*, *C. multilineata* and *S. sanctipauli* were concentrated in the 0-10 m depth stratum of the SPSPA. It is suggested here that shallow reefs of the SPSPA, like shallow reef habitats elsewhere (Nagelkerken et al. 2000a, b), work as nurseries for some reef fish species. The opposite trend (i.e. decreased body size with depth) was recorded for *B. insularis*. Several species of *Bodianus* are recognized as having juveniles mostly or exclusively associated with mesophotic habitats (Lobel 1981, Randall & Chen 1985, Sazima et al. 2010). Mesophotic reefs are also important settlement habitats for *Clepticus parrae* (Labridae) and *Chromis insolata* (Pomacentridae) in Isla Desecheo, Puerto Rico (Garcia-Sais 2010). The extent to which different species rely on shallow or deep reefs

for completing their life cycle in isolated oceanic locations is still unknown, with important implications for population maintenance (see below).

Major shifts in trophic structure of reef fish assemblages were recorded across the depth gradient in the SPSPA. The general pattern recorded here (i.e. decreased abundance of herbivores and increased abundance of piscivores with depth, as well as greater abundance of planktivores at intermediate depths), is similar to that recorded in previous studies (e.g. Dennis & Bright 1988, Garcia-Sais 2010). Greater abundance of herbivores in shallow reefs dominated by photosynthetic algae is an expected and widely recognized pattern (Choat 1991), and herbivores are indeed scarce at mesophotic habitats (Kahng *et al.* 2010). Piscivorous fish such as *C. lugubris* are generally more protected from fishing in mesophotic than shallower reefs (Fitzpatrick *et al.* 2012). In addition, reduced light with increasing depth may facilitate prey capture by piscivores (Collete & Talbolt 1972, Hobson 1972).

Garcia-Sais (2010) explained the high abundance of planktivores (particularly *Chromis cyanea*) in the upper limit of the mesophotic zone of Isla Desecheo, Puerto Rico, by the high availability of zooplankton arriving from the shelf edge. Variations in wind regime have been suggested to induce surfacing of the Equatorial Undercurrent in the SPSPA (Bowen 1966). During this study, abrupt drops in temperature of up to 5 °C were recorded in depths between 30-40 m. Therefore, high zooplankton availability coming from the relatively cold Equatorial Undercurrent is a plausible explanation for the increased abundances of planktivores between 20-40 m depth in the SPSPA. While *C. multilineata* was by far the most important species driving this latter pattern, *C. enchrysur* was also a conspicuous element of the fish assemblage between 30-40 m depth. In fact, the genus *Chromis* includes the few pomacentrid species known to occur

at mesophotic habitats, a pattern largely attributed to their diet based in zooplankton (Pyle *et al.* 2008).

Mesophotic reefs are generally considered to be less susceptible to local and global disturbances, such as overfishing, pollution and climate change, than shallow reefs. Thus, they may function as refuges and potential sources of individuals for the biota in shallow and more threatened reefs (the so called “deep reef refugia” hypothesis; Lesser *et al.* 2009, Bongaerts *et al.* 2010). The level of connectivity between shallow and mesophotic zones (via larval dispersal or juvenile/adult migration) is a central question regarding the mesophotic refuge hypothesis, with most benefits expected for species inhabiting both zones (Bongaerts *et al.* 2010, Slattery *et al.* 2011). Half of the reef fish species studied here showed a nearly homogeneous abundance distribution across the euphotic to mesophotic gradient (see Fig. 2). On the other hand, some species may use deep or shallow habitats only in parts of their life cycle, implying they may not survive in case of major disturbances eliminating shallow populations. Species primarily associated with shallow reefs of the SPSPA, such as the herbivores *S. sanctipauli*, *Kyphosus* sp. and *Ophioblennius trinitatis*, may be more susceptible to local extinction than species with broader depth distributions and mesophotic specialists (Fitzpatrick *et al.* 2012). There is a clear need to improve knowledge on levels of connectivity between euphotic and mesophotic reefs, including aspects regarding larval dispersal, genetic connectivity and juvenile/adult migrations (Lesser *et al.* 2009, Slattery *et al.* 2011). *Carcharhinus galapagensis* is a common reef shark in many isolated oceanic locations in the Atlantic (e.g. Randall 1963) and the Pacific (e.g. Papastamatiou *et al.* 2006, Williams *et al.* 2011, Friedlander *et al.* 2013). Historical accounts indicate that the abundance of sharks, particularly *Carcharhinus galapagensis*, was unusually high in the SPSPA (Edwards & Lubbock 1982, Luiz & Edwards 2011). However, there

is strong evidence that the local population of *C. galapagensis* in the SPSPA went extinct in the late 90's due to overfishing (Luiz & Edwards 2011). In fact, no sharks were sighted during the entire period of this study. Luiz & Edwards (2011) suggest that the demise of *C. galapagensis* may have led to increased abundance of the whitespot moray *Muraena pavonina* and carangids in the SPSPA. This is a plausible hypothesis, as *C. galapagensis* is known to frequently include muraenids and carangids in its diet (Wetherbee *et al.* 1996, Papastamatiou *et al.* 2006).

Total biomass of mesopredator fish obtained here was $149.2 \pm \text{SE } 48.1 \text{ g.m}^{-2}$, a relatively high estimate in comparison to those from other areas in the Atlantic and the Pacific. For example, maximum biomass of mesopredator reef fish ranged between about $50\text{-}70 \text{ g.m}^{-2}$ in the Netherlands Antilles, south Caribbean (Sandin *et al.* 2008b). A study conducted at the Pacific-wide scale showed that biomass of piscivorous fish (including sharks) ranged from 9.4 to 231.6 g.m^{-2} at remote areas, and from 0.8 to 9.8 g.m^{-2} at populated islands (Williams *et al.* 2011). In a striking comparison, biomass of *C. lugubris* in the SPSPA ($86.8 \pm 29.2 \text{ g.m}^{-2}$) was about 13 times greater than the biomass of this same species in similar habitats of the Salas y Gómez Island (6.7 g.m^{-2}), a small (0.15 km^2) and isolated area in the south Pacific in which *C. galapagensis* is still relatively abundant (Friedlander *et al.* 2013). Mesopredator release may lead to increased predation pressure upon the small endemic fish species of the SPSPA, raising concern over their conservation (Luiz & Edwards 2011).

The small area and relatively high proportion of endemic species (~10%) make the SPSPA a priority area for biodiversity conservation in the Atlantic (Floeter *et al.* 2008, Ferreira *et al.* 2009). The SPSPA is included within the “Fernando de Noronha/Rocas/São Pedro e São Paulo Environmental Protected Area”, but there are no fishery regulations in place, and this MPA adds to the list of Brazilian “paper parks”

(Moura *et al.* 2013). Considering the importance of the SPSPA and the worldwide trend of escalating threats to rocky and coralline reefs (Bellwood *et al.* 2004, Sala *et al.* 2012), there is an urgent need to implement conservation measures for the SPSPA, such as the establishment of a permanent no-take zone surrounding the archipelago.

1.7. Acknowledgments

We thank E.O.C. Coni, C.M. Ferreira, M. Villela, A.P.B. Moreira, L.S. Rodrigues and D. Sartor for field assistance and data collection. APA Fernando de Noronha/Rocas/São Pedro e São Paulo/ICMBio for providing research permits. The crew of Transmar I and Transmar III, as well as Secretaria de Comissão Interministerial para os Recursos do Mar (SECIRM) for logistical support. Financial support was provided by the Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq (grant 557185/09-2 to RBFF). BPF, FLT, GMAF, PYGS, RBFF and RSR acknowledge individual grants from CNPq. GMAF, FLT and RLM acknowledge individual grants from Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ). MRR acknowledges a doctoral fellowship from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES).

1.8. Literature cited

- Aburto-Oropeza O., Balart E.F. (2001) Community structure of reef fish in several habitats of a rocky reef in the Gulf of California. *Marine Ecology*, 22, 283–305.
- Allen G.R. (2008) Conservation hotspots of biodiversity and endemism for Indo-Pacific coral reef fishes. *Aquatic Conservation Marine and Freshwater Ecosystems*, 18, 541–556.
- Anderson W.D., Heemstra P.C. (2012) Review of Atlantic and Eastern Pacific Anthiine fishes (Teleostei:Perciformes: Serranidae), with descriptions of two new genera. *Transactions of the American Philosophical Society*, 102, 173p.
- Bak R.P.M., Nieuwland G., Meesters E.H. (2005) Coral reef crisis in deep and shallow reefs: 30 years of constancy and change in reefs of Curacao and Bonaire. *Coral Reefs*, 24, 475–479.
- Beets J (1997) Effects of a predatory fish on the recruitment and abundance of Caribbean coral reef fishes. *Marine Ecology Progress Series*, 148, 11–21.
- Bellwood D.R., Hughes T.P., Folke C., Nyström M. (2004) Confronting the coral reef crisis. *Nature*, 429, 827–833.
- Boland R.C., Parrish F.A. (2005) A description of fish assemblages in the black coral beds off Lahaina, Maui, Hawai'i. *Pacific Science*, 59, 411–420.
- Bongaerts P., Ridgeway T., Sampayo E.M., Hoegh-Guldberg O. (2010) Assessing the 'deep reef refugia' hypothesis: focus on Caribbean reefs. *Coral Reefs*, 29, 309–327.

- Bouchon-Navaro Y., Harmelin-Vivien M.L. (1981) Quantitative distribution of herbivorous reef fishes in the Gulf of Aqaba (Red Sea). *Marine Biology*, 63, 79–86.
- Bowen V.T. (1966) St. Paul's on the subway. *Oceanus*, 12, 2–4.
- Brokovich E., Einbinder S., Shashar N., Kiflawi M., Kark S. (2008) Descending to the twilight-zone: coral reef fish assemblages change along a depth gradient down to 65 m. *Marine Ecology Progress Series*, 371, 253–262.
- Carr M.H., Hixon M.A. (1995) Predation effects on early post-settlement survivorship of coral-reef fishes. *Marine Ecology Progress Series*, 124, 31–42.
- Choat J.H. (1991) The biology of herbivorous fishes on coral reefs. In: Sale PF (Ed) *The ecology of fishes on coral reefs*. Academic Press, San Diego: 120-155.
- Clarke K.R., Warwick R.M. (1994) *Change in marine communities: an approach to statistical analysis and interpretation*. Plymouth Marine Laboratory: Plymouth.
- Colin P.L. (1974) Observation and collection of deep reef fishes off the coasts of Jamaica and Honduras. *Marine Biology*, 24, 29–38.
- Collette B.B., Talbolt F.H. (1972) Activity patterns of coral reef fishes with emphasis on nocturnal-diurnal changeover. *Natural History Museum of Los Angeles County*, 14, 98–124.
- Dahlgren C.P., Eggleston D.B. (2000) Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology*, 81, 2227–2240.
- Dennis G.D., Bright T.J. (1988) Reef fish assemblages on hard banks in the northwest Gulf of Mexico. *Bulletin of Marine Science*, 43, 280–307.

- Edwards A.J., Lubbock H.R. (1982) The shark population of Saint Paul's Rocks. *Copeia*, 1, 223–225.
- Edwards A., Lubbock R. (1983a) Marine zoogeography of St. Paul's Rocks. *Journal of Biogeography*, 10, 65–72.
- Edwards A., Lubbock R. (1983b) The ecology of Saint Paul's Rocks (Equatorial Atlantic). *Journal of Zoology*, 200, 51–69.
- Feitoza B.M., Rocha L.A., Luiz O.J., Floeter S.R., Gasparini J.L. (2003) Reef fishes of St. Paul's Rocks: new records and notes on biology and zoogeography. *Aqua Journal of Ichthyology and Aquatic Biology*, 7, 61–82.
- Ferreira C.E.L., Luiz-Jr O.J., Feitoza B., Ferreira C.G.W., Gasparini J.L., Noguchi R.C., Godoy E.A., Joyeux, J.C., Rangel C.A., Rocha L.A., Floeter S.R., Carvalho-Filho A. (2009) Peixes recifais: síntese do atual conhecimento. In: Viana D.L., Hazin F.H.V., Souza M.A.C. (Eds.). *O Arquipélago de São Pedro e São Paulo: 10 anos de estação científica*. Brasília, SECIRM: 244-340.
- Fitzpatrick B.M., Harvey E.S., Heyward A.J., Twiggs E.J., Colquhoun J. (2012) Habitat specialization in tropical continental shelf demersal fish assemblages. *PLoS ONE*, 7, e39634.
- Floeter S.R., Rocha L.A., Robertson D.R., Joyeux J.C., Smith-Vaniz W.F., Wirtz P., Edwards A.J., Barreiros J.P., Ferreira C.E.L., Gasparini J.L., Brito A., Falcón J.M., Bowen B.W., Bernardi G. (2008) Atlantic reef fish biogeography and evolution. *Journal of Biogeography*, 35, 22–47.

- Francini-Filho R.B., Moura R.L. (2008) Dynamics of fish assemblages on coral reefs subjected to different management regimes in the Abrolhos Bank, eastern Brazil. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 18, 1166–1179.
- Francini-Filho R.B., Coni E.O.C., Meirelles P.M., Amado-Filho G.M., Thompson F.L., Pereira-Filho G.H., Bastos A.C., Abrantes D.P., Ferreira C.M., Gibran F.Z., Güth A.Z., Sumida P.Y.G., Oliveira N.L., Kaufman L., Minte-Vera C.V., Moura R.L. (2013) Dynamics of coral reef benthic assemblages of the Abrolhos Bank, eastern Brazil: inferences on natural and anthropogenic drivers. *PLoS ONE*, 8, e54260.
- Friedlander A.M., DeMartini E.E. (2002) Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian Islands: the effects of fishing down apex predators. *Marine Ecology Progress Series*, 230, 253–264.
- Friedlander A.M., Ballesteros E., Beets J., Berkenpas E., Gaymer C.F., Gorny M., Sala E. (2013) Effects of isolation and fishing on the marine ecosystems of Easter Island and Salas y Gómez, Chile. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 23, 515–531.
- Froese R, Pauly D (Eds) (2006) FishBase. <http://www.fishbase.org>. Version June 13 2013.
- Garcia-Sais J.R. (2010) Reef habitats and associated sessile-benthic and fish assemblages across a euphotic-mesophotic depth gradient in Isla Desecheo, Puerto Rico. *Coral Reefs*, 29, 277–288.
- Harris P.T., Bridge T.C.L., Beaman R.J., Webster J.M., Nichol S.L., Brooke B.P. (2013) Submerged banks in the Great Barrier Reef, Australia, greatly increase available coral reef habitat. *ICES Journal of Marine Science*, 70, 284–293.

- Hazin F.H.V., Viana D., Pinheiro P., Fischer A., Macena B., Vêras D., Oliveira P., Carvalho F., Vaske-Jr T., Branco I. (2009) Ecologia de grandes peixes pelágicos. In: Viana DL, Hazin FHV, Souza MAC (Eds.). O Arquipélago de São Pedro e São Paulo: 10 anos de estação científica. Brasília, SECIRM: 226-233.
- Hinderstein L.M., Marr J.C.A., Martinez F.A., Dowgiallo M.J., Puglise K.A., Pyle R.L., Zawada D.G., Appeldoorn R. (2010) Introduction to mesophotic coral ecosystems: characterization, ecology, and management. *Coral Reefs*, 29, 247–251.
- Hobson E.S. (1972) Activity of Hawaiian reef fishes during the evening and during transition between daylight and darkness. *Fishery Bulletin*, 70, 715–740.
- Kahng S.E., Spalding H.L., Brokovich E., Wagner D., Weil E., Hinderstein L., Toonen R.J. (2010) Community ecology of mesophotic coral reef ecosystems. *Coral Reefs*, 29, 255–275.
- Kohler K.E., Gill S.M. (2006) Coral Point Count with Excel extensions (CPCe): A visual basic program for the determination of coral and substrate coverage using random point count methodology. *Computers & Geosciences*, 32, 1259–1269.
- Krajewski J.P., Floeter S.R. (2011) Reef fish community structure of the Fernando de Noronha Archipelago (Equatorial Western Atlantic): the influence of exposure and benthic composition. *Environmental Biology of Fishes*, 92, 25–40.
- Lesser M.P., Slattery M. (2011) Invasive lionfish causes a phase shift to algal dominated communities at mesophotic depths on a Bahamian coral reef. *Biological Invasions*, 13, 1855–1868.

- Lesser M.P., Slattery M., Leichter J.J. (2009) Ecology of mesophotic coral reefs. *Journal of Experimental Marine Biology and Ecology*, 375, 1–8.
- Lobel P.S. (1981) *Bodianus prognathus* (Labridae, Pisces), a new longnose hogfish from the Central Pacific. *Pacific Science*, 35, 45–50.
- Luiz-Jr O., Edwards A.L. (2011) Extinction of a shark population in the Archipelago of Saint Paul's Rocks (equatorial Atlantic) inferred from the historical record. *Biological Conservation*, 144, 2873–2881.
- McGehee M.A. (1994) Correspondence between assemblages of coral reef fishes and gradients of water motion, depth, and substrate size off Puerto Rico. *Marine Ecology Progress Series*, 105, 243–255.
- Menza C., Kendall M., Rogers C., Miller J. (2007) A deep reef in deep trouble. *Continental Shelf Research*, 27, 2224–2230.
- Minte-Vera C.V., Moura R.L., Francini-Filho R.B. (2008) Nested sampling: an improved visual-census technique for studying reef fish assemblages. *Marine Ecology Progress Series*, 367, 283–293.
- Moura R.L., Francini-Filho R.B., Chaves E.M., Minte-Vera C.V., Lindeman K. (2011) Use of riverine through reef habitat systems by dog snapper (*Lutjanus jocu*) in eastern Brazil. *Estuarine, Coastal and Shelf Science*, 95, 274–278.
- Moura R.L., Secchin N.A., Amado-Filho G.M., Francini-Filho R.B., Freitas M.O., Minte-Vera C.V., Teixeira J.B., Thompson F.L., Dutra G.F., Sumida P.Y.G., Guth A.Z., Lopes R.M., Bastos A.C. (2013) Spatial patterns of benthic megahabitats and conservation planning in the Abrolhos Bank. *Continental Shelf Research*, DOI:10.1016/j.csr.2013.04.036.

- Nagelkerken I., van der Velde G., Gorissen M.W., Meijer G.J., van't Hof T., den Hartog C. (2000a) Importance of mangroves, seagrass beds, and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. *Estuarine, Coastal and Shelf Science*, 51, 31–44.
- Nagelkerken I., Dorenbosch M., Verberk W.C.E.P., Cocheret de la Morinière E., van der Velde G. (2000b) Importance of shallow-water biotopes of a Caribbean bay for juvenile coral reef fishes: Patterns in biotope association, community structure and spatial distribution. *Marine Ecology Progress Series*, 202, 175–192.
- Papastamatiou Y.P., Wetherbee B.M., Lowe C.G., Crow, G.L. (2006) Distribution and diet of four species of carcharhinid shark in the Hawaiian Islands: evidence for resource partitioning and competitive exclusion. *Marine Ecology Progress Series*, 320, 239-251.
- Pereira-Filho G.H., Amado-Filho G.M., Guimarães S.M.P.B., Moura R.L., Sumida P.Y.G., Abrantes D.P., Bahia R.G., Guth A.Z., Jorge R.R., Francini Filho R.B. (2011) Reef fish and benthic assemblages of the Trindade and Martin Vaz island group, southwestern Atlantic. *Brazilian Journal of Oceanography*, 59, 201–212.
- Pinheiro H.T., Ferreira C.E.L., Joyeux J.C., Santos R.G., Horta P.A. (2011) Reef fish structure and distribution in a south-western Atlantic Ocean tropical island. *Journal of Fish Biology*, 79, 1984–2006.
- Pyle R.L., Early J.L., Greene B.D. (2008) Five new species of the damselfish genus *Chromis* (Perciformes: Labroidae: Pomacentridae) from deep coral reefs in the tropical western Pacific. *Zootaxa*, 1671, 3–31.

- Randall J.E. (1963) A fatal attack by the shark *Carcharhinus galapagensis* at St. Thomas, Virgin Islands. *Caribbean Journal of Science*, 3, 201–205.
- Randall R.E., Chen C. (1985) First Record of the labrid fish *Bodianus cylindriatus* (Tanaka) from the Hawaiian Islands. *Pacific Science*, 39, 291–293.
- Roberts C.M. (2002) Deep impact: the rising toll of fishing in the deep sea. *Trends in Ecology & Evolution*, 17, 242–245.
- Rosa R.S., Moura R.L. (1997) Visual assessment of reef fish community structure in the Atol das Rocas Biological Reserve, off north-eastern Brazil. *Proceedings of the 8th International Coral Reef Symposium*, 1, 983–986.
- Sala E., Ballesteros E., Dendrinos P., Di Franco A., Ferretti F., Foley D., Fraschetti S., Friedlander A., Garrabou J., Güçlüsoy H., Guidetti P., Halpern B.S., Hereu B., Karamanlidis A.A., Kizilkaya Z., Macpherson E., Mangialajo L., Mariani S., Micheli F., Pais A., Riser K., Rosenberg A.A., Sales M., Selkoe K.A., Starr R., Tomas F., Zabala M. (2012) The structure of Mediterranean rocky reef ecosystems across environmental and human gradients, and conservation implications. *PLoS ONE*, 7, e32742.
- Sandin S.A., Smith J.E., DeMartini E.E., Dinsdale E.A., Donner S.D., Friedlander A.M., Konotchick T., Malay M., Maragos J.E., Obura D., Pantos O., Paulay G., Richie M., Rohwer F., Schroeder R.E., Walsh S., Jackson J.B.C., Knowlton N., Sala E. (2008a) Baselines and degradation of coral reefs in the northern Line Islands. *PLoS ONE*, 3, e1548.

- Sandin S.A., Sampayo E.M., Vermeij M.J.A. (2008b) Coral reef fish and benthic community structure of Bonaire and Curaçao, Netherlands Antilles. *Caribbean Journal of Science*, 44, 137-144.
- Sazima I., Grossman A., Sazima C. (2010) Deep cleaning: a wrasse and a goby clean reef fish below 60 m depth in the tropical south-western Atlantic. *Marine Biodiversity Records*, 3, e60-3.
- Slattery M., Lesser M.P., Brazeau D., Stokes M.D., Leichter J.J. (2011) Connectivity and stability of mesophotic coral reefs. *Journal of Experimental Marine Biology and Ecology*, 408, 32–41.
- Sokal R.R., Rohlf F.J. (1995) *Biometry: The principles and practice of statistics in biological research*. Third edition, Freeman, New York
- Ter Braak C.J.F. (1996) *Unimodal methods to relate species to environment*. Centre for Biometry Wageningen (DLO Agricultural Mathematics Group), Wageningen, the Netherlands.
- Thompson G. (1981) St. Peter and St. Paul's Rocks (Equatorial Atlantic) and the surrounding sea floor. Woods Hole Oceanographic Institute Technical Reports, WHOI-81-98.
- Vaske-Jr. T, Lessa R.P.T., Ribeiro A.C.B., Nóbrega M.F., Pereira A.A., Andrade C.D.P. (2006) A pesca comercial de peixes pelágicos no arquipélago de São Pedro e São Paulo, Brasil. *Tropical Oceanography*, 34, 31–41.
- Wetherbee B.M., Crow G.L., Lowe C.G. (1996) Biology of the Galapagos shark, *Carcharhinus galapagensis*, in Hawai'i. *Environmental Biology of Fishes*, 45, 299-310.

- Williams I.D., Richards B.L., Sandin S.A., Baum J.K., Schroeder R.E., Nadon M.O., Brainard R.E. (2010) Differences in reef fish assemblages between populated and remote reefs spanning multiple archipelagos across the central and western Pacific. *Journal of Marine Biology*, ID 826234, doi:10.1155/2011/826234.
- Wilson S.K., Graham N.A.J., Polunin N.V.C. (2007) Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Marine Biology*, 151, 1069 – 1076.
- Zar J.H. (1999) *Biostatistical analysis*, 4th edition. New Jersey: Prentice-Hall.

1.9. Legend for figures

Figure 1 – 1. Map showing: A) the location of the St. Peter and St. Paul's Archipelago (SPSPA) and other Brazilian oceanic islands in the South Atlantic Ocean, as well as the coastal area of the Abrolhos Bank and B) Detail of the SPSPA showing the study area (light grey).

Figure 1 – 2. Fish abundance (mean + SE) across the depth gradient. ANOVA results: *P < 0.05, **P < 0.01, ***P < 0.001, ns - not significant. Homogeneous groups are identified by equal letters.

Figure 1 – 3. Non-metric multi-dimensional scaling (MDS) ordination based on similarities (Bray-Curtis) in fish abundance between three distinct depth strata as defined by Analysis of Similarities (ANOSIM) (see Results).

Figure 1 – 4. Size frequency distribution of fish across the depth gradient. Significant differences in size distribution were determined using pairwise Kolmogorov–Smirnov tests (alpha set at 0.003 after Bonferroni correction). Homogeneous groups within each depth stratum are linked by equal number of signals.

Figure 1 – 5. Abundance (mean + SE) of fish within different trophic categories across the depth gradient. ANOVA results: *P < 0.05, **P < 0.01, ***P < 0.001, ns - not significant. Homogeneous groups are identified by equal letters.

Figure 1 – 6. Biomass (mean + SE) of piscivorous fish in three Brazilian locations: the St. Peter and St. Paul's Archipelago (SPSPA), the Trindade/Martim Vaz Insular Group (TMVIG) and the coastal no-take zone of the National Marine Park of Abrolhos

(Abrolhos Archipelago plus Parcel dos Abrolhos Reef). ANOVA results: $P < 0.001$ in all cases. Homogeneous groups are identified by equal letters.

Figure 1 – 7. Canonical Correspondence Analysis (CCA) plot showing (A) habitat characteristics and depth strata, and (B) fish species. Abbreviations of species names: genus indicated by tree first letter and specific epithet by the tree following letters (see full names in Table 1).

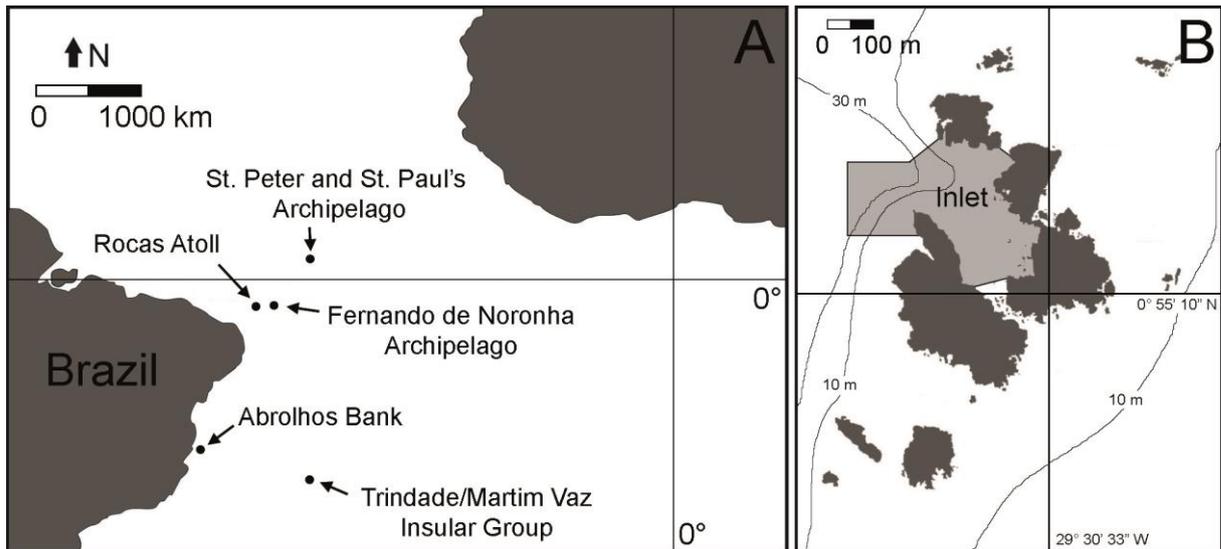


Figure 1 – 1.

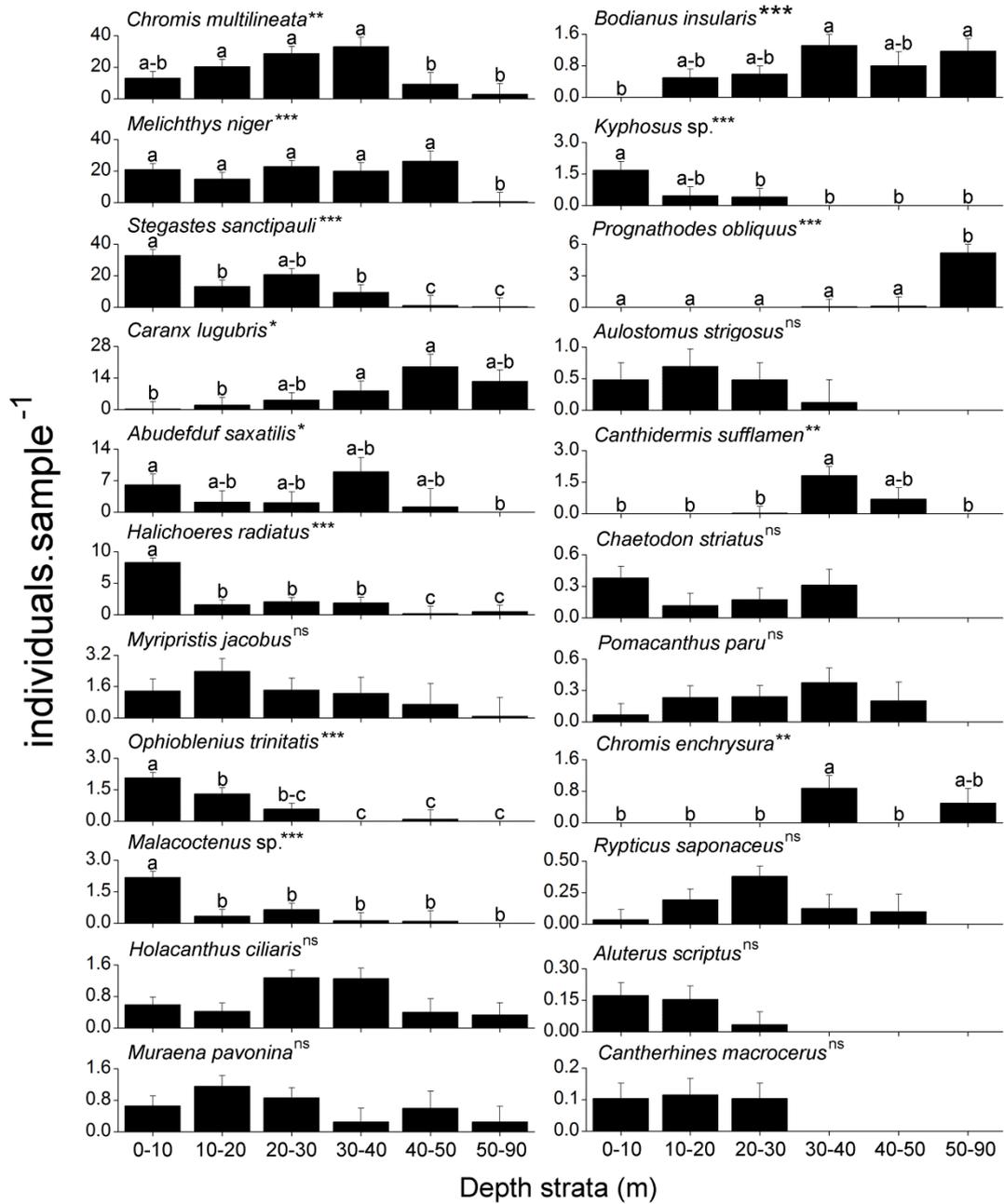


Figure 1 – 2.

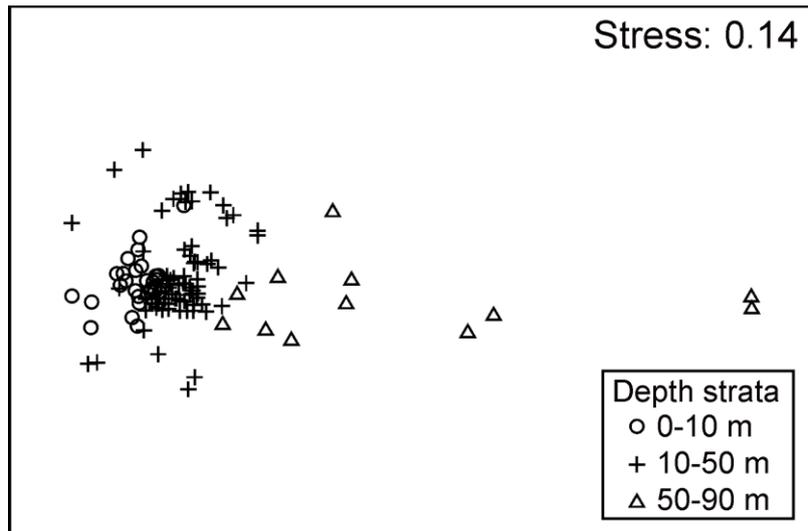


Figure 1 – 3.

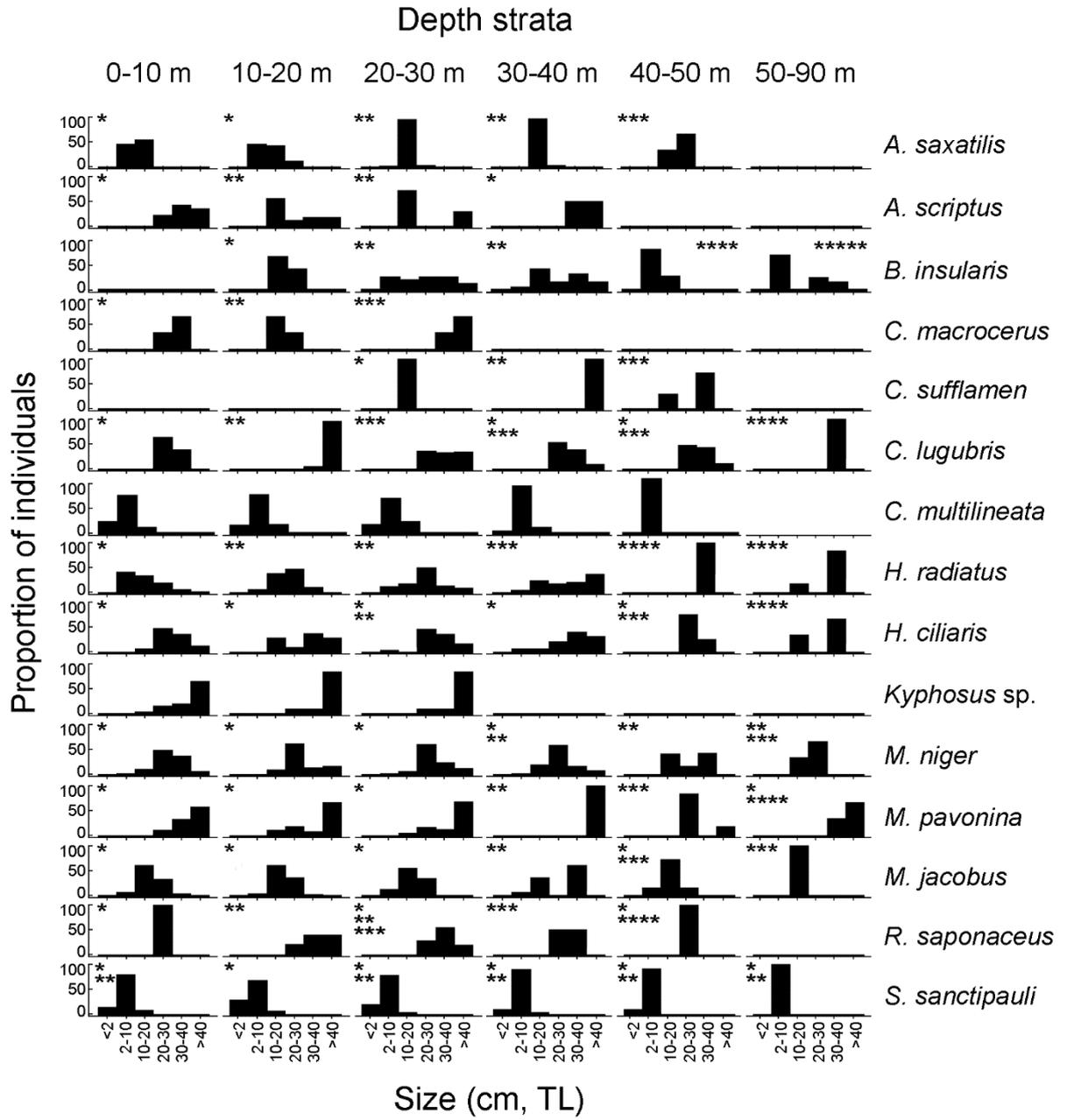


Figure 1 – 4.

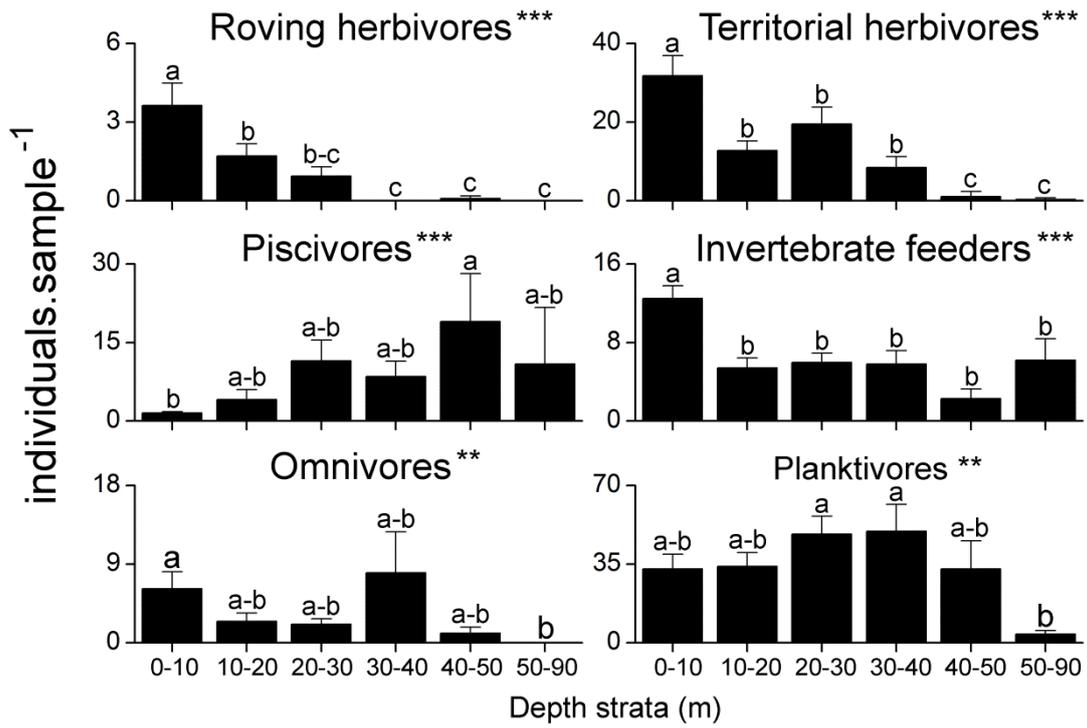


Figure 1 – 5.

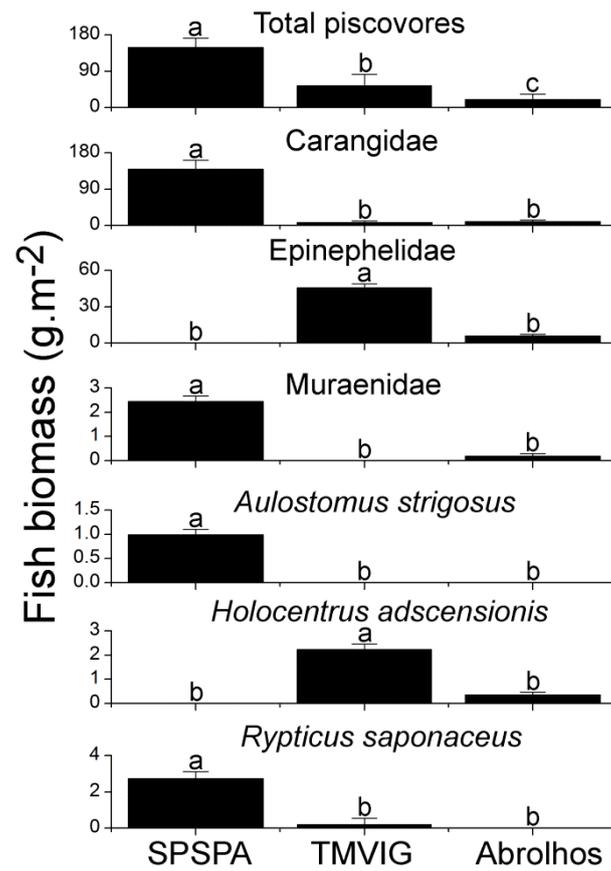


Figure 1 – 6.

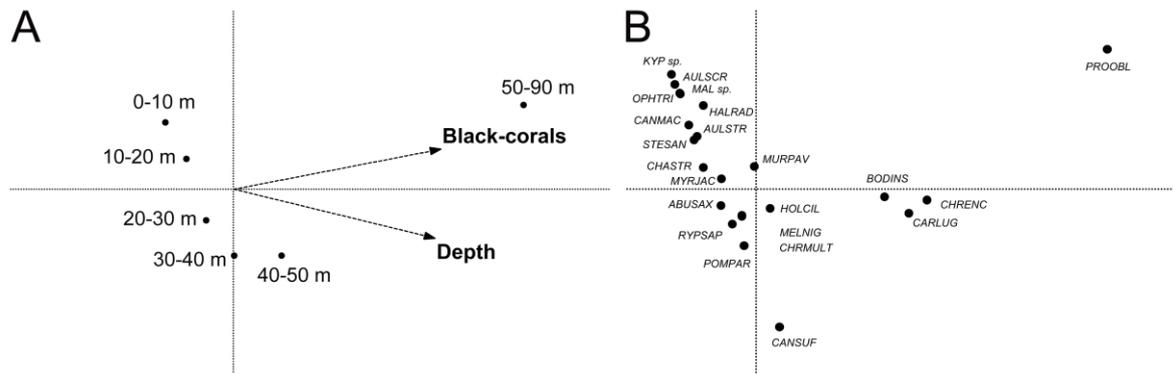


Table 1 – 1. Reef fish species recorded in the St. Peter and St. Paul's Archipelago and their respective trophic groups. N – Total number of individuals recorded, FO – frequency of occurrence in samples. Species arranged according to total N. Bold denotes species retained for quantitative analyses (see text).

| Family | Species | N | FO | Trophic group |
|-----------------------|----------------------------------------|-------------|-----------|------------------------------|
| Pomacentridae | <i>Chromis multilineata</i> | 2393 | 78 | Planktivore |
| Balistidae | <i>Melichthys niger</i> | 2247 | 96 | Omnivore |
| Pomacentridae | <i>Stegastes sanctipauli</i> | 2071 | 85 | Territorial herbivore |
| Carangidae | <i>Caranx lugubris</i> | 657 | 37 | Piscivore |
| Pomacentridae | <i>Abudefduf saxatilis</i> | 454 | 55 | Omnivore |
| Labridae | <i>Halichoeres radiatus</i> | 381 | 77 | Invertebrate feeder |
| Holocentridae | <i>Myripristis jacobus</i> | 171 | 34 | Planktivore |
| Carangidae | <i>Caranx latus</i> | 130 | 2 | Piscivore |
| Blenniidae | <i>Ophioblennius trinitatis</i> | 112 | 41 | Territorial herbivore |
| Labrisomidae | <i>Malacoctenus</i> sp. | 94 | 29 | Invertebrate feeder |
| Pomacanthidae | <i>Holacanthus ciliaris</i> | 93 | 50 | Invertebrate feeder |
| Muraenidae | <i>Muraena pavonina</i> | 87 | 44 | Piscivore |
| Labridae | <i>Bodianus insularis</i> | 73 | 33 | Invertebrate feeder |
| Kyphosidae | <i>Kyphosus</i> sp. | 73 | 20 | Roving herbivore |
| Chaetodontidae | <i>Prognathodes obliquus</i> | 64 | 9 | Invertebrate feeder |
| Carangidae | <i>Carangoides crysos</i> | 58 | 3 | Piscivore |
| Aulostomidae | <i>Aulostomus strigosus</i> | 48 | 21 | Piscivore |
| Balistidae | <i>Canthidermis sufflamen</i> | 37 | 7 | Planktivore |
| Chaetodontidae | <i>Chaetodon striatus</i> | 24 | 13 | Invertebrate feeder |
| Pomacanthidae | <i>Pomacanthus paru</i> | 23 | 14 | Omnivore |
| Pomacentridae | <i>Chromis enchrysur</i> | 20 | 6 | Planktivore |
| Serranidae | <i>Rypticus saponaceus</i> | 20 | 17 | Piscivore |
| Monacanthidae | <i>Aluterus scriptus</i> | 10 | 8 | Omnivore |
| Carangidae | <i>Carangoides bartholomaei</i> | 10 | 1 | Piscivore |
| Monacanthidae | <i>Cantherhines macrocerus</i> | 9 | 9 | Omnivore |
| Serranidae | <i>Choranthias salmopunctatus</i> | 8 | 1 | Planktivore |
| Labridae | <i>Clepticus brasiliensis</i> | 7 | 2 | Planktivore |
| Sphyraenidae | <i>Sphyraena barracuda</i> | 7 | 4 | Piscivore |
| Carangidae | <i>Elagatis bipinnulata</i> | 4 | 2 | Invertivore |
| Muraenidae | <i>Channomuraena vittata</i> | 2 | 1 | Piscivore |
| Muraenidae | <i>Gymnothorax miliaris</i> | 2 | 2 | Piscivore |
| Balistidae | <i>Balistes vetula</i> | 1 | 1 | Invertebrate feeder |
| Muraenidae | <i>Gymnothorax funebris</i> | 1 | 1 | Piscivore |
| Blenniidae | <i>Scartella itajobi</i> | 1 | 1 | Territorial herbivore |
| Labridae | <i>Thalassoma noronhanum</i> | 1 | 1 | Omnivore |

Chapter 2

This chapter was submitted for publication in Bulletin of Marine Science. The leading author is Gabriela Machado Magalhães. Gilberto Menezes Amado-Filho, Marcos Rogerio Rosa, Rodrigo Leão de Moura, Poliana Silva Brasileiro, Fernando Coreixas de Moraes, Ronaldo Bastos Francini-Filho, Guilherme Henrique Pereira-Filho are coauthors.

Changes in benthic communities across a depth gradient in the remote St. Peter and St. Paul Archipelago (Mid-Atlantic Ridge, Brazil): The influence of biotic and abiotic factors

2.1. Abstract

Isolated reefs are usually characterised by a high fish biomass and by benthic communities dominated by reef-building organisms. This study presents the first detailed quantitative assessment of benthic communities across an abrupt depth gradient (euphotic to mesophotic) on one of the smallest and most isolated rocky reefs in the world, the St. Peter and St. Paul Archipelago (SPSPA). The influence of biotic (i.e., the abundance of fish trophic groups) and abiotic (i.e., benthic complexity, depth and light) variables on the structure of the benthic communities was evaluated. SCUBA and a Remotely Operated Vehicle were used to access shallow (<30 m) and mesophotic reefs (30-60 m), respectively. We recorded 77 benthic taxa belonging to six groups

(macroalgae, Porifera, Cnidaria, Annelida, Bryozoa and Tunicata). Macroalgae was the richest group (41 infrageneric taxa), with 17 new records for the SPSPA. Turf algae were the most abundant group on both shallow and mesophotic reefs. However, of the 26 turf-forming species, only eight occurred deeper than 30 m. Despite the high coverage of turf algae across the entire depth gradient, two distinct communities were detected: a shallow one composed primarily by the zoanthid *Palythoa caribaeorum* (Duchassaing and Michelotti, 1861), the fleshy alga *Caulerpa racemosa* (Forsskål) J. Agardh, crustose coralline algae (CCA) and *Bryopsis* spp., and another deeper community dominated by CCA, bryozoans and scleractinian corals. Abiotic variables were the most important predictors of benthic community structure. The data presented do not support the hypothesis that substantial changes have occurred since the 70's. However, a long-term monitoring programme is suggested.

Key words: Black-corals, endemic reef fish, mesophotic reef ecosystems, reef ecology, substrate cover, *Tanacetipathes hirta* and *T. tamnea*.

2.2. Introduction

Benthic reef communities are highly dynamic as a result of natural variations in predation, competition for space, the frequency of disturbance (e.g., storms, hurricanes and earthquakes) and physical factors, such as wave energy, temperature and light (Hughes 1989, Hughes and Connel 1999, Mumby and Steneck 2008). For example, the irradiance of photosynthetically active radiation (PAR) in the Bahamas is approximately $2,100 \mu\text{mol m}^{-2} \text{sec}^{-1}$ at the sea surface and only $45 \mu\text{mol m}^{-2} \text{sec}^{-1}$ at 100 m depth (Lesser et al. 2010). As a consequence of light variation, the distribution of autotrophic organisms, such as algae and scleractinian corals, is highly influenced by depth (e.g., Huston 1985, Francini-Filho et al. 2013).

Reef-building organisms (e.g., scleractinian corals and crustose coralline algae) are primarily found in shallow waters (<30 m depth) due to light limitations. However, some of these organisms can be found at depths between 30 and 150 m, where they compete for space with non-autotrophic organisms, such as black corals and sponges (Reed and Pomponi 1997). Because of their depth range and the presence of both photosynthetic and non-photosynthetic organisms, reefs from 30-150 m are recognised as Mesophotic Reef Ecosystems (MREs), which generally represent extensions of shallow reefs (Lesser et al. 2009, Hinderstein et al. 2010).

MREs harbour species that are particularly associated with this habitat (i.e., mesophotic specialists) and species that also occur on shallow reefs (“depth generalists”; Hinderstein et al. 2010). Thus, MREs represent potentially important refugia; additionally, they represent sources/sinks for shallow-water populations of many reef taxa (the so-called “deep reef refugia” hypothesis) (Slattery et al. 2011, Slattery and Lesser 2012). These ecosystems are relatively less susceptible to anthropogenic disturbances but are not immune to human impacts (Hinderstein et al.

2010). For example, although reefs in Curaçao and Bonaire have been described as lacking human impacts deeper than 30-40 m (Bak et al. 2005), recent evidence suggests that MREs may suffer with extreme weather (White et al. 2013) and invasive species (Lesser and Slattery 2011).

MREs occur at continental shelf breaks as well as around oceanic islands/archipelagos and seamounts (Kahng et al. 2010, Pereira-Filho et al. 2012). In Brazil, there are four major oceanic reef systems: one built primarily by coralline algae (Rocas Atoll) (Figueiredo et al. 2008, Fonseca et al. 2012) and three archipelagos associated with rocky bottoms (Fernando de Noronha, Trindade/Martin Vaz and St. Peter and St. Paul Archipelago (SPSPA)). At both Fernando de Noronha and Trindade/Martin Vaz, the MREs are primarily horizontal and are formed by free-living coralline algae (rhodolith beds) interspersed with a number of rocky reefs (Amado-Filho et al. 2012, Pereira-Filho et al. 2011). In contrast, the MREs of the SPSPA are exclusively formed by rocks. The rocky reefs of the SPSPA show a nearly vertical slope starting at a depth of approximately 30 m with an abrupt gradient from the shallows downwards to the mesophotic zone. Thus, the SPSPA provides a unique opportunity to evaluate the influence of depth on the structure of benthic communities across a depth gradient including both shallow and mesophotic zones.

Although the SPSPA is one of the world's smallest and most isolated oceanic reefs (Edwards and Lubbock 1983a, b, Serafini et al. 2010), evidence indicates that the archipelago suffers from overfishing, which has resulted in the local extinction of the top predator *Charcharinus galapagensis* (Snodgrass and Heller, 1905) (Ferreira et al. 2009, Luiz-Jr and Edwards 2011). In the Mediterranean, predatory fishes play critical roles in controlling the abundance of herbivores (Sala et al. 2012). Increased grazing activity of herbivores in predation-free areas is recognised as a major driver of shifts in

dominance, resulting in transitions from erect algal assemblages to coralline barrens (Sala et al. 1998).

Grouping macroalgae species into defined morphological categories based on their growth type, morphology and, thus, on their ecological function has become a very popular approach to examine several types of disturbance impact on benthic communities (e.g. Littler and Littler 1980, Steneck and Dethier 1994, Lacey et al. 2013). However, morphological categories may be subject to certain degree of subjectivity and does not agree with phylogenetic relationships (Balata et al 2011). For example, turfs are composed by an aggregate of some filamentous growth type morphology that can be from different evolutionary lineages (Littler and Littler 1980, Steneck and Dethier 1994). However, red algae (Rhodophyta) are more common than green (Chlorophyta) and brown (Phaeophyceae) at greater depths (Kirk 1994). This can be explained, in part, because of the red pigments (Phycoerythrin) has a higher absorption efficiency for blue and green wavelengths, which penetrate deeper in the oceans (Hanelt et al. 2003). Even on the light of this knowledge, many filamentous algae are still nowadays treated as turf forming algae, independently of its evolutionary history (e.g. Sandin et al. 2008, Fraschetti et al. 2012, Sala et al. 2012).

Balata et al. (2011) proposed an expansion to the morphological groups proposed by Steneck and Dethier (1994) that takes in account evolutionary lineages, thallus structure, growth form and branching pattern. In additions, these authors showed that turf assemblages are much more complex than it was believed and its high abundance are not always related to depredated sites as it has been largely considered (see also Bruno et al. 2013).

In this study, we used the most world's smallest and most isolated oceanic rocky reefs with recent evidences of overfishing as model; and the morphological functional

groups of marine macroalgae proposed by Balata et al. (2011) to test the hypothesis that MREs are less susceptible to anthropogenic changes. In addition, we present the first detailed quantitative assessment of the benthic communities of both the shallow and mesophotic reefs of the SPSPA. We also evaluated the influence of biotic (i.e., the abundance of fish trophic levels) and abiotic variables (i.e., benthic complexity, depth and PAR) in predicting benthic community structure across an abrupt gradient of depth up to 60 m. In addition, we discuss the importance of continuous monitoring programmes on isolated reefs for understanding the decline of reef systems as a consequence of anthropogenic global changes.

2.3. Methods

The SPSPA is a remote group of five islets located on the Mid-Atlantic Ridge, approximately 1,000 km from the Brazilian northeast mainland (Figure 2 – 1A). The reef area at depths shallower than 100 m is approximately 0.5 km². The archipelago is under the influence of both the South Equatorial Current (between 0-40 m and westwards) and the Equatorial Undercurrent (between 40-150 m and eastwards) (Edwards and Lubbock 1983a, b).

Two expeditions were conducted on September 2010 and May 2011, including a total of 30 days of fieldwork. We used both SCUBA and a Remotely Operated Vehicle (ROV) to access shallow (<30 m) and mesophotic reefs (30-60 m depth), respectively. Stratified random sampling was performed, with at least 10 samples obtained per depth stratum (5-10, 10-20, 20-30, 30-40, 40-50 and 50-60 m). A HOBO UA-002-64 (Onset Company) data logger system was used to measure the photosynthetically active radiation (PAR) along the depth gradient.

All samples were obtained on the NW side of the SPSPA (Figure 2 – 1B) from the cove to the nearby vertical wall. This area is characterised by a small inlet (approximately 4,500 m²) with a nearly horizontal slope down to 20 m depth followed by an abrupt vertical wall (Figure 2 – 1C and 2 – 2A). The PAR values near the sea surface ranged between 4,500 and 3,500 $\mu\text{mol m}^2 \text{s}^{-1}$. Only 10 % of the surface irradiance reached a depth of 5 m, and less than 2 % (i.e., 70 $\mu\text{mol m}^2 \text{s}^{-1}$) reached 30 m. At depths greater than 30 m, the decrease in light was less pronounced, with 0.4 % of PAR reaching a depth of 60 m (Figure 2 – 1C).

Due to logistical limitations, we did not survey other sites around the SPSPA. However, the area sampled represents 15 % of the perimeter of the archipelago and encompassed 80 % and 51 % of the total species richness known for benthic algae and sponges, respectively (see Results).

In the shallow zone, we obtained photo-quadrats (cf. Francini-Filho et al. 2013) and a stationary visual census (cf. Minte-Vera et al. 2008) that were used to characterise benthic communities and fish functional groups (see below), respectively. Benthic cover was estimated through the identification of organisms (at the lowest possible taxonomic level) below 300 randomly distributed points per 0.7 m² quadrat using the Coral Point Count with Excel Extensions software (CPCe v. 4.1) (Kohler and Gill 2006). Because certain species could not be accurately identified in the images, we collected material for laboratory identification, specially the turf forming algae. Voucher specimens of algae have been deposited in the Herbarium of the Rio de Janeiro Botanical Garden (RB), Brazil.

The benthic communities of the mesophotic zone were assessed using videos obtained with the Remotely Operated Vehicle (ROV – VideoRay Explorer). Benthic cover was quantified from 30 still frames obtained at 10 second intervals, a total of

approximately 0.7 m² per sample. We also used the CPCe software to analyse the video still frames, using 10 randomly distributed points per frame (a total of 300 points per sampling unit). For both, shallow and mesophotic zones, macroalgae (specially turf forming species which was the most abundant taxa - see results) were classified according the morphological functional groups proposed by Balata et al. (2011).

We also classified the benthic organisms in three groups according to their dependence of light: phototrophic (e.g. all macroalgae), non-phototrophic (e.g. Porifera, Bryozoa and Tunicata) and symbiont organisms (e.g. scleractinian corals). Percent covers of these three categories were evaluated by simple linear regression analysis between them and depth (Quinn and Keough 2001), thereafter, we used an ANOVA to test the significance of the regression. Data were transformed into $\arcsin \sqrt{x}$.

Fish species on both shallow and mesophotic reefs were quantified and classified according to their predominant diet in one of the following trophic categories: roving herbivores, territorial herbivores, invertebrate feeders, omnivores or piscivores (see chapter 1 in this thesis).

Quantitative analyses were performed for only the benthic taxa that presented a mean relative cover greater than 0.5 % (Quinn and Keough 2001). Based on this criterion, the 26 most abundant taxa were retained for the final analyses. After a fourth-root transformation (Quinn and Keough 2001), we used a non-metric multidimensional scaling (nMDS) ordination to summarise similarities (Bray-Curtis) in the structure of benthic communities (i.e., the relative abundance of various taxa) according to depth strata. An analysis of similarities (ANOSIM) was applied to evaluate differences between depths, and a Similar Percentages (SIMPER) analysis was used to identify the species that contributed most heavily to the average similarity within a group (Clarke and Warwick 1994). An analysis of variance (ANOVA) was applied to test differences

in each variable among the depth strata. A Tukey *a posteriori* test was applied when necessary (Quinn and Keough 2001).

We used a Canonical Correspondence Analysis (Ter Braak 1996) to evaluate the relative influence of environmental (benthic complexity, depth and light) and biotic variables (the biomass of different fish trophic groups) on the structure of benthic communities. We applied a forward selection procedure, and only the independent variables that contributed to increase the explanatory power of the model, defined by a Monte Carlo permutation test (999 permutations), were included in the final model.

2.4. Results

We recorded a total of 77 benthic taxa belonging to six major groups (macroalgae, Porifera, Cnidaria, Annelida, Bryozoa and Tunicata). Macroalgae was the richest group, with 43 infrageneric taxa, including 31 Rhodophyta, 9 Chlorophyta and 3 Phaeophyceae. Rhodophyta constituted nearly 75 % of the total identified algae (Table 2 – 1). Seventeen algal species represented new records for the SPSPA, namely, two Chlorophyta (*Caulerpa mexicana* and *Struvea elegans*) and 15 Rhodophyta (*Amphiroa beauvoisii*, *Anotrichium tenue*, *Botryocladia wynnei*, *Centroceras* sp., *Ceramium affine*, *Ceramium comptum*, *Ceramium vegans*, *Ceratodictyon planicaule*, *Gloiocladia iyocensis*, *Herposiphonia tenella*, *Heterosiphonia crispella*, *Jania cubensis*, *Kallymenia limminghei*, *Polysiphonia denudata* and *Sahlingia subintegra*).

Fleshy and turf algae were the most abundant benthic organisms on shallow reefs (relative cover = $33.4 \pm \text{SE } 3.9 \%$ and $27.9 \pm \text{SE } 3.5 \%$, respectively), whereas turf algae ($25.1 \pm \text{SE } 1.7 \%$) and bryozoans ($19.2 \pm \text{SE } 2.3 \%$) dominated mesophotic reefs (Figure 2 – 3A). Twenty-six turf-forming species were identified, all of them occurring on shallow reefs but only eight occurring below 30 m (Table 2 – 1). The most frequent

morphological functional groups of turf forming algae on shallow zone were “filamentous uniseriate and pluriseriate with erect thallus” (major *Ceramium* spp., *Antithamnion antillanum* and *P. denudata*), “blade-like with one or few layers of cells” (major “*Hypoglossum hypoglossoides* and *Nitophyllum wilkinsoniae*), “smaller-sized corticated” (major *Gloiocladia iyoensis*) and “smaller-sized filamentous pluriseriate” (*Sphacelaria rigidula*) (Table 2 – 1). On the mesophotic zone most of turf forming algae belong to the “smaller-sized corticated”, “filamentous uniseriate and pluriseriate with erect thallus” (i.e. *P. denudate*, *C. affine* and *Asparagopsis taxiformis*), “smaller-sized filamentous pluriseriate” (i.e. *Sphacelaria rigidula*) and “Corticated with hollow thallus” (i.e. *Champia parvula*) (Table 2 – 1).

On the shallow reefs, we also recorded high coverage of the zoanthid *Palythoa caribaeorum* (11.7 ± 3.6 %), the green stoloniferous alga *Caulerpa racemosa* var. *peltata* (11.2 ± 2.9 %), CCA (10.5 ± 6.7 %), the green filamentous macroalgae *Bryopsis* spp. (8.0 ± 2.4 %) and the fleshy macroalga *Dictyota menstrualis* (5.8 ± 1.9 %) (Figure 2 – 2B-C and Figure 2 – 3A-B). On the mesophotic reefs, we observed an increase in CCA coverage (19.6 ± 2.0 %). Other groups with a relatively high coverage on the mesophotic reefs were bryozoans (19.2 ± 2.3 %) (primarily *Margaretta buski*), scleractinian corals (13.1 ± 1.2 %) (only *Madracis decactis* and *Scolymia wellsii*) (Figure 2 – 2D) and sponges (9.2 ± 0.8 %; total of 18 species) (Fig. 2 and Table 2).

The structure of the benthic communities differed along the depth gradient (ANOSIM, $R = 0.464$, $P < 0.05$) (Table 2 – 3). Although we observed two distinct groups of samples at a 20 % similarity level (Figure 2 – 4A), the ANOSIM pairwise test indicated differences among all depth strata except between the 20-30 and 30-40 m ones, which appear to constitute a transitional zone (Table 2 – 3). We also observed that the similarity among samples increased with depth, indicating a higher spatial

homogeneity within mesophotic benthic communities (Table 2 – 3). Turf algae, CCA and *C. racemosa* var. *peltata* were the main organisms that contributed (>50 %) to these similarities between depths of 5 and 20 m (SIMPER), whereas turfs, CCA, *M. buski*, *Clathria calla* and *M. decactis* contributed more than 50 % to the within-group similarities between depths of 20 and 60 m. However, we observed that *D. menstrualis* was among the most strongly contributing organisms only in the 20-30 m depth stratum. Although colonies of black corals, *Tanacetipathes* sp., were observed at 40 m depth, this species was quantitatively recorded only below 50 m depth (Figure 2 – 2E-F). Using additional ROV footage, we observed a clear increase in black coral abundance below 60 m depth.

Simple linear regression analysis showed a significant decrease in the abundance of phototrophic organisms ($y = -0.009x + 1.1714$; $R^2 = 0.966$; ANOVA $P < 0.001$) while both non-phototrophic ($y = 0.0101x + 0.1773$; $R^2 = 0.8895$; ANOVA $P < 0.001$) and symbiont organisms ($y = 0.0098x - 0.0884$; $R^2 = 0.904$; ANOVA $P < 0.01$) increased according to depth (Figure 2 – 4B). Turf forming algae were the major phototrophic organisms on the mesophotic zone studied (Figuras 2 – 3A-B). Although less than $70 \mu\text{mol m}^2 \text{s}^{-1}$ reaches below 40 m depth, phototrophic organisms were more abundant than non-phototrophic ones down to 50 m depth (Figure 2 – 4B).

A Canonical Correspondence Analysis showed that the depth, light, biomass of roving herbivorous fishes (primarily *Kyphosus* sp.) and biomass of territorial herbivorous fishes (primarily *Stegastes sanctipauli* Lubbock and Edwards, 1981) were, in decreasing order, the principal predictors of benthic community structure. No other independent variables were significant according to the Monte Carlo test. The first two axes explained nearly 70 % of the data variance. We observed a clear gradient of samples (depth strata) following the depth gradient. Macroalgae, primarily of the genus

Caulerpa and *Laurencia*, were associated with shallow reefs (< 20 m) with high irradiance and a high abundance of herbivorous fish (both territorial and roving), whereas scleractinian corals (*M. decactis* and *S. wellsi*), sponges, bryozoans and black corals were associated with deeper strata (Figure 2 – 5).

2.5. Discussion

We added 17 new species records of macroalgae to SPSPA, increasing from 53 (Pereira 2006, Burgos et al. 2009) to 70 the total number of known species to the area.

Despite the high coverage of turf-forming algae at all depths, our analyses detected two distinct benthic communities: i) one consisting primarily of *P. caribaeorum*, *C. racemosa* var. *peltata*, CCA and *Bryopsis* spp. at depths shallower than 30 m and ii) another dominated by CCA, bryozoans (primarily *M. buski*) and the scleractinian corals *M. decactis* and *S. wellsi* at depths greater than 30 m. Edward and Lubbock (1983b) described almost the same pattern, identifying shallower reefs as the “*Caulerpa* zone” and “sub-*Caulerpa* zone”. These authors did not mention the presence of turf algae in the SPSPA and only provided qualitative data on the most prominent benthic features. However, they described high abundances of the damselfish *S. sanctipauli*, a species generally known as a turf algae farmer (e.g., Hinds and Ballantine 1987, Emslie et al. 2012). Thus, it is plausible that turfs were already an important benthic component in the 70’s in the SPSPA, as they are in most rocky and biogenic systems worldwide (Bruno et al. 2013). In contrast, turfs are considered opportunistic algae (Steneck and Dethier 1994), and many authors have associated their increased cover with declining reef health (e.g., Smith et al. 2006, Sandin et al. 2008, Kenyon et al. 2012, Lacey et al. 2013).

Bruno et al. (2013) argue that the use of remote Pacific and Caribbean reefs as global baselines has several limitations, as they are, most likely, not representative of the reefs of other regions. In fact, in six years monitoring the largest coralline reefs of the Southwestern Atlantic Ocean (Abrolhos Bank), Francini-Filho et al. (2013) recorded an increase in turf algae cover and a positive relationship between turf algae and coral cover. In contrast, Sala et al. (2012) observed a high coverage of turfs in non-enforced marine protected areas and areas open to fishing on Mediterranean rocky reefs. Furthermore, “turf algae” has been treated as a functional group, and little attention has been given to the taxonomic composition within this group. Our data indicate that Rhodophyta is the major group forming turf on both shallow and mesophotic zone of the SPSPA and that the composition of the turf algal species varies with depth (Table 1).

Balata et al. (2011) showed that different morphologies of turf forming algae presented different responses to disturbances. The more frequent morphology of turf forming algae on the shallow zone was filamentous uniseriate and pluriseriate forms with erect thallus while more complex morphology of flattened Rhodophyta with cortication, often used as indicative of low-stressed sites (Sala et al. 2012, Fraschetti et al. 2012), were abundant in mesophotic zone.

According to Balata et al. (2011), the most abundant turf assemblages under stress conditions are filamentous forms with extensive prostate filaments. It occurs likely because they reproduce mostly by vegetative propagation and can rapidly spread horizontally on the substratum after a disturbance (Balata et al. 2011, Airoidi 2000). At the SPSPA, our data show that turf forming with prostate filaments were conspicuous and restrict to the shallow zone.

Despite the evidence for the effects of intense industrial fishing activities during the past three decades (Vaske Jr. et al. 2006; Hazin et al. 2009) including the local extinction of the top predator *C. galapagensis*, our data indicate no major changes in benthic communities since the 70's (Edwards and Lubbock 1983a; b). In rocky reefs of the Mediterranean, several studies show that overfishing of predators increase by top-down control the abundance of herbivorous and, consequently, large areas covered by CCA, barren rocks and rapidly growing turf algae are found (e.g., Sala et al. 1998, Fraschetti et al. 2012, Sala et al. 2012). In the other hand, the overfishing of herbivores is known to promote the proliferation of macroalgae in many reef systems (Mumby and Steneck 2008). After these changes, few successful cases of recovery at the ecosystem level have been described for rocky reefs (e.g., Fraschetti et al. 2012). Most cases of successful recovery have consisted of fishery exclusions resulting from the implementation of no-take zones (i.e., areas in which any extractive activities are prohibited) (Bevilacqua et al. 2006, Guidetti 2006, Francini-Filho and Moura 2008, Libralato et al. 2010). However, for the SPSPA our canonical correspondence analysis indicated abiotic variables as the principal contributors to the explanation of local benthic community structure.

We observed two major benthic communities: the first between 5 and 20 m and the second between 40 and 60 m, with a transitional zone between 20 and 40 m. Many authors consider that the 40 m isobath represents the upper boundary of mesophotic reefs (Hinderstein et al. 2010). However, many authors argue that this boundary can vary according to the region and the light penetration in water (Lesser et al. 2009, Slattery and Lesser 2012).

The highest decrease in PAR occurred at depths of < 40 m, with only 10 % of the surface irradiance reaching the 5 m depth and a sharp decrease in irradiance between 5

and 40 m. Below 40 m, PAR decreased more slowly, with at least 20 % of incident PAR at 40 m ($70 \mu\text{mol m}^{-2} \text{s}^{-1}$) reaching the 60 m isobath. The Canonical Correspondence Analysis indicated that abiotic variables (depth and light) were the most important ones for explaining variation in benthic community structure across the depth gradient. Depths between 5 and 20 m, where light varied most abruptly, harboured a more heterogeneous community (see the high dispersion of shallow samples in Figure 2 – 4).

In contrast, at depths between 40 and 60 m, at which the rates of light decrease were relatively low, we observed a more homogeneous benthic community dominated by photosynthetic organisms (turf algae, CCA, scleractinian corals) and non-photosynthetic organisms such as bryozoans (primarily *M. buski*). Human influences are usually associated with increasing in patchy landscape, loss habitat and susceptibility to invasive species establishment (Bulleri et al. 2010, Claudet and Fraschetti 2010). However, habitat diversity and fragmentation are not always results of anthropogenic influence (Boström et al. 2011) and many times are consequences of natural processes like grazing, hydrodynamics and physical features (e.g. light and bottom topography) (Tamburello et al. 2012). In fact, we observed that below 40 m depth, where lower physical features variations occurred (i.e. light and complexity), the benthic communities were also more homogeneous.

In rocky reefs of the Mediterranean, large areas covered by CCA are associated with a high abundance of benthic herbivores, especially sea urchins, as a consequence of the overfishing of species exerting top-down control (e.g., Sala et al. 1998, Fraschetti et al. 2012, Sala et al. 2012). Despite the evidence of overfishing in the SPSPA (Ferreira et al. 2009, Luiz-Jr and Edwards 2011), sea urchins (*Eucidaris tribuloides* Lamarck, 1816) are rare and we did not recognise any other macro-invertebrates grazing on CCA. Crustose coralline algae are slow-growing organisms (Amado-Filho et al. 2012b). They

have previously been found living and photosynthesising at a depth of 268 m (Littler et al. 1985). Both *S. wellsi* and *M. decactis* corals have also been observed in association with mesophotic Brazilian reefs (Pereira-Filho et al. 2011) or with low light intensities (Francini-Filho et al. 2013). The presence of zooxanthellae corals in low light habitats is likely related to the photosynthetic properties of the symbiont.

Scleractinian species can harbour many clades of *Symbiodinium*. However, the genus *Madracis* is apparently restricted to only B7, B13 and B15 ones, which are physiologically distinct but phylogenetically closely related (Frade et al. 2008a, b). For Caribbean reefs, *M. decactis* harbours symbiont with physiological capacities to a more efficient production under shallow depths (Frade et al. 2010). In the other hand, Diekmann et al. (2002) did not observe correlations among the symbiont clades and depths on Curaçao reefs. Our data showed an increase in zooxanthellate corals according to the depth towards to mesophotic reefs. Data about symbionts physiology from SPSPA and also about its clades could reveal new important informations, including some biogeographical and evolutionary questions about these corals.

Due to its geographical isolation and the presence of endemic species, such as two sponges (*Hemimycale insularis* and *Plakortis petrupaulensis*) and four fishes (*Choranthias salmopunctatus*, *Prognathodes obliquus*, *Enneanectes smithi* and *S. sanctipauli*) (Feitoza et al. 2003, Ferreira et al. 2009, Moraes 2011, Anderson and Heemstra 2012, Reis et al. 2013, Domingos et al. 2013), SPSPA is an area of high conservation interest and is already included in the Fernando de Noronha/Rocas/São Pedro e São Paulo Environmental Protected Area. Despite the scientific relevance of SPSPA for the understanding of biogeographical and ecological patterns, there is evidence that enforcement is still not adequate and that, indeed, changes in fish

assemblages have already been detected (Vaske Jr et al. 2006, Hazin et al. 2009, Ferreira et al. 2009, Luiz-Jr and Edwards 2011, Rosa et al. unpubl data).

Although our data did not show substantial changes in benthic community structure at SPSPA in the past four decades, reef systems have been declining as consequence of global anthropogenic changes. Continuous monitoring programmes taking in account the turfs morphological function and taxonomic refinement for these systems will provide the necessary relevant understanding of this question, especially when such programmes are implemented on isolated reefs such as the SPSPA. A comprehensive understanding of this remote Atlantic rocky reef will help to improve worldwide compilations on the health of rocky reefs, for which most available knowledge is based on studies of the Mediterranean Sea.

2.6. Acknowledgements

We thank A Alves, C Moitinho, E Coni, D Sartor, L Silva, M Villela and AP Moreira for logistical assistance and data collection; APA Fernando de Noronha/Rocas/São Pedro e São Paulo/ICMBio for providing research permits; the crew of Transmar I and Transmar II, as well as Secretaria da Comissão Interministerial para os Recursos do Mar (SECIRM), for logistical support; and MB Barros Barreto for *Ceramium* identification. Financial support was provided by the Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq (grant 557185/09-2 to RBFF and 484875/2011-6 to GHPF). GMAF, RBFF and RLM acknowledge individual grants from CNPq. RLM and GMAF acknowledge individual grants from Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ). GMM, MRR and PSB acknowledge post-graduate fellowships from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and from FAPERJ. FCM acknowledges a fellowship (DTI-A) from CNPq.

2.7. Literature Cited

- Airoidi L. 2000. Effects of disturbance, life-history and overgrowth on coexistence of algal crusts and turfs. *Ecology*. 8:798-814.
- Amado-Filho GM, Pereira-Filho GH, Bahia RG, Abrantes DP, Veras PC, Matheus Z. 2012a. Occurrence and distribution of rhodolith beds on Fernando de Noronha Archipelago of Brazil. *Aqua. Bot.* 101:41-45.
- Amado-Filho GM, Moura RL, Bastos AC, Salgado LT, Sumida PY, Guth AZ, Francini-Filho RB, Pereira-Filho GH, Abrantes DP, Brasileiro PS, Bahia RG, Leal RN, Kaufman L, Kleypas JA, Farina M, Thompson FL. 2012b Rhodolith beds are major CaCO₃ bio-factories in the tropical south west Atlantic. *PLoS ONE* 7(4):e35171.
- Anderson WD, Heemstra PC. 2012. Review of Atlantic and Eastern Pacific Anthiine fishes (Teleostei:Perciformes: Serranidae), with descriptions of two new genera. *Trans Am Phil Soc.* 102:1–173.
- Bak RPM, Nieuwland G, Meesters EH. 2005. Coral reef crisis in deep and shallow reefs: 30 years of constancy and change in reefs of Curacao and Bonaire. *Coral Reefs*. 24:475-479.
- Balata D, Piazzzi L, Rindi F. 2011. Testing a new classification of morphological functional groups of marine macroalgae for the detection of responses to stress. *Mar Biol.* 158:2459-2469.
- Bevilacqua S, Terlizzi A, Fraschetti S, Russo GF, Boero F. 2006. Mitigating human disturbance: Can protection influence trajectories of recovery in benthic assemblages? *J Anim Ecol.* 75:908-920.

- Boström C, Pittman SJ, Simenstad C, Kneib RT. 2011. Seascape ecology of coastal biogenic habitats: advances gaps, and challenges. *Mar Ecol Prog Ser.* 427:191-217.
- Bulleri F, Balata D, Bertocci I, Tamburello L, Benedetti-Cecchi L. 2010. The seaweed *Caulerpa racemosa* on Mediterranean rocky reefs: from passenger to driver of ecological change. *Ecology.* 91:2205-22-12.
- Burgos DC, Pereira SMB, Bandeira-Pedrosa ME. 2009. Levantamento florístico das rodofíceas do Arquipélago de São Pedro e São Paulo (ASPSP) – Brasil. *Act Bot Bras.* 23:1110-1118.
- Bruno JF, Precht WF, Vroom PS, Aronson RB. 2013. Coral reef baselines: how much macroalgae is natural?. *PeerJ.* 1:e19v1.
- Clarke KR, Warwick RM. 1994. Change in marine communities: an approach to statistical analysis and interpretation. Plymouth: Plymouth Marine Laboratory.
- Claudet J, Fraschetti S. 2010. Human-driven impacts on marine habitats: a regional meta-analysis in the Mediterranean Sea. *Biol Conserv.* 143:2195-2206.
- Diekmann OE, Bak RPM, Tonk L, Stam WT, Olsen JL. 2002. No habitat correlation of zooxanthellae in the coral genus *Madracis* on Curaçao reef. *Mar Ecol Prog Ser.* 227:221-232.
- Domingos C, Moraes F, Muricy G. 2013. Four new species of Plakinidae (Porifera: Homoscleromorpha) from Brazil. *Zootaxa.* 3718:530-544.
- Edwards A, Lubbock R. 1983a. Marine zoogeography of St. Paul's Rocks. *J Biogeogr.* 10:65-72.
- Edwards A, Lubbock R. 1983b. The ecology of Saint Paul's Rocks (Equatorial Atlantic). *J Zool.* 200:51-69.

- Emslie MJ, Logan M, Ceccarelli DM, Cheal AJ, Hoey AS, Miller L, Sweatman HPAS. 2012. Regional-scale variation in the distribution and abundance of farming damselfishes on Australia's Great Barrier Reef. *Mar Biol.* 159:1293-1304.
- Feitoza BM, Rocha LA, Luiz OJ, Floeter SR, Gasparini JL. 2003. Reef fishes of St. Paul's Rocks: new records and notes on biology and zoogeography. *Aqua J Ichthyol Aquatic Biol.* 7:61-82.
- Ferreira CEL, Luiz-Jr OJ, Feitoza B, Ferreira CGW, Gasparini JL, Noguchi RC, Godoy EA, Joyeux, JC, Rangel CA, Rocha LA, Floeter SR, Carvalho-Filho A. 2009. Peixes recifais: síntese do atual conhecimento. *In: Viana DL, Hazin FHV, Souza MAC (eds) O Arquipélago de São Pedro e São Paulo: 10 anos de estação científica.* Brasília: SECIRM.
- Figueiredo MAO, Horta PA, Pedrini AG, Nunes JMC. 2008. Benthic marine algae of the coral reefs of Brazil: a literature revision. *Oecol Bras.* 12:258-269.
- Frade PR, De Jongh F, Vermeulen F, Van Bleijswijk J, Bak RPM. 2008a. Variation in symbiont distribution between closely related coral species over large depth ranges. *Mol Ecol.* 17:691-703.
- Frade PR, Bongaers P, Winkelhagen AJS, Tonk L, Bak RPM. 2008b. In situ photobiology of corals over large depth ranges: a multivariate analysis on the roles of environment, host, and algal symbiont. *Limnol Oceanogr.* 53:2711-2723.
- Frade PR, Reyes-Nivia MC, Faria J, Kaandorp JA, Luttikhuizen PC, Bak RPM. 2010. Semi-permeable species boundaries in the coral genus *Madracis*: introgression in a brooding coral system. *Mol Phylogen Evol.* 57:1072-1090.
- Francini-Filho RB, Moura RL. 2008. Dynamics of fish assemblages on coral reefs subjected to different management regimes in the Abrolhos Bank, eastern Brazil. *Aquatic Conserv Mar Freshwater Ecosys.* 18:1166-1179.

- Francini-Filho RB, Coni, EOC, Meirelles PM, Amado-Filho GM, Thompson FL, Pereira-Filho GH, Bastos AC, Abrantes DP, Ferreira CM, Gibran FZ, Güth AZ, Sumida PYG, Oliveira NL, Kaufman L, Minte-Vera CV, Moura RL. 2013. Dynamics of coral reef benthic assemblages of the Abrolhos Bank, eastern Brazil: Inferences on natural and anthropogenic drivers. PLoS ONE. 8:e54260.
- Fraschetti S, Bevilacqua S, Guarnieri G, Terlizzi A. 2012. Idiosyncratic effects of protection in a remote marine reserve. Mar Ecol Prog Ser. 466:21-34.
- Fonseca AC, Villaça R, Knoppers B. 2012. Reef flat community structure of Atol das Rocas, northeast Brazil and southwest Atlantic. J Mar Biol. 12:ID179128.
- Guidetti P. 2006. Marine reserves reestablish lost predatory interactions and cause community changes in rocky reefs. Ecol Appl. 16:963-976.
- Hanelt D, Wiencke C, Bischof K. 2003. Photosynthesis in marine macroalgae. *In*: Larkum AW, Douglas SE, Raven JA (eds). Photosynthesis in Algae. The Netherlands: Kluwer Academic Publishers.
- Hazin FHV, Viana D, Pinheiro P, Fischer A, Macena B, Vêras D, Oliveira P, Carvalho F, Vaske Jr. T, Branco I. 2009. Ecologia de grandes peixes pelágicos. *In*: Viana DL, Hazin FHV, Souza MAC (eds) O Arquipélago de São Pedro e São Paulo: 10 anos de estação científica. Brasília: SECIRM.
- Hinderstein LM, Marr JCA, Martinez FA, Dowgiallo MJ, Puglise KA, Pyle RL, Zawada DG, Appeldoorn R. 2010. Introduction to mesophotic coral ecosystems: characterization, ecology, and management. Coral Reefs. 29:247-251.
- Hinds P, Ballantine D. 1987. Effects of the caribbean threespot damselfish, *Stegastes planifrons* (Cuvier), on algal lawn composition. Aquat Bot. 27:299-308.
- Hughes TP. 1989. Community structure and diversity of coral reefs: the role of history. Ecology. 70:275-279.

- Hughes TP, Connell JH. 1999. Multiple stressors on coral reefs: a long-term perspective. *Limnol Oceanogr.* 44:932–940.
- Huston MA. 1985. Patterns of species diversity on coral reefs. *Annu Rev Ecol Syst.* 16:149–177.
- Kahng SE, Spalding HL, Brokovich E, Wagner D, Weil E, Hinderstein L, Toonen RJ. 2010. Community ecology of mesophotic coral reef ecosystems. *Coral Reefs.* 29:255–275.
- Kenyon J, Maragos JE, Vroom P. 2012. Monitoring supports establishment of Pacific Remote Islands Marine National Monument. Proc 12th Int Coral Reef Symp. Cairns, Australia.
- Kirk, JTO. 1994. Light and photosynthesis in aquatic ecosystems. New York: Cambridge University Press.
- Kohler KE, Gill SM. 2006. Coral Point Count with Excel extensions (CPCe): A visual basic program for the determination of coral and substrate coverage using random point count methodology. *Comput Geosci.* 32:1259-1269.
- Lacey EA, Fourqurean JW, Collado-Vides L. 2013. Increased algal dominance despite presence of *Diadema antillarum* populations on a caribbean coral reef. *Bull Mar Sci.* 89:603-620.
- Lesser MP, Slattery M, Leichter JJ. 2009. Ecology of mesophotic coral reefs. *J Exp Mar Biol Ecol.* 375:1-8.
- Lesser MP, Slattery M. 2011. Phase shift to algal dominated communities at mesophotic depths associated with lionfish (*Pterois volitans*) invasion on Bahamian coral reef. *Biol Invasions.* 13:1855-1868.

- Lesser MP, Slattery M, Stat M, Ojimi M, Gates R, Grotoli A. 2010. Photoacclimatization by the coral *Montastraea cavernosa* in the mesophotic zone: Light, food, and genetics. *Ecology*. 91:990-1003.
- Libralato S, Coll M, Tempesta M, Santojanni A, Spoto M, Palomera I, Arneri E, Solidoro C. 2010. Food-web traits of protected and exploited areas of the Adriatic Sea. *Biol Conserv*. 143:2182-2194.
- Littler MM, Littler DS. 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. *Am Nat*. 116:25-44.
- Littler MM, Littler DS, Hanisak MD. 1985.. Deepest known plant life discovered on an uncharted seamount. *Science*. 227:57-59.
- Luiz-Jr O, Edwards AL. 2011. Extinction of a shark population in the Archipelago of Saint Paul's Rocks (equatorial Atlantic) inferred from the historical record. *Biol Cons*. 144:2873-2881.
- Minte-Vera CV, Moura RL, Francini-Filho RB. 2008. Nested sampling: an improved visual-census technique for studying reef fish assemblages. *Mar Ecol Prog Ser*. 367:283-293.
- Moraes FC. 2011. Esponjas das ilhas oceânicas brasileiras. Rio de Janeiro: Museu Nacional.
- Mumby PJ, Steneck RS. 2008. Coral reef management and conservation in light of rapidly-evolving ecological paradigms. *Trends Ecol Evol*. 23:555–563.
- Pereira SMB. 2006. Algas marinhas bentônicas do Arquipélago de Fernando de Noronha (PE) e Arquipélago de São Pedro e São Paulo. *In*: Alves RJV, Castro JWA (eds) *Ilhas oceânicas brasileiras: da pesquisa ao manejo*, 2nd Brasília: Ministério do Meio Ambiente.

- Pereira-Filho G, Amado-Filho G, Guimarães S, Moura RL, Sumida P, Abrantes DP, Bahia RG, Güth AZ, Jorge RR, Francini Filho RB. 2011. Reef fish and benthic assemblages of the Trindade and Martin Vaz island group, Southwestern Atlantic. *Braz J Oceanogr.* 59:201–212.
- Quinn GP, Keough, MJ. 2001. *Experimental design and data analysis for biologists.* Cambridge: Cambridge University Press.
- Reed JK, Pomponi SA. 1997. Biodiversity and distribution of deep and shallow water sponges in the Bahamas. *Proc 8th Int Coral Reef Sym* 2:1387-1392.
- Reis F, Moraes F, Batista D, Villaça R, Aguiar A, Muricy G. 2013. Diet of the queen angelfish *Holacanthus ciliaris* (Pomacanthidae) in São Pedro e São Paulo Archipelago, Brazil. *J Mar Biol Ass UK.* 93:453-460.
- Sala E, Boudouresque CF, Harmelin-Vivien M. 1998. Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. *Oikos.* 82:425-439.
- Sala E, Ballesteros E, Dendrinos P, Franco AD, Ferretti F, Foley D, Fraschetti S, Friedlander A, Garrabou J, Güclüsoy H, Guidetti P, Halpern BS, Hereu B, Karamanlidis AA, Kizilkaya Z, Macpherson E, Mangialajo L, Mariani S, Micheli F, Pais A, Riser K, Rosenberg AA, Sales M, Selkoe KA, Starr R, Tomas F, Zabala M. 2012. The structure of Mediterranean rocky reef ecosystems across environmental and human gradients, and conservations implications. *PLoS ONE.* 7:e32742.
- Sandin SA, Smith JE, DeMartini EE, Dinsdale EA, Donner SD, Friedlander AM, Konotchick T, Malay M, Maragos JE, Obura D, Pantos O, Paulay G, Richie M, Rohwer F, Schroeder RE, Walsh S, Jackson JBC, Knowlton N, Sala E. 2008.

- Baselines and degradation of coral reefs in the northern Line Islands. *PLoS ONE*. 3:e1548.
- Serafini TZ, França GB, Andriquetto-Filho JM. 2010. Brazilian oceanic islands: known biodiversity and its relation to the history of human use and occupation. *J Int Coast Zone Manag.* 10:281-301.
- Slattery M, Lesser MP, Brazeau D, Stokes MD, Leichter JJ. 2011. Connectivity and stability of mesophotic coral reefs. *J Exp Mar Biol Ecol.* 408:32-41.
- Slattery M, Lesser MP. 2012. Mesophotic coral reefs: a global model of community structure and function. *Proc 12th Int Coral Reef Symp.* Cairns, Austrália.
- Smith JE, Shaw M, Edwards RA, Obura D, Pantos O, Sala E, Sandin SA, Smriga S, Hatay M, Rohwer FL. 2006. Indirect effects of algae on coral: algae-mediated, microbe-induced coral mortality. *Ecol Lett.* 9:835–845.
- Steneck RS, Dethier MN. 1994. A functional group approach to the structure of algal-dominated communities. *Oikos.* 69:476-498.
- Tamburello L, Benedetti-Cecchi L, Ghedini G, Alestra T, Bulleri F. 2012. Variation in the structure of subtidal landscapes in the Mediterranean Sea. *Mar Ecol Prog Ser.* 457:29-41.
- Ter Braak CJF. 1996. Unimodal methods to relate species to environment. The Netherlands: Centre for Biometry Wageningen (DLO Agricultural Mathematics Group).
- Vaske Jr. T, Lessa RPT, Ribeiro ACB, Nóbrega MF, Pereira AA, Andrade CDP. 2006. A pesca comercial de peixes pelágicos no arquipélago de São Pedro e São Paulo, Brasil. *Tropical Oceanogr.* 34: 31-41.

- Vroom PS, Braun CL. 2010. Benthic composition of a healthy subtropical reef: baseline species-level cover, with an emphasis on algae, in the Northwestern Hawaiian Islands. *PLoS ONE*. 5:e9733.
- Vroom PS, Musburger CA, Cooper SW, Maragos JE, Page-Albins KN, Timmers MAV. 2010. Marine biological community baselines in unimpacted tropical ecosystems: spatial and temporal analysis of reefs at Howland and Baker Islands. *Biod Cons*. 19:797–812.
- White KN, Ohara T, Fujii T, Kawamura I, Mizuyama M, Montenegro J, Shikiba H, Naruse T, McClelland T, Denis V, Reimer JD. 2013. Typhoon damage on a shallow mesophotic reef in Okinawa, Japan. *PeerJ*. 1:e151.
- Williams GJ, Smith JE, Conklin EJ, Gove JM, Sala E, Sandin SA. 2013. Benthic communities at two remote Pacific coral reefs: effects of reef habitat, depth, and waver energy gradients on spatial patterns. *PeerJ*. 1:e81.

2.8. Table Legends

Table 2 – 1: Group/Taxa found per depth stratum in the SPSPA. * represents turf-forming algae that were classified as: ^a corticated with hollow thallus, ^b filamentous uniseriate and pluriseriate with extensive prostate filaments, ^c siphonous with thin separate filaments, ^d smaller-sized corticated, ^e smaller-sized filamentous pluriseriate, ^f filamentous uniseriate and pluriseriate with erect thallus and ^g blade-like with one or few layers of cells (according Balata et al., 2011). ⁺ indicates new records for the SPSPA. (x) presence and (-) absence.

| Group/Taxa | 5-10 | 10-20 | 20-30 | 30-40 | 40-50 | 50-60 |
|--------------------------------------------------------------------------------------|------|-------|-------|-------|-------|-------|
| Chlorophyta (9) | | | | | | |
| <i>Bryopsis plumosa</i> (Hudson) C.Agardh | x | x | x | - | - | - |
| <i>Bryopsis pennata</i> J.V.Lamouroux | x | x | x | x | x | - |
| <i>Caulerpa mexicana</i> Sonder ex Kützing ⁺ | x | - | - | - | - | - |
| <i>Caulerpa racemosa</i> var. <i>peltata</i> (J.V.Lamouroux) Eubank | x | x | x | - | - | - |
| <i>Caulerpa</i> sp. | x | x | - | - | - | - |
| <i>Caulerpella ambigua</i> (Okamura) Pru d'homme van Reine & Lokhorst * ^c | x | - | - | - | - | - |
| <i>Cladophora</i> aff. <i>vagabunda</i> (Linnaeus) Hoek * ^c | x | - | - | - | - | - |
| <i>Derbesia marina</i> (Lyngbye) Solier * ^c | - | x | - | - | - | - |
| <i>Struvea elegans</i> Børgesen * ^c ⁺ | x | x | - | - | - | - |
| Heterokontophyta (3) (Classe Phaeophyceae) | | | | | | |
| <i>Dictyota menstrualis</i> (Hoyt) Schnetter, Hörning and Weber-Peukert | - | x | x | x | x | - |
| <i>Lobophora variegata</i> (J.V. Lamouroux) Womersley ex E.C. Oliveira | x | x | - | - | - | - |
| <i>Sphacelaria rigidula</i> Kützing * ^d | x | x | - | x | - | x |
| Rhodophyta (31) | | | | | | |
| <i>Amphiroa beauvoisii</i> J.V.Lamouroux ⁺ | - | x | - | - | - | - |
| <i>Anotrichium tenue</i> (C.Agardh) Nägeli * ^f ⁺ | - | x | - | - | - | - |
| <i>Antithamnion antillanum</i> Børgesen * ^f | x | x | x | - | - | - |
| <i>Asparagopsis taxiformis</i> (Delile) Trevisan de Saint-Léon * ^f | x | - | - | x | - | x |
| <i>Botryocladia wynnei</i> Ballantine ⁺ | - | x | - | - | - | x |

| | | | | | | |
|-------------------------------------------------------------------------------------------|---|---|---|---|---|---|
| <i>Centroceras</i> spp. * ^{f+} | X | - | - | - | - | - |
| <i>Ceramium affine</i> Setchell & N.L.Gardner* ^{f+} | X | X | X | X | - | - |
| <i>Ceramium comptum</i> Børgeesen* ^{f+} | X | X | - | - | - | - |
| <i>Ceramium dawsonii</i> A.B.Joly* ^f | X | X | - | - | - | - |
| <i>Ceramium flaccidum</i> (Harvey ex Kützing) Ardisson* ^f | X | X | X | - | - | - |
| <i>Ceramium vagans</i> P.C.Silva* ^{f+} | X | X | X | - | - | - |
| <i>Ceratodictyon planicaule</i> (W.R.Taylor)M.J.Wynne* ^{d+} | X | X | - | - | - | - |
| <i>Champia parvula</i> (C.Agardh) Harvey* ^a | X | X | - | - | - | X |
| <i>Champia vieillardii</i> Kützing* ^a | X | X | - | - | - | - |
| <i>Gelidium pusillum</i> (Stackhouse) Le Jolis | X | - | X | - | - | X |
| <i>Gloiocladia iyoensis</i> (Okamura) R.E.Norris* ^{d+} | - | X | X | X | X | X |
| <i>Herposiphonia tenella</i> (C.Agardh) Ambronn* ^{b+} | X | - | - | - | - | - |
| <i>Heterosiphonia crispella</i> (C.Agardh) M.J.Wynne* ^{f+} | X | X | - | - | - | - |
| <i>Hypoglossum hypoglossoides</i> (Stackhouse) F.S.Collins and Hervey* ^g | - | X | X | X | X | X |
| <i>Jania adhaerens</i> J.V.Lamouroux | X | X | X | - | - | X |
| <i>Jania capillacea</i> Harvey | X | X | X | X | X | - |
| <i>Jania rubens</i> (Linnaeus) J.V.Lamouroux | - | X | - | - | - | - |
| <i>Jania cubensis</i> Montagne ex Kützing ⁺ | - | X | - | - | - | - |
| <i>Jania pumila</i> J.V.Lamouroux | X | X | X | - | - | - |
| <i>Kallymenia limminghei</i> Montagne ⁺ | - | - | X | X | X | X |
| <i>Laurencia</i> spp. | X | - | - | - | - | - |
| <i>Neosiphonia ferulacea</i> (Suhr ex J.Agardh) S.M.Guimarães and M.T.Fujii* ^f | X | X | - | - | - | - |
| <i>Nitophyllum wilkinsoniae</i> F.S.Collins & Hervey* ^g | - | X | X | X | X | X |
| <i>Polysiphonia denudata</i> (Dillwyn) Greville ex Harvey* ^{f+} | X | - | X | X | X | X |
| <i>Sahlingia subintegra</i> (Rosenvinge) Kornmann* ^{b+} | X | X | - | - | - | - |
| <i>Stylonema alsidii</i> (Zanardini) K.M.Drew* ^f | X | - | - | - | - | - |
| Porifera (18) | | | | | | |
| <i>Aplysina fulva</i> (Pallas, 1766) | - | X | - | - | - | - |
| <i>Asteropus niger</i> Hajdu and Van Soest, 1992 | X | X | - | - | - | - |
| <i>Chelonaplysilla erecta</i> (Row, 1911) | - | X | - | X | X | X |
| <i>Chondrosia collectrix</i> (Schmidt, 1870) | X | X | X | X | X | X |
| <i>Clathria calla</i> (de Laubenfels, 1934) | X | X | X | X | X | X |
| <i>Clathria</i> sp. | - | - | X | - | - | X |
| <i>Crella brasiliensis</i> Moraes, 2011 | - | X | X | X | X | X |
| <i>Darwinella rosacea</i> Hechtel, 1965 | - | - | X | - | X | X |
| Demospongiae | - | - | X | X | - | - |
| <i>Dercitus (Stoeba) latex</i> (Moraes and Muricy, 2007) | - | - | X | - | - | - |
| <i>Didiscus oxedata</i> Hechtel, 1983 | - | X | X | - | X | X |

| | | | | | | |
|----------------------------------------------------------------------------------------|---|---|---|---|---|---|
| <i>Discodermia dissoluta</i> Schmidt, 1880 | - | - | - | - | - | X |
| <i>Dysidea etheria</i> (de Laubenfels, 1936) | - | - | X | X | X | X |
| <i>Hemimycale insularis</i> Moraes, 2011 | X | X | X | X | X | X |
| <i>Hexadela</i> sp. | - | X | - | - | - | - |
| <i>Scopalina ruetzleri</i> (Wiedenmayer, 1977) | X | X | X | X | X | X |
| <i>Spirastrella hartmani</i> Boury-Esnault, Klautau, Bézac, Wulff & Solé-Cava, 1999 | X | X | X | X | X | X |
| <i>Clathrina</i> sp. | - | X | X | - | X | X |
| Cnidaria (10) | | | | | | |
| <i>Aiptasia pallida</i> Verrill 1864 | X | - | - | - | - | - |
| <i>Anemonia sargassensis</i> Hargitt 1908 | X | - | - | - | - | - |
| <i>Tanacetipathes</i> sp. | - | - | - | - | - | X |
| <i>Carijoa riisei</i> (Duchassaing and Michelotti, 1860) | - | - | X | X | - | - |
| <i>Epizoanthus</i> sp. | X | - | - | - | - | - |
| <i>Madracis decactis</i> (Lyman 1859) | - | - | X | X | X | X |
| <i>Palythoa caribaeorum</i> (Duchassaing and Michelotti 1860) | X | X | X | - | - | - |
| <i>Protopalythoa</i> sp. | X | - | - | - | - | - |
| <i>Scolymia wellsi</i> Laborel 1967 | - | - | X | X | X | X |
| Hydrozoa | X | X | X | X | X | X |
| Tunicata (3) | | | | | | |
| <i>Didemnum</i> sp. | X | - | X | X | X | X |
| <i>Lissoclinum fragile</i> (Van Name, 1902) | - | X | - | X | X | X |
| <i>Trididemnum</i> sp. | X | X | X | X | - | - |
| Bryozoa (2) | | | | | | |
| <i>Crisia</i> spp. | - | - | X | X | X | X |
| <i>Margaretta buski</i> Harmer, 1957 | - | X | X | X | X | X |
| Annelida (1) | | | | | | |
| <i>Hermodice carunculata</i> (Pallas, 1766) | - | X | X | - | X | X |

Table 2 – 2. Mean and standard deviation of the 26 most abundant benthic organisms in the St. Peter and St. Paul Archipelago according to depth strata. * indicates significant between-strata differences (ANOVA). Letters indicate homogeneous groups according to the Student-Newman-Keuls *a posteriori* test.

| Taxa | Abbreviations | 5–10 m | 10–20 m | 20–30 m | 30–40 m | 40–50 m | 50–60 m |
|---------------------------------------------|---------------|-----------------|------------------|------------------|-----------------|------------------|---------------|
| Turf algae | TURF | 32.7(±7.8) | 34.1(±5.1) | 14.3(±2.5) | 25.4(±3.1) | 26.7 (±2.2) | 23.3(±3.4) |
| <i>C. racemosa</i> var. <i>peltata</i> * | Crac v. | 23.4(±6.4) a | 9.6(±4.2) a | 0.1(±0.1) b | 0.0(±0.0) b | 0.0(±0.0) b | 0.0(±0.0) b |
| <i>Caulerpa</i> sp.* | CAU | 2.0(±1.0) a | 0.1(±0.1) b | 0.0(±0.0) b | 0.0(±0.0) b | 0.0(±0.0) b | 0.0(±0.0) b |
| <i>Bryopsis</i> spp. | BRY | 1.5(±0.9) | 10.9(±2.4) | 11.1(±7.4) | 1.1(±0.8) | 0.1(±0.1) | 0.0(±0.0) |
| <i>Lobophora</i> <i>variegata</i> * | Lvar | 0.4(±0.3) ab | 1.7(±0.5) a | 0.0(±0.0) b | 0.0(±0.0) b | 0.0(±0.0) b | 0.0(±0.0) b |
| <i>Dictyota</i> <i>menstrualis</i> * | Dmen | 0.0(±0.0) a | 0.6(±0.3) a | 19.1(±4.7) b | 8.4(±4.4) ab | 0.9(±0.2) a | 0.0(±0.0) a |
| <i>Laurencia</i> spp.* | LAU | 11.3(±3.9) a | 2.5(±0.9) b | 0.0(±0.0) b | 0.0(±0.0) b | 0.0(±0.0) b | 0.0(±0.0) b |
| Crustose Coralline Algae | CCA | 8.1(±1.7) a | 11.0(±1.8) ac | 12.4(±1.7) ac | 25.5(±3.5) b | 20.0(±2.9) bc | 13.8(±3.5) ac |
| <i>Jania</i> spp.* | JAN | 0.7(±0.3) a | 2.7(±0.8) b | 0.3(±0.1) a | 0.4(±0.1) a | 0.3(±0.1) a | 0.1(±0.0) a |
| <i>Kallymenia</i> <i>limminghei</i> * | Klimm | 0.0(±0.0) a | 0.0(±0.0) a | 2.2(±1.0) b | 0.6(±0.2) ab | 0.8(±0.5) ab | 0.2(±0.1) ab |
| <i>Palythoa</i> <i>caribaeorum</i> | Pcar | 9.7(±6.4) | 16.0(±6.2) | 7.8(±6.6) | 0.0(±0.0) | 0.0(±0.0) | 0.0(±0.0) |
| <i>Madracis</i> <i>decactis</i> * | Mdec | 0.0(±0.0) a | 0.0(±0.0) a | 2.2(±1.8) a | 5.3(±2.5) ab | 13.7(±4.2) b | 13.3(±2.9) b |
| <i>Tanacetipathes</i> sp.* | Ahir | 0.0(±0.0) a | 0.0(±0.0) a | 0.0(±0.0) a | 0.0(±0.0) a | 0.0(±0.0) a | 2.2(±1.5) b |
| <i>Scolymia wellsi</i> * | Swel | 0.0(±0.0) a | 0.0(±0.0) a | 0.0(±0.0) a | 4.8(±2.7) b | 1.7(±1.3) ab | 0.3(±0.1) ab |
| <i>Margaretta</i> <i>buski</i> * | Mbus | 0.0(±0.0) a | 0.4(±0.2) a | 11.4(±2.9) b | 9.3(±4.0) ab | 6.8(±1.2) ab | 11.4(±3.1) b |
| <i>Crisia</i> spp.* | CRI | 0.0(±0.0) a | 0.0(±0.0) a | 2.3(±0.7) a | 3.2(±1.5) ab | 10.8(±2.5) bc | 15.0(±3.6) c |
| Hydrozoa * | Hydro | 0.3(±0.1) a | 0.2(±0.1) a | 2.1(±0.7) b | 1.7(±0.5) ab | 1.5(±0.6) ab | 0.4(±0.2) ab |
| Demospongiae* | Demos | 0.0(±0.0) a | 0.2(±0.4) a | 0.0(±0.0) a | 0.0(±0.0) a | 0.2(±0.1) a | 1.4(±0.4) b |
| <i>Scopalina</i> <i>ruetzleri</i> * | Srue | 0.8(±0.2) a | 1.2(±0.3) ab | 2.7(±0.8) ab | 3.1(±0.6) ab | 3.3(±0.7) b | 1.8(±0.3) ab |
| <i>Clathria calla</i> * | Ccal | 0.9(±0.5) a | 1.1(±0.4) a | 2.8(±0.7) ab | 1.4(±0.3) ab | 2.7(±0.4) ab | 3.2(±0.6) b |

| | | | | | | | |
|-------------------------------|------|-------------------------|------------------------|-------------------------|-------------------------|-------------------------|-------------------------|
| <i>Hemimycale insularis</i> * | Hin | 0.2(±0.1) ^a | 0.0(±0.0) ^a | 1.7(±0.5) ^b | 1.3(±0.4) ^{ab} | 2.8(±0.5) ^b | 2.5(±0.2) ^b |
| <i>Chondrosia collectrix</i> | Ccol | 0.4(±0.2) | 1.3(±0.4) | 1.4(±0.5) | 1.0(±0.3) | 0.4(±0.2) | 0.6(±0.2) |
| <i>Spirastrella hartmani</i> | Shar | 0.2(±0.1) | 0.4(±0.2) | 0.1(±0.0) | 0.1(±0.1) | 0.3(±0.1) | 0.4(±0.1) |
| <i>Trididemnum</i> sp. | TRI | 1.5(±0.8) | 1.8(±0.7) | 0.1(±0.1) | 0.4(±0.4) | 0.0(±0.0) | 0.0(±0.0) |
| <i>Didemnum</i> sp.* | DID | 0.0(±0.0) ^{ab} | 0.0(±0.0) ^a | 0.1(±0.0) ^{ab} | 1.1(±0.7) ^b | 0.6(±0.5) ^{ab} | 0.7(±0.1) ^{ab} |
| Polychaeta tube* | Pol | 0.0(±0.0) ^a | 0.1(±0.0) ^a | 2.8(±1.1) ^b | 3.5(±1.3) ^b | 3.0(±0.6) ^b | 1.3(±0.4) ^{ab} |

2.9. Figure Legends

Figure 2 – 1: Maps showing: (A) the location of the St. Peter and St. Paul Archipelago (SPSPA) and other Brazilian oceanic islands in the South Atlantic Ocean; (B) detail of the sampling area (light grey); the arrow indicates the depth gradient sampled; (C) schematic depth profile of photosynthetically active radiation incident in each depth strata.

Figure 2 – 2: Panoramic and close-up views of rocky reefs, St. Peter and St. Paul Archipelago. (A) Belmonte Islet with the Scientific Station and the cove; (B) shallow vertical rocky wall covered by *P. caribaeorum* (bottom right) and *C. racemosa* (centre) (13 m depth); (C) algal turf (centre), *Dictyota menstrualis* (brown) and sponges; (D) distinct specimens of *S. wellsi* (green), CCA (pink) and sponges (35 m); (E) characteristic mesophotic vertical reefs where the incident light decreases (40 m); (F) colony of black coral *Tanacetipathes* sp. (50 m).

Figure 2 – 3: Benthic cover at St. Peter and St. Paul Archipelago: (A) major benthic categories (mean + SE) for both shallow (<30 m depth) (white bar) and mesophotic (>30 m) (black bar) reefs; (B) relative cover of the 26 most abundant taxa across the depth gradient.

Figure 3 – 4: Benthic community structure in the remote St. Peter and St. Paul Archipelago. (A) Non-metric multi-dimensional scaling (nMDS) ordination based on benthic cover and Bray-Curtis similarity index. Groups are circled at a 20 % similarity level. (B) Simple linear regression analysis of the three groups of organisms according to their light dependence: phototrophic (full circle), non-phototrophic (empty circle) and symbiont organisms (grey triangle). *P* values are indicated for each regression according the ANOVA.

Figure 4 – 5: Canonical Correspondence Analysis plot showing (a) predictive variables and depth strata, TERH – territorial herbivorous fish and ROVH – roving herbivorous fish; (b) benthic attributes. See full names of benthic attributes in Table 2 – 2.

Figure 2 – 1.

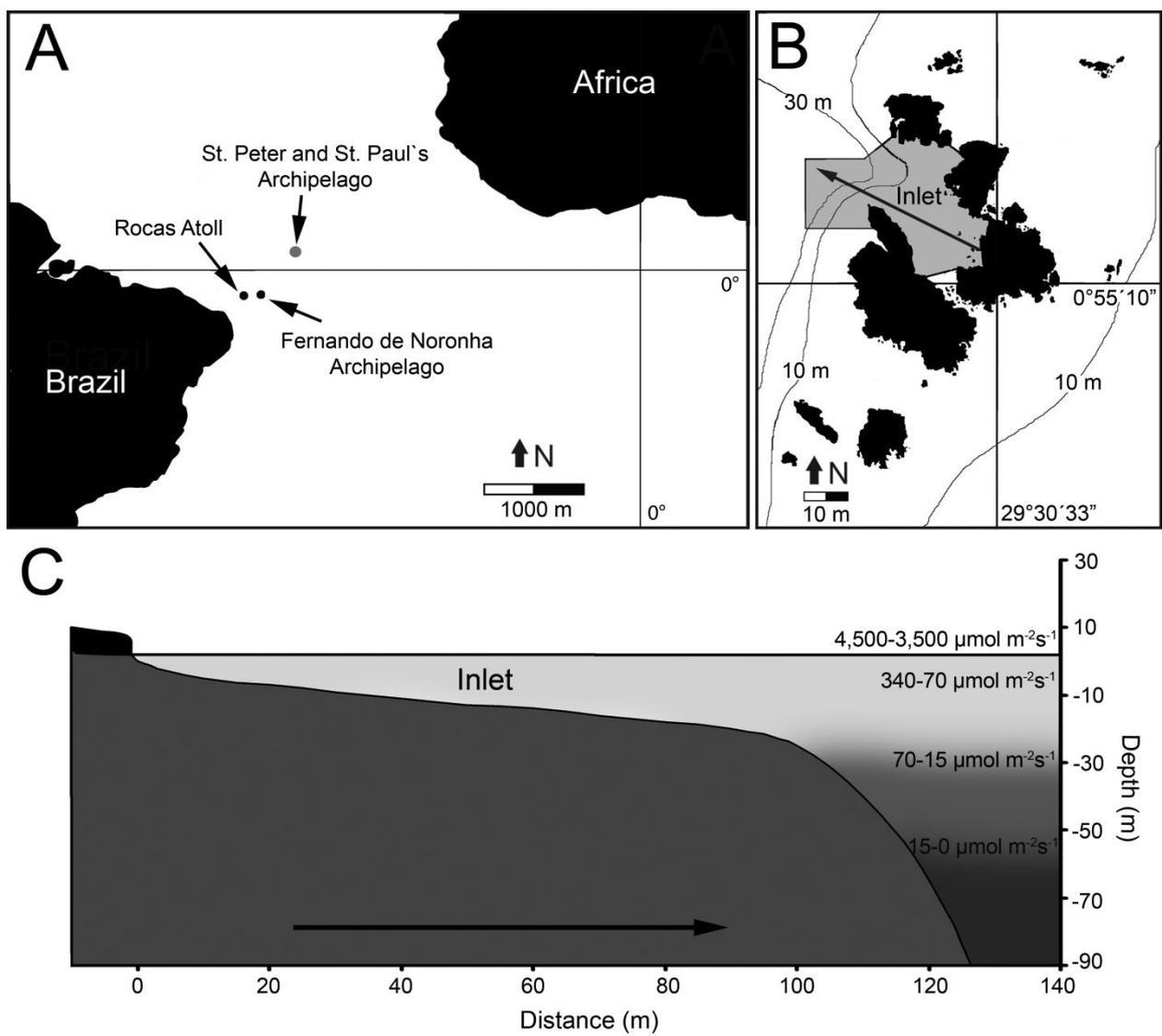


Figure 2 – 2.

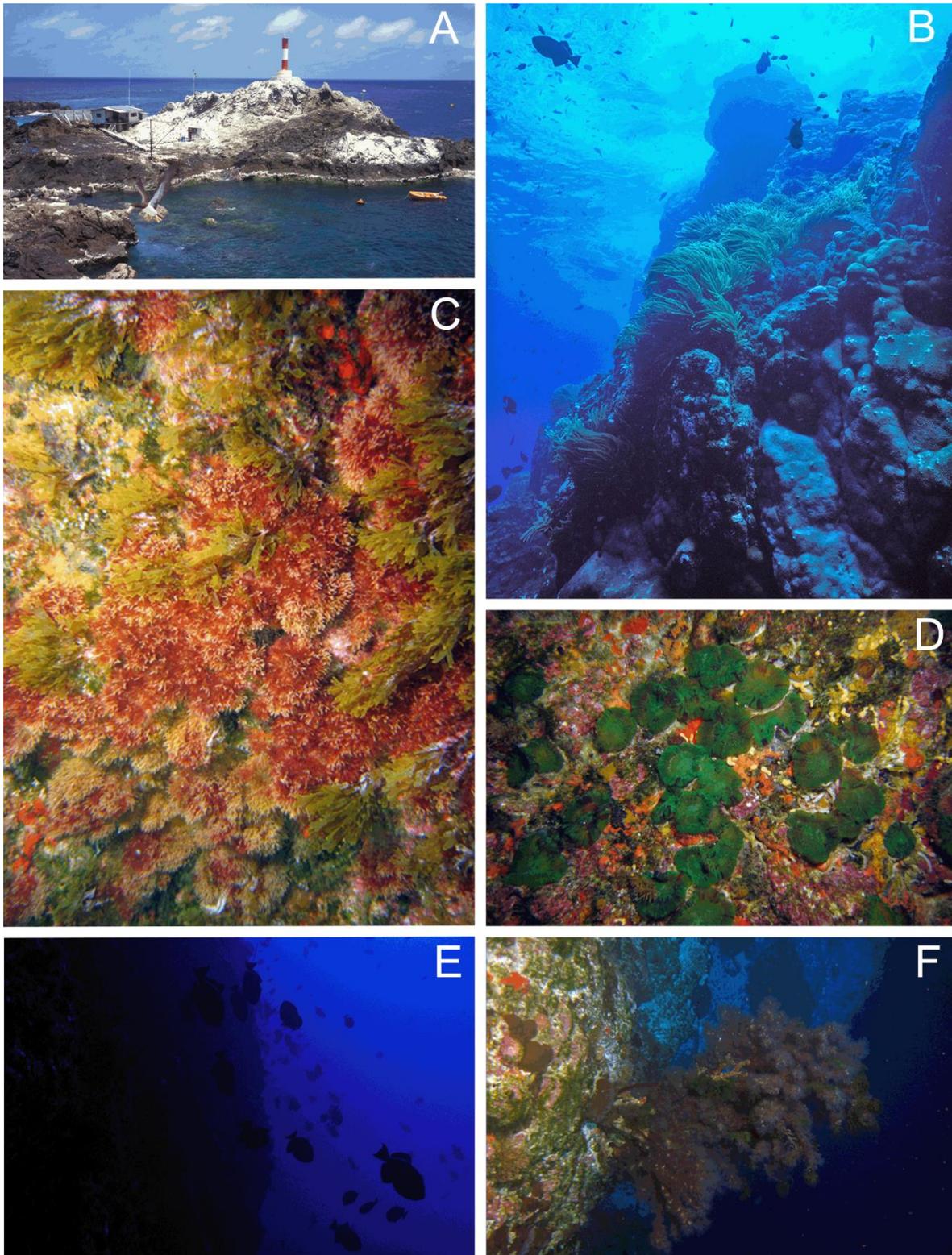


Figure 2 – 3.

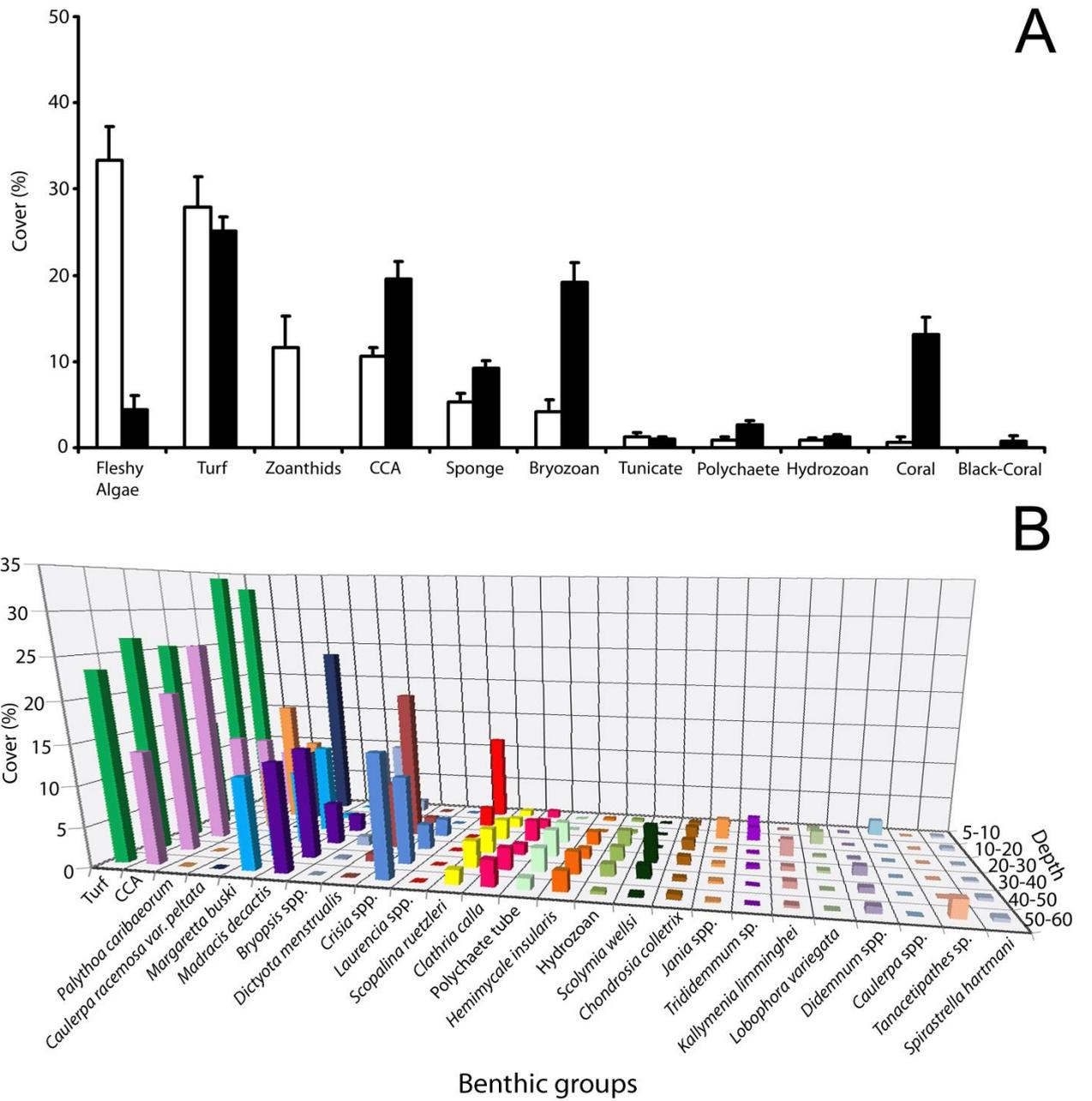


Figure 2 – 4.

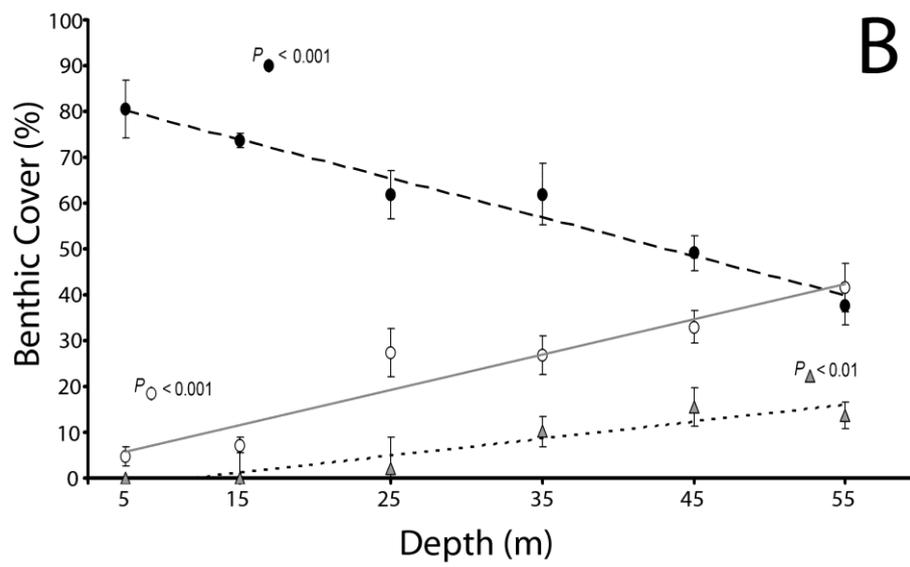
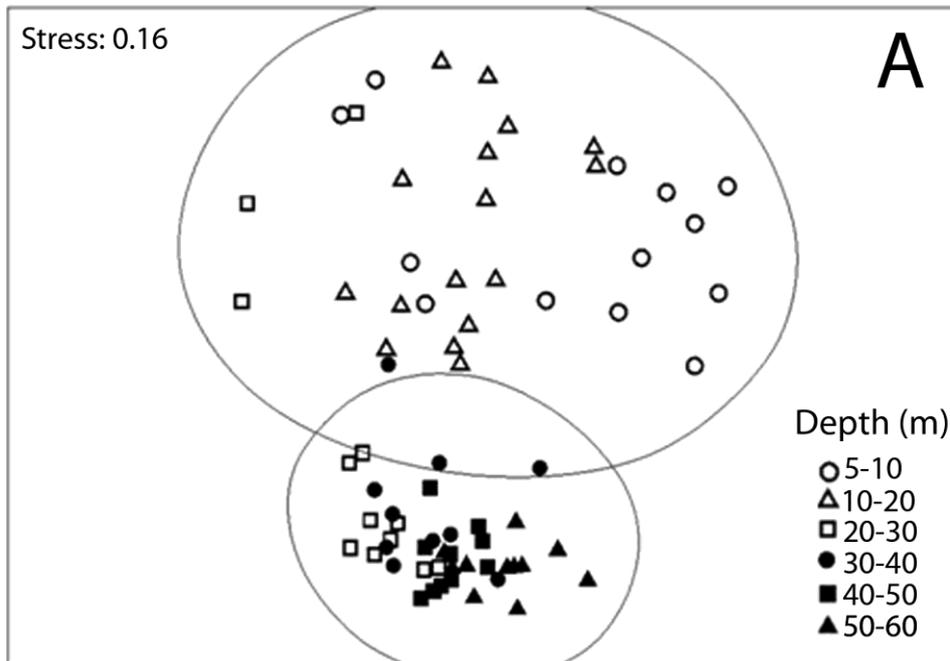
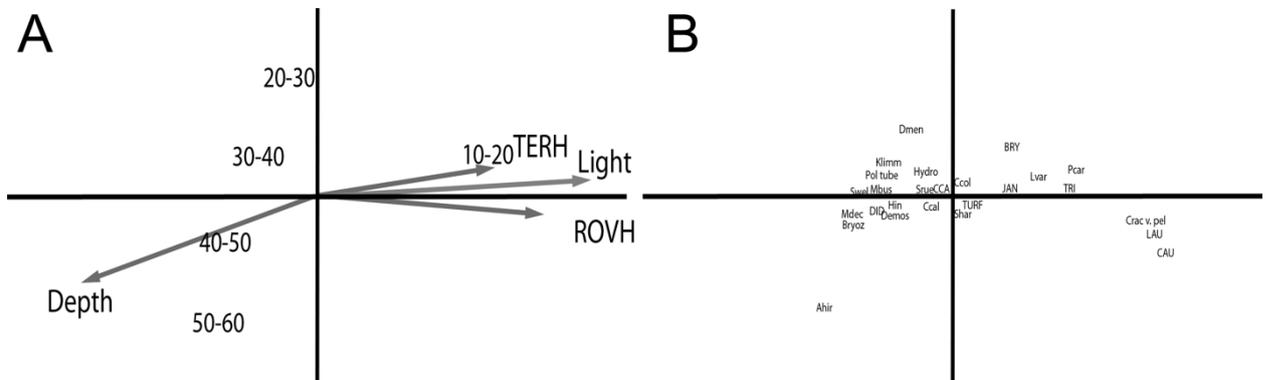


Figure 2 – 5.



Chapter 3

This chapter was prepared to be submitted for the Journal of the Marine Biological Association of the United Kingdom (JMBA). The leading author is Marcos Rogerio Rosa. Erica Oliveira Cavalcanti Coni, Paulo Yukio Gomes Sumida, Fabiano Lopes Thompson, Gilberto Menezes Amado-Filho & Ronaldo Bastos Francini-Filho are coauthors.

Bathimetric distribution, abundance, epibiosis, vitality and size of branching black-corals (Cnidaria: Antipatharia) in the mesophotic zone of the remote St. Peter and St. Paul's Archipelago (Mid Atlantic Ridge, Brazil)

3.1. Abstract

Branching black-corals, also called “precious corals”, provide an important 3-dimensional habitat for the associated biota, increasing benthic complexity and providing to reef organisms with key refuge at mesophotic depths (30-150 m). The ecology (depth distribution, abundance, epibiosis, vitality and size) of the antipatharian fauna of St. Peter and St. Paul's Archipelago (SPSPA), one of the most isolated oceanic archipelagos on the planet, was studied using a Remotely Operated Vehicle (ROV) in depths ranging between 0-90 m. Two black-coral species, *Tanacetipathes hirta* (Gray, 1857) and *T. thamnea* (Warner, 1981), were recorded continuously between 45-90 m depth. Overall density of colonies was $0.14 \pm (\text{SE}) 0.027 \text{ colonies.m}^{-2}$ with a maximum of $0.23 \pm (\text{SE}) 0.019 \text{ colonies.m}^{-2}$ between 70-90 m depth. Epibiosis by parasitic zoanthids (*Protopalythoa* sp.), bryozoans and sponges decreased vitality (i.e. proportion

of live tissue) of colonies. Black-corals were intensively used as microhabitat by seven species of reef fish, particularly the endemics *Prognathodes obliquus* (100% of all individuals observed), *Bodianus insularis* (33%) and *Stegastes sanctipauli* (10%). A single black-coral colony monitored for ten years showed a decrease in vitality, mainly because of overgrowth by algal detritus coming from the shallows and entanglement by fishing monofilament, this latter commonly found wrapping up colonies in the SPSPA. Because black-corals create important 3-dimensional microhabitats that serve as refuge and feeding grounds for several reef fish species (particularly threatened endemic species) in the mesophotic zone of the SPSPA, urgent conservation measures, such as banning the use of monofilament near the SPSPA, are suggested.

Keywords: Benthic complexity, endemic species, mesophotic reefs, microhabitat use, *Prognathodes obliquus*, *Tanacetipathes*.

3.2. Introduction

Branching corals increase benthic complexity and refuge availability, being thus widely recognized as a critical functional group on coral and rock reefs, as well as seamounts (Bellwood *et al.* 2004; Bo *et al.* 2008; Coni *et al.* 2013). Branching corals also provide fish with shelter against water motion (Johansen *et al.* 2008), as well as suitable microhabitat for small predators to ambush their prey (Holbrook and Schmitt 2002; Coni *et al.* 2013). Some fish species are highly dependent on branching corals for their survival (Ben-Tzvi *et al.* 2008), while other species may use several microhabitats (e.g. macroalgal and gorgonians) (Pollux *et al.* 2007; Tazioli *et al.* 2007; Salvati *et al.* 2010). Over large spatial scales, branching corals is generally an important variable affecting the structure of fish assemblages as a whole (Bell and Galzin 1984; Coni *et al.* 2013).

Black-corals (Antipatharians) are also called “precious corals” because they have a high monetary value, being harvested to manufacture jewelry and other art work, considered one of the most valuable living marine resources (Grigg, 1974; 1976; Huang and Ou, 2010; Tsounis *et al.*, 2010).

Black-coral beds have been suffering with anthropogenic impacts all over the world in the last decades, mainly by bottom trawling (Koslow *et al.*, 2001; Murillo *et al.*, 2011) and extraction for the ornamental trade (Grigg, 1974; 1976; 2001; Huang and Ou, 2010, Tsounis *et al.*, 2010). Many areas are currently overexploited and the harvesting of black-corals was banned by the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES) since 1981 (Olsen and Wood, 1980; Romero, 1997; Green and Hendry, 1999; Bruckner, 2001; Harriott, 2003; Maldonado, 2003; Padilla and Lara, 2003; Wagner and Tönen, 2012). However, information on the main

threats to black-corals is still relatively scarce, mostly due to the difficulties in accessing their habitats (Wagner and Tonen, 2012).

Besides studies on overexploitation impacts, most research about black-corals to date have focused on their taxonomy (Opresko, 1972; 1974; Loiola and Castro, 2001; Castro *et al.*, 2006; 2010). Available ecological studies include information on bathymetric distribution, new occurrences, associated fauna and physical factors influencing population parameters, with data for Hawaii (Sánchez *et al.*, 1998; Grigg, 1965; 1993; Khang *et al.*, 2005; Wagner *et al.*, 2010), the Caribbean (Warner, 1981; Sanchez, 1999; Padilla and Lara, 2003), the Red Sea (Bo *et al.*, 2011; Salvati *et al.*, 2010; Tarzioli *et al.*, 2007) and the Great Barrier Reef (Bridge *et al.*, 2011a, b; Bungaerts *et al.*, 2011).

In Brazil, black-corals occur throughout the Southeast and Northeast coasts (Loiola and Castro, 2001; Castro *et al.*, 2006; 2010) and have been studied only in terms of taxonomy (Castro, 1994; Echeverría and Castro, 1995; Loiola and Castro, 2001; 2005; Echeverría, 2002). Despite their importance, little is known about the basic biology and ecology of black-corals in Brazil, and about the *Tanacetipathes* genus in Brazil and elsewhere (Wagner and Tonen, 2012).

While shallow euphotic reefs (0-30 m depth) are characterized by the dominance of scleractinian corals and algae, mesophotic reef ecosystems (MREs) are characterized by the presence of specific light-dependent corals and associated communities in tropical and subtropical regions. Sponges, calcareous algae, gorgonians and black-corals dominate MREs at depths ranging from 30 to over 150 m (Boland and Parrish 2005; Bo *et al.*, 2008; 2011a; Hinderstein *et al.*, 2010; Kahng *et al.*, 2010) and MREs are considered transition zones between shallow and deep reefs (Lang, 1974; Liddell and

Ohlhorst, 1988). Branching black-corals are key organisms of MREs and act as ecosystem engineers, since they attain relatively large sizes, from just a few centimetres to a few meters in height, and increase benthic complexity, thus providing refuge for several organisms, including arthropods, annelids, echinoderms, mollusks, sponges, cnidarians and fish, several of which are adapted to live exclusively over/within black-coral colonies and to show particular co-evolutionary strategies (Boland & Parrish 2005; Bo *et al.*, 2008; 2009; 2011a, b; Tazioli *et al.*, 2007; 2010).

This is the first work focusing on the ecology of branching black-corals from Brazilian waters. The aim here is to quantitatively describe the depth distribution, abundance, epibiosis, vitality and size of these organisms in the Saint Peter and Saint Paul's Archipelago (SPSPA) in order to discuss the hypothesis that they may function as an important microhabitat for endemic and threatened reef fish.

3.3. Materials and methods

3.3.1. Study area

The SPSPA is a small group of five islets and rocks (total emerged area ~15,000 m²) located in the central equatorial Atlantic Ocean, just above the Mid Atlantic Ridge and about 1,000 km off the northeastern Brazilian coast of (Figure 3 – 1) (Edwards & Lubbock 1983a, b, Feitoza *et al.* 2003). The SPSPA is influenced by the South Equatorial Current, which flows westward, as well as by the Equatorial Undercurrent, which flows eastward below the surface, in depths between 40-150 m. The area of reefs <100 m depth is about 0.5 km² (Edwards & Lubbock 1983a, b). Shallow rocky reefs of the SPSPA are covered mainly by the zoanthid *Palythoa caribaeorum* and species of

algae of the genera *Bryopsis*, *Caulerpa* and *Dictyota*. In depths > 30 m, most common organisms are the scleractinian corals *Madracis decactis* and *Scolymia wellsi*, crustose calcareous algae and bryozoans. Sponges and black-corals of the genus *Tanacetipathes* are relatively abundant in depths > 40 m (Edwards & Lubbock 1983a, b, Feitoza *et al.* 2003).

3.3.2. Sampling procedures

Sampling was performed using video image records obtained with a Remote Operated Vehicle (ROV; VideoRay Explorer equipped with external lights and a laser scale) during four expeditions between September 2010 and June 2011. A total of 60 days of fieldwork and 52 5-min ROV video samples were obtained. Abundance of black-corals was estimated in about 4 m radius for each 5 min sample. A single conspicuous colony at 45 m depth was monitored at irregular time-intervals in 2003, 2010, 2011 and 2013. Vitality is defined here as the proportion of live tissue versus dead, injured (unusual color and presence of dark spots or bands) and tissue overgrown by epibionts. The two different *Tanacetipathes* species that occur in the SPSPA could be only occasionally identified to the species level according to their general morphology (area and messiness) and colour, being thus pulled for the quantitative analyses.

Relative cover of black-corals was quantified from 30 still frames obtained from each 5-min video sample. Frames were captured from video images every 10 seconds avoiding overlap between frames. The total analyzed area was ca. 0.7 m². The following categories were used to characterize benthic cover: bare rock, black-corals, *Caulerpa* spp., crustose coralline algae, fleshy macroalgae (other than *Caulerpa* spp.),

hydrozoans, live scleractinian corals, sediment, turf algae and zoanthids (see Chapter 2). The inclination of colonies in relation to the substrate was visually estimated.

3.3.3. Data analyses

Analyses were performed considering depth strata of 10 m intervals. Samples between 70 and 90 m depth were grouped into a single category in order to satisfy ANOVA assumptions.

One-way analysis of variance (ANOVA) was applied to evaluate variations in black-coral abundance (number of colonies per sample), relative cover and colony size (colony height) between depth strata. Student-Newman-Keuls (SNK) multiple comparisons of means were performed as a *post-hoc* test (Zar 1999). Separate multiple regressions were applied to evaluate the influence of depth, benthic complexity and cover of different benthic organisms on the abundance, size and vitality of black-corals.

3.4. Results

A total of 134 black coral colonies were recorded, with a global average density of $0.14 \pm (\text{SE}) 0.027$ colonies.m⁻² (Table 3 – 2). Black-corals were recorded from 40 m to 90 m depth. The colonies were fixed on rocky substrates with an average angle of $104^\circ \pm (\text{SE}) 2.37^\circ$. No significant differences in abundance (absolute abundance and relative benthic cover), vitality (proportion of live tissue) and size of colonies (height) were recorded between depth strata (Figure 3 – 2 and 3).

The multiple regression showed a significant ($p < 0.000$) positive relationships between number of black-coral colonies and depth ($\beta = 0.28$, $p = 0.017$), and negatively relationships with abundance of zoantids ($\beta = -0.79$, $p < 0.000$), *Caulerpa racemosa* ($\beta = -0.77$, $p < 0.000$), bryozoans ($\beta = -0.77$, $p < 0.000$), crustose coralline algae ($\beta = -0.64$, $p < 0.000$), other corals ($\beta = -0.61$, $p < 0.000$), sediment ($\beta = -0.25$, $p = 0.00065$), polychaeta tubes ($\beta = -0.16$; $P = 0.015$), bare rocky ($\beta = -0.12$, $p < 0.000$) and turf algae ($\beta = -0.10$, $p < 0.000$).

From all the studied colonies, 82.6% were classified as fully healthy and 17.4% were considered as either partially dead or injured, with all colonies below 70 meters health. Shallower colonies (40-50 m depth) were less healthy than deeper ones, although no significant difference on healthy status according to depth strata were found (ANOVA, $p > 0.05$). The multiple regression model showed that substrate inclination positively influenced the health of the colonies ($\beta = 0.35$, $p = 0.00072$). The amount of epibiosis varied significantly with depth (ANOVA, $p < 0.005$) with colonies within the deepest strata (> 70 m) showing no signs of epibiosis. Epibionts were detected in 52.3% of colonies, mainly the zoanthid *Protopalythoa* sp., sponges and bryozoans. The overall average of colonies covered by epibionts was $7.86\% \pm$ (SE) 3.9%. Drifting algae and sediments (“sediment snow”) from shallow reefs were recorded over 8.8% of the colonies, but never at depths > 70 meters.

The single black-coral colony monitored between 2003 to 2013 showed a decrease of 50% in vitality during the sampling period (Figure 3 – 2). During this period we observed an increase of algal detritus coming from the surface (45%), a sponge growing on its base (5%), and the impact of a nylon fishing line wrapped up on the colony.

Seven reef fish species were recorded using black-corals as shelter and/or feeding grounds, mainly the endemic species *Prognathodes obliquus* (oblique butterflyfish; 37 individuals), *Stegastes sanctipauli* (Saint Paul's gregory; 6 individual) and *Bodianus insularis* (island hogfish; 3 individuals). Other species included the Queen angelfish *Holocanthus ciliaris*, the black triggerfish *Melichthys niger*, the yellowtail reef fish *Chromis enchrysur* and the brown chromis *C. multilineata*.

3.5. Discussion

This is the first ecological study of antipatharian corals in the South Atlantic Ocean, including a detailed description of a unique oceanic black-coral meadow off Brazil. It is also the first evaluation of the population structure of the genus *Tanacetipathes* (see Wagner and Tonen, 2012).

Black-corals of the SPSPA form a mixture of colonies of two *Tanacetipathes* species, which were indistinguishable in video analyses. Considering the Myriopathidae family, the abundance estimates presented here are many times higher than those available for *Plumapathes pennacea* from the Mediterranean Sea (Olsen and Wood, 1980; Sanches, 1999), similar to those for *Antipathella* spp. from New Zealand (Grange, 1985) and much lower than those for *Myriopathes ulex* from Hawaii (Wagner *et al.*, 2011) and *Antipathella subpinnata* from the Mediterranean Sea (Bo *et al.*, 2008; 2009b). Black-coral beds are a common feature on seamounts, lower fringe reefs, deep rocky banks and other hard bottoms in the mesophotic zone with favorable hydrodynamic conditions (Bo *et al.*, 2008; 2009; 2011; 2013). They propitiate a unique three-dimensional forest-like habitat, essential for a huge variety of organisms that use

them as feeding grounds, refuge and nursery habitats (Roberts *et al.*, 2006, Wagner and Tonen, 2012; Bo *et al.*, 2013).

Factors limiting the distribution of black-corals have been discussed in several studies (Bo *et al.*, 2008, Wagner and Tonen, 2012; Tazioli *et al.*, 2007; Grange and Singleton, 1988). Bo *et al.* (2008) working on the distribution of *Antipathella subpinnata*, emphasize that the main factor shaping the distribution of black-corals is temperature, and that 15°C is a maximum limit for them. However, Wagner and Tonen (2012) argue that light is the main limiting factor, with most species occurring below 50 meters, with those living in shallower water inhabit mainly crevices, caves or turbid waters where light levels are low. On the other hand, Tarzioli *et al.* (2007) showed rich and abundant antipatharian faunas living in well-lit high, constant temperature (27-28°C) shallow reefs. Tarzioli *et al.* (2007) suggest that competition for space can be the main factor shaping the distribution of some species of black-corals.

The substrate cover of shallow zone of SPSPA is dominated by the zoanthid *Palythoa caribaeorum* and by the fleshy macroalgae *Caulerpa racemosa* and *Bryopsis* spp. (see Chapter 2 in this thesis), impeding the fixation/growth of others organisms. Cover of benthic organisms become more sparse in depths greater than 30 meters, suggesting that black-corals may escape competition with photosynthetic fast growing organism at mesophotic depths where bare rock become more common (McCook *et al.* 2001). This latter hypothesis was supported by the results of the multiple regression analysis. Although there are some evidences that black-coral have secondary metabolites and may make use of allelopathy to compete for space (Qi *et al.*, 2009; Bai *et al.*, 2011), macroalgae and zoanthids are known to be competitively superior to most other benthic organisms at shallow depths (Suchanek and Green, 1982; McCook, *et al.* 2001), while black-corals have, comparatively, limited abilities to compete for space

(Wagner and Tonen, 2012). The arborescent shape of *Tanacetipathes*, may also cause difficulties in substrate fixation, growth and permanence in shallow, turbulent waters (Tarzioli *et al.*, 2007, Wagner and Tonen, 2012). In the SPSPA, black-coral colonies were recorded exclusively where the slope is steep, nearly 90° from horizontal, in depths > 40 m depth. It has been suggested that particular wind regimes may induce surfacing of the Equatorial Undercurrent in the SPSPA (Bowen, 1966), possibly enriching the mesophotic zone with zooplankton. This is supported by the abrupt drops in temperature of up to 5 °C recorded in depths between 30-40 m in this study, and by large number of planktivorous fish recorded at this depth strata (see chapter 1 on this thesis). The angle of fixation of the black-coral colony in the substrate is important to its survival (Tarzioli *et al.*, 2007; Salvati *et al.*, 2010; Bo *et al.* 2008; 2010; 2011). They may also select for favorable sites in which topography accelerates currents, such as the borders of seamounts, pinnacles and steep slopes of oceanic islands, areas generally enriched with zooplankton used by these suspension feeders (Grigg, 1964; Grange and Singleton, 1988; Parrish and Baco, 2007; Tarzioli *et al.*, 2007; Bo, 2008).

Branching black-corals are known to host a diverse fauna (Buhl-Mortensen, 2004; Salvati *et al.*, 2010; Bo *et al.* 2010; 2011; Gori *et al.*, 2011), being thus a key functional group in MREs (Bo *et al.*, 2007). The black-coral beds of the SPSPA appears to be essential for reef fish, especially for *Prognathodes obliquus* and *Bodianus insularis*, both endemic species, which can use them for feeding and refuge (Chapter 1 in this thesis).

The main predators of black-corals in the SPSPA are the endemic oblique butterflyfish *Prognathodes obliquus* and the bearded fireworm *Hermodice carunculata*, both abundant at mesophotic depths (Chapter 1 and 4 in this thesis). *Prognathodes obliquus* was frequently recorded foraging over black-coral colonies, but we could not

distinguish if they are preying upon the black-corals and/or over epibiontes. Fish are the most common vertebrates observed biting on black-corals, but the reports are sporadic, indicating that it is not regular component of fish diet or that additional studies are necessary (Wagner and Tönen 2012). In contrast to the sporadic nature of records of vertebrate preying upon black-corals, some invertebrates appear to be specialized to predate on them, including molluscan families Muricidae (*Rhizochilus* sp., *R. antipathum*, *R. teramachii* and *Coralliophila kaofitorum*), and the ovullid *Phenacovolva carnepicta* and *Phenacovolva weaver* (Totton, 1923; Rees, 1969; Okamura and Habe, 1976; Poorman, 1981; Vega *et al.*, 2002). With the exception of a few predators such as gastropods, parrotfishes, butterflyfishes and the green sea turtle, antipatharians appear to be little impacted by predation (Goenaga, 1977; Grange and Singleton, 1988; Tazioli *et al.*, 2007; Bo, 2008). A production of deterrent compounds by Antipatharia are also described (Qi *et al.*, 2009; Al-Lihaibi *et al.*, 2011; Bai *et al.*, 2011), additionally the tissue of black-corals are of low nutritional value (Goldberg, 1976). Because of the extremely high abundances of *Hermodice carunculata* in the SPSPA, and because they are frequently seen preying upon black-corals (Pers. Obs), further studies on this relationship are warranted.

On the other hand, more attention is being given to the impact of black-coral harvesting (Grigg, 1976; Bruckner *et al.*, 2008) and to the damage caused by fishing gears (Mortensen and Buhl-Mortensen, 2004; Bo *et al.*, 2009), leading to the application of a series of protective measures around the globe (Bruckner *et al.*, 2008; Deidun *et al.*, 2010; Tsounis *et al.*, 2012, Aguilar and Marin, 2013). The entanglement of black-coral colonies with monofilament is a problem that deserves urgent attention, which may be mitigated with simple measures (e.g. banning line fishing around the ASPSP).

This is the first study about the ecology of black-corals in Brazil, and the first one to focus on the ecology of *Tanacetipathes*, precluding more detailed comparisons. The occurrence of Antipatharians range from tropical to polar latitudes (Wagner and Tonen, 2012), but the logistical challenging to access the habitats in which they live (most bellow 50 m) impedes detailed studies (Wagner and Tonen, 2012). Thus, most of the available information is based on type locality of museum housed specimens, taxonomic description and reports material collected during oceanographic expedition (Opresko, 1972; 1974; Loiola and Castro, 2001; Castro *et al.*, 2006; 2010; Wagner and Tonen, 2012). There is a clear need of additional studies on MREs with larger sample sizes and focusing on different geographical regions, in order to allow broader biological and ecological generalizations regarding the ecology and biogeography of antipatharians (Wagner and Tonen, 2012).

In several places around the world, fully-protection of black-coral beds have been implemented (Grigg *et al.*, 1977; 1984; 1989; Aguilar & Marin, 2013) and held as special ecological ecosystems, requiring protection contemplated under the Convention of Biological Diversity (UNEP, 2007). In addition, the Food and Agriculture Organization of the United Nations (FAO) considered black-coral beds as sensitive habitats, classifying them as Vulnerable Marine Ecosystems (VMEs) potentially impacted by human actions (FAO, 2009). Considering the essential habitat created by black-corals and that they represent the most characteristic component of the mesophotic zone of the SPSPA, there is an urgent need to protect them, which could be done by excluding line fishing activities around the archipelago.

3.6. Literature cited

- Adams, A. J.; Ebersole, J. P. 2002. Use of back-reef and lagoon habitats by coral reef fishes. *Marine Ecology Progress Series*, v. 228, p. 213-226.
- Aguilar, R.; Marin, P. 2013. Mediterranean deep-sea corals: reasons for protection under the Barcelona Convention. *Oceana* (September 2013) http://oceana.org/sites/default/files/euo/OCEANA_Brief_Deep-sea_Corals.pdf
- Al-Lihaibi, S. S.; Ayyad, S.-E. N.; Shaher, F.; Alarif, W. M. 2011. ChemInform abstract: Antibacterial sphingolipid and steroids from the black coral *Antipathes dichotoma*. *ChemInform*, v. 42.
- Bai, X., Chen, Y., Lei, H., and Shi, G. 2011. Volatile constituents, inorganic elements and primary screening of bioactivity of black coral cigarette holders. *Marine Drugs*, v. 9, 863–878.
- Bellwood, D. R.; Hoey, A. S.; Choat, J. H. 2003. Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecology Letters*, v. 6, p. 281-285.
- Bo, M.; Tazioli, S.; Spanò, N.; Bavestrello, G. 2008. *Antipathella subpinnata* (Antipatharia, Myriopathidae) in Italian seas. *Italian Journal of Zoology*, v. 75, p. 185–195.
- Bo, M.; Bavestrello, G.; Canese, S.; Giusti, M.; Salvati, E.; Angiolillo, M.; Greco S. 2009. Characteristics of a black coral meadow in the twilight zone of the central Mediterranean Sea. *Marine Ecology Progress Series*, v. 397, p. 53-61
- Bo, M.; Bertolino, M.; Borghini, M.; Castellano, M.; Harriague, A. C.; Di Camillo, C. G. 2011. Characteristics of the mesophotic megabenthic assemblages of the Vercelli seamount (North Tyrrhenian Sea). *PloS one*, v. 6, n. 2, e16357.
- Bo, M.; Bavestrello, G.; Canese, S.; Giusti, M.; Angiolillo, M.; Cerrano, C.; Salvati, E. 2011. Coral assemblage off the Calabrian Coast (South Italy) with new observations on living colonies of *Antipathes dichotoma*. *Italian Journal of Zoology*, v. 78, n. 2, p. 231-242

- Bo, M.; Cerrano, C.; Canese, S.; Salvati, E. Angiolillo, M.; Santangelo, G.; Bavestrello, G. 2013. The coral assemblages of an off-shore deep Mediterranean rocky bank (NW Sicily, Italy). *Marine Ecology*,
- Boland, R. C.; Parrish, F. A. 2005. A description of fish assemblages in the black coral beds off Lahaina, Maui, Hawai'i. *Pacific Science*, 59, 411–420.
- Bonatti, E. 1990. Subcontinental mantle exposed in the Atlantic Ocean on St Peter-Paul islets. *Nature*, v. 345, p. 800-802.
- Bridge, T. C. L.; Done, T. J.; Beaman, R. J.; Friedman, A.; Williams, S. B.; Pizarro, O.; Webster, J. M. 2011a. Topography, substrate and benthos relationships on a tropical mesophotic shelf margin. *Coral Reefs*, v. 30, p. 143–153.
- Bridge, T. C. L.; Done, T. J.; Friedman, A.; Beaman, R. J.; Williams, S. B.; Pizarro, O.; Webster, J. M. 2011b. Variability in mesophotic coral reef communities along the Great Barrier Reef. *Mar Ecol Prog Ser*, v. 428, p. 63–75.
- Bruckner, A. W. 2001. Tracking the trade in ornamental coral reef organisms: The importance of CITES and its limitations. *Aquarium Sciences and Conservation*, v. 3, p. 79–94.
- Bruckner, A.; De Angelis, P.; Montgomery, T. 2008. Case study for black coral from Hawaii. International Expert Workshop on CITES Non-detriment Findings, Cancun, Mexico (November 2008). http://www.conabio.gob.mx/institucion/cooperacion_internacional/TallerNDF/Links-Documentos/WG-CS/WG9-AquaticInvertebrates/WG9-CS1%20BlackCoral/WG9-CS1.pdf
- Buhl-Mortensen, L.; Buhl-Mortensen, P. 2004. Symbiosis in deep-water corals. *Symbiosis*, v. 37, p. 33–61.
- Bungaerts, T. C. L.; Bridge, D. I.; Kline, P. R.; Muir, C. C.; Wallace, R. J.; Hoegh-Guldberg, O. 2011. Mesophotic coral ecosystems on the walls of Coral Sea atolls. *Coral Reefs*, v. 30, n. 2.

- Caley, M. J.; Buckley, K. A. Jones, G. P. 2001. Separating ecological effects of habitat fragmentation, degradation, and loss on coral commensals. *Ecology*, v. 82, p. 3435-3448.
- Castro, C. B.; Pires, D. O.; Medeiros, M. S.; Loiola, L. L.; Arantes, R. C. Cnidaria: Corais. In: Lavrado HP, Ignácio BL. Biodiversidade bêntica da costa central brasileira. Rio de Janeiro: Museu Nacional – UFRJ. p. 147-192. 2006.
- Castro, C. B.; Medeiros, M. S.; Loiola, L. L. 2010. Octocorallia (Cnidaria: Anthozoa) from Brazilian reefs. *Journal of Natural History*, v. 44, p. 763-827
- Chappell, J. 1980. Coral morphology, diversity, and reef growth. *Nature*, v. 286, p. 249-252.
- Clarke, K. R.; Warwick, R. M. 1994. Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory: Plymouth.
- Deidun, A.; Tsounis, G.; Balzan, F.; Micallef, A. 2010. Records of black coral (*Antipatharia*) and red coral (*Corallium rubrum*) fishing activities in the Maltese Islands. *Marine Biodiversity Records*, v. 3, p. 90.
- Dubinsky, Z.; Stambler, N. (Eds.) 2011. *Coral Reefs: An Ecosystem in Transition* Springer Dordrecht Heidelberg, London, New York. 549 pp.
- Echeverría, C. A.; Castro, C. B. 1995. *Antipathes* (Cnidaria, Antipatharia) from Southeastern Brazil. *Boletim do Museu Nacional. Zoologia*, Rio de Janeiro, n. 364, p. 1-7.
- Echeverría, C. A. 2002. Black corals (Cnidaria: Anthozoa: Antipatharia): first records and a new species from the Brazilian coast. *Rev. Biol. Trop.* V. 50, p. 1067–1077.
- Edwards A, Lubbock R. 1983a. Marine zoogeography of St. Paul's Rocks. *J Biogeogr* 10:65-72
- Edwards A, Lubbock R. 1983b. The ecology of Saint Paul's Rocks (Equatorial Atlantic). *J Zool*, v. 200, p. 51-69.
- FAO. 2009. *International Guidelines for the Management of Deep-sea Fisheries in the High Seas*. FAO, Rome, Italy, 73pp.

- Feitoza, B. M.; Rocha, L. A.; Luiz, O. J.; Floeter, S. R.; Gasparini, J. L. 2003. Reef fishes of St. Paul's Rocks: new records and notes on biology and zoogeography. *Aqua J Ichthyol Aquatic Biol*, v. 7, p. 61-82.
- Ferner, M. C.; Smee, D. L.; Weissburg, M. J. 2009. Habitat complexity alters lethal and nonlethal olfactory interactions between predators and prey. *Mar Ecol-Prog Ser*, v. 374, p. 13-22.
- Folke, C.; Carpenter, S.; Walker, B.; Scheffer, M.; Elmqvist, T.; Gunderson, L.; Holling, C. S. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annu Rev Ecol Evol Syst*, v. 35, p. 557-581.
- Gori, A.; Rossi, S.; Linares, C.; Berganzo, E.; Orejas, C.; Dale, M. R. T.; Gili, J. M. 2011. Size and spatial structure in deep versus shallow populations of the Mediterranean gorgonian *Eunicellasingularis* (Cap de Creus, northwestern Mediterranean Sea). *Marine Biology*, v. 158, n. 8, p. 1721-1732.
- Grange, K. R.; Singleton, R. J. 1988. Population structure of a black coral, *Antipathes aperta*, in the southern fiords of New Zealand. *NZ J Zool*, v. 15, p. 481-489.
- Green, E. P.; Hendry, H. 1999. Is CITES an effective tool for monitoring trade in corals? *Coral Reefs*, v. 18, p. 403-407.
- Grigg, R. W. 1964. A contribution to the biology and ecology of the black coral, *Antipathes grandis* in Hawai'i. MS Thesis in Zoology, p. 74. Hawai'i, Honolulu.
- Grigg, R. W. 1965. Ecological studies of black coral in Hawai'i. *Pacific Science* 19, 244-260.
- Grigg, R. W. 1974. Distribution and abundance of precious corals. *Proceedings of the Second International Coral Reef Symposium*, v. 2, p. 235-240.
- Grigg, R. W. 1976. Fishery management of precious and stony corals in Hawaii. Sea Grant Technical Report. UNHI-SEAGRANT-TR-77-03 p. 48.
- Grigg, R. W. 1977. Population dynamics of two gorgonian corals. *Ecology*, n. 1991, n. 58, p. 278-290.

- Grigg, R. W. 1984. Resource management of precious corals: A review and application to shallow water reef building corals. *Marine Ecology*, v. 5, p. 57–74.
- Grigg, R. W. 1988. Recruitment limitation of a deep benthic hard-bottom octocoral population in the Hawaiian Islands. *Mar. Ecol. Prog. Ser.*, v. 45, p. 121-126.
- Grigg, R. W. 1989. Precious coral fisheries of the Pacific and Mediterranean. In J. F. Caddy (Editor), *Marine invertebrate fisheries: Their assessment and management*, p. 637-645.
- Grigg, R. W. 1993. Precious coral fisheries of Hawaii and the U.S. Pacific Islands. *Mar. Fish. Rev.*, v. 55, p. 50-60.
- Grigg, R. W. 2001. Black coral: History of a sustainable fishery in Hawai‘i. *Pacific Science*, v. 55, p. 291–299.
- Harriott, V. J. 2003. Can corals be harvested sustainably? *Ambio*, v. 32, p. 130–133.
- Hinderstein, L. M.; Marr, J. C. A.; Martinez, F. A.; Dowgiallo, M. J.; Puglise, K. A.; Pyle, R. L.; Zawada, D. G.; Appeldoorn, R. 2010. Introduction to mesophotic coral ecosystems: characterization, ecology, and management. *Coral Reefs*, v. 29, p. 247-251.
- Huang, M. H.; Ou, C. H. 2010. Precious coral fisheries management in Taiwan – past, present & future. *Marine Policy*, v. 34, p. 1002–1009.
- Hughes, T. P.; Tanner, J. E. 2000. Recruitment failure, life histories, and long-term decline of Caribbean corals. *Ecology*, v. 81, p. 2250-2263.
- Huston, M. A. 1985. Patterns of species diversity on coral reefs. *Annual Review of Ecology and Systematics*, v. 16, p. 149–177.
- Jones, G. P.; McCormick, M. I.; Srinivasan, M.; Eagle, J. V. 2004. Coral decline threatens fish biodiversity in marine reserves. *Proc Natl Acad Sci U S A*, v. 101, p. 8251-8253.
- Kahng, S. E., Grigg, R. W. 2005. Impact of an alien octocoral (*Carijoa riisei*) on black corals in Hawaii. *Coral Reefs*, v. 24, n. 4, p. 556-562.

- Kahng, S. E., Spalding, H. L.; Brokovich, E.; Wagner, D.; Weil, E.; Hinderstein, L.; Toonen, R. J. 2010. Community ecology of mesophotic coral reef ecosystems. *Coral Reefs*, v. 29, p. 255-275.
- Koslow, J. A.; Gowlett-Holmes, K.; Lowry, J. K.; O'Hara, T.; Poore, G. C. B.; Williams, A. 2001. Seamount benthic macrofauna off southern Tasmania: Community structure and impacts of trawling. *Marine Ecology Progress Series*, v. 213, p. 111–125.
- Lang, J. C. 1974. Biological zonation at the base of a reef. *Am Sci*, v. 62, p. 272-281.
- Liddell, W. D.; Ohlhorst, S. L. 1988. Hard substrata community patterns, 1–120 M, North Jamaica. *Palaios*, v. 3, p. 413–423.
- Loiola, L. L.; Castro, C. B. 2001. Three new records of Antipatharia (Cnidaria) from Brazil, including the first record of a Schizopathidae. *Boletim do Museu Nacional*, v. 455, p. 1–10.
- Loiola, L. L.; Castro, C. B. 2005. *Tanacetipathes* Opresko, 2001 (Cnidaria: Antipatharia: Myriopathidae) from Brazil, including two new species. *Zootaxa*, v. 1081, p. 1–31.
- Loiola, L. L. 2007. Black corals (Cnidaria: Antipatharia) from Brazil: an overview. *Bulletin of Marine Science*, v. 81, p. 253-264.
- Lumpkin, R.; Garzoli, S. L. 2005. Near-surface Circulation in the Tropical Atlantic Ocean. *Deep-Sea Res.*, v. 52, n. 3, p. 495-518.
- McCook, L.; Jompa, J.; Diaz-Pulido, G. 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs*, v. 19, n. 4, p 400-417.
- Maldonado, A. 2003. Cuba's environment: today and tomorrow - an action plan. *Coral Gables, Florida*. p. 63-73.
- Ménard, A.; Turgeon, K.; Roche, D. G.; Binning, S. A.; Kramer, D. L. 2012. Shelters and Their Use by Fishes on Fringing Coral Reefs. *PLoS ONE*, v. 7, n. 6, p. e38450 .

- Mumby, P. J.; Dahlgren, C. P.; Harborne, A. R.; Kappel, C. V.; Micheli, F.; Brumbaugh, D. R.; Holmes, K. E.; Mendes, J. M.; Box, S.; Broad, K.; Sanchirico, J. N.; Buch, K.; Stoffle, R. W.; Gill, A. B. 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. *Science*, v. 311, p. 98-101.
- Murillo, F. J.; Dura'n Muñoz, P.; Altuna, A.; Serrano, A. 2011. Distribution of deep-water corals of the Flemish Cap, Flemish Pass and the Grand Banks of Newfoundland (northwest Atlantic Ocean): interaction with fishing activities. *ICES Journal of Marine Science*, v. 68, p. 319–332.
- Okamura, S. I.; Habe, T. 1976. The strange habit of *Rhizochilus teramachii* Kuroda. *Venus* 35, 91–92.
- Olsen, D. A.; Wood, R. S. 1980. Investigations on black coral in Salt River Submarine Canyon Saint Croix, U.S. Virgin Islands (Final Scientific Report 80-12), National Undersea Laboratory System, St. Croix, Virgin Islands.
- Opresko, D. M. 1972. Redescriptions of antipatharia described by L.F. Pourtales. *Bull. Mar. Sci.*, v. 22, n. 4, p. 950-1017.
- Opresko, D. M. A 1974. study of the classification of the Antipatharia (Coelenterata: Anthozoa) with redescriptions of eleven species. Ph.D. Diss, University of Miami, Coral Gables. 194 p.
- Padilla, C.; Lara, M. 2003. Banco Chinchorro: The last shelter for black coral in the Mexican Caribbean. *Bulletin of Marine Science*, v. 73, p. 197–202.
- Pandolfi, J. M.; Jackson, J. B. C. 2006. Ecological persistence interrupted in Caribbean coral reefs. *Ecology Letters*, v. 9, n. 7, p. 818–826.
- Parrish, F. A.; Baco, A. R. 2007. State of Deep Coral Ecosystems in the U.S. Pacific Islands Region: Hawaii and the U.S. Pacific Territories. pp. 155–194. In “The State of Deep Coral Ecosystems in the United States” (S. E. Lumsden, T. F. Hourigan, A. W. Bruckner and G. Dorr, eds), p. 365. NOAA Technical Memorandum CRCP-3, Silver Spring, MD.
- Poorman, L. H. 1981. *Rhizochilus* in the Gulf of California. *Veliger*, v. 24, p. 165–166.

- Qi, S. H.; Su, G. C.; Wang, Y. F.; Liu, Q. Y.; Gao, C. H. 2009. Alkaloids from the South China Sea black coral *Antipathes dichotoma*. *Chemical & Pharmaceutical Bulletin* 57, 87–88.
- Rees, W. J. 1969. A brief survey of the symbiotic associations of Cnidaria with Mollusca. *Proceedings of the Malacological Society of London*, v. 37, p. 213–231.
- Romero, X. M. 1997. Ecuador's vanishing black corals. *Aquaticus: Journal of the Shedd Aquarium*, v. 26, p. 21–25.
- Roberts, J. M.; Wheeler, A. J.; Freiwald, A. 2006. Reefs of the Deep: The Biology and Geology of Cold-Water Coral Ecosystems. *Science*, v. 312, p. 543.
- Rotjan RD, Lewis SM (2008) The impact of coral predators on tropical reefs. *Marine Ecology Progress Series*. 367: 73-91.
- Sale, P. F. 2002. Coral reef fishes/dynamics and diversity in a complex ecosystems. Edited by P. F. Sale. xiv 549 pp. Published by Academic Press, San Diego, 2002.
- Salvati E.; Angiolillo, M.; Bo, M.; Bavestrello, G.; Giusti, M.; Cardinali, A.; Puce, S.; Spaggiari, C.; Greco, S.; Canese, S. 2010. The population of *Errina aspera* (Hydrozoa: Stylasteridae) of the Messina Strait (Mediterranean Sea). *Journal of the Marine Biological Association of the United Kingdom*, v. 90, p. 1331-1336.
- Sánchez, J. A.; Zea, S.; Díaz, J. M. 1998. Patterns of octocoral and black coral distribution in the oceanic barrier reef-complex of Providencia Island, southwestern Caribbean. *Caribb. J. Sci.*, v. 34, p. 250-264.
- Sokal, R. R.; Rohlf, F. I. 1995. *Biometry: the principles and practice of statistics in biological research*. San Francisco: W.H. Freeman, 776 p.
- Spalding, M. D.; Ravilious, C.; Green, E. P. 2001. *World Atlas of Coral Reefs*. University of California Press, Berkeley, California.
- Suchanek, T. H.; Green, D. J. 1982. Interspecific competition between *Palythoa caribaeorum* and other sessile invertebrates on St. Croix reefs, U. S. Virgin Islands. *Proc. Fourth Int. Coral Reef Symp., Manila*, v. 2, p. 679-684.

- Syms, C.; Jones, G. P. 2000. Disturbance, habitat structure, and the dynamics of a coral-reef fish community. *Ecology*, v. 81, p. 2714-2729.
- Tazioli, S.; Bo, M.; Boyer, M.; Rotinsulu, H.; Bavestrello, G. 2007. Ecological observations of some common antipatharian corals in the marine park of Bunaken (North Sulawesi, Indonesia). *Zoological Studies*, v. 46, p. 227–241.
- Totton, A. K. 1923. Coelenterata. Part III-Antipatharia (and their cirripede commensals). British Antarctic (“Terra Nova”) Expedition, 1910, Natural History Report. *Zoology*, v. 5, p. 97–120.
- Tsounis, G.; Rossi, S.; Grigg, R. W.; Santangelo, G.; Bramanti, L.; Gili, J. M. 2010. The exploitation and conservation of precious corals. *Oceanography and Marine Biology: An Annual Review*, v. 48, p. 161–212.
- UNEP. 2007. Report on the expert workshop on ecological criteria and biogeographic classification system for marine areas in need of protection. UNEP/CBD/EWS.MPA/1/2.URL: <http://www.cbd.int/doc/meetings/mar/ewsebm-01/official/ewsebm-01-02-en.pdf>.
- Vega, R.; Luque, A. A. 2002. *Coralliophila kaofitorum*, a new species (Gastropoda: Coralliophilidae) from the Canary Islands living on *Antipathes wollastoni* (Cnidaria: Anthozoa: Antipatharia). *Nautilus*, v. 116, p. 50–55.
- Wagner, D.; Brugler, M. R.; Opresko, D. M.; France, S. C.; Montgomery, A. M.; Toonen, R. J. 2010. Using morphometrics, in situ observations and genetic characters to distinguish among commercially valuable Hawaiian black coral species; a redescription of *Antipathes grandis* Verrill, 1928 (Antipatharia: Antipathidae). *Invertebr. Syst.*, v. 24, p. 271 – 290.
- Wagner, D.; Papastamatiou, Y. P.; Kosaki, R. K.; Gleason, K. A.; McFall, G. B.; Boland, R. C; Pyle, R. L.; Toonen, R. J. 2011. New records of commercially valuable black corals (Cnidaria: Antipatharia) from the Northwestern Hawaiian Islands at mesophotic depths. *Pac Sci*, v. 65, p. 249–255.
- Wagner, D.; Toonen, R. M. R.; Brugler, D. M; Opresko, S. C.; France, A. D. 2010. Using Morphometrics, In Situ Observations and Genetic Characters to Distinguish Among Commercially Viable Hawaiian Black Coral Species; A Redescription of

Antipathes grandis Verrill, 1928 (Antipatharia: Antipathidae). *Invertebrate Systematics*, v. 24, n. 3, p. 271-290.

Warner, G. F. 1981. Species descriptions and ecological observations of black corals (Antipatharia) from Trinidad. *Bulletin of Marine Science*, v. 31, p. 147-163.

Wilkinson, C. 2004. *Status of Coral Reefs of the World: 2004*. Australian Institute of Marine Science, Townsville, Australia.

Wilson, S. K.; Graham, N. A. J.; Pratchett, M. S.; Jones, G. P.; Polunin, N. V. C. 2006. Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Global Change Biol.*, v.12, p. 2220-2234.

Zar, J. H. 1999. *Biostatistical analysis*, 4th edition. New Jersey: Prentice-Hall.

3.7. Legend for figures

Figure 3 – 1. Maps showing: (A) the location of the St. Peter and St. Paul Archipelago (SPSPA) and other Brazilian oceanic islands in the South Atlantic Ocean; (B) detail of the sampling area (light grey); the arrow indicates the depth gradient sampled; (C) schematic depth profile of photosynthetically active radiation incident in each depth strata.

Figure 3 – 2. Abundance and distribution of black-corals between 0 -100 m depth. The occurrence of colonies started at 45 m to over 90 m depth.

Figure 3 – 3. a) Relative cover of branching black-corals (mean + SE) according to depth strata and b) Height of black-corals (cm) (mean + SE) according to depth strata.

Figure 3 – 4. The single black-coral colony monitored in 2003, 2010 and 2013.

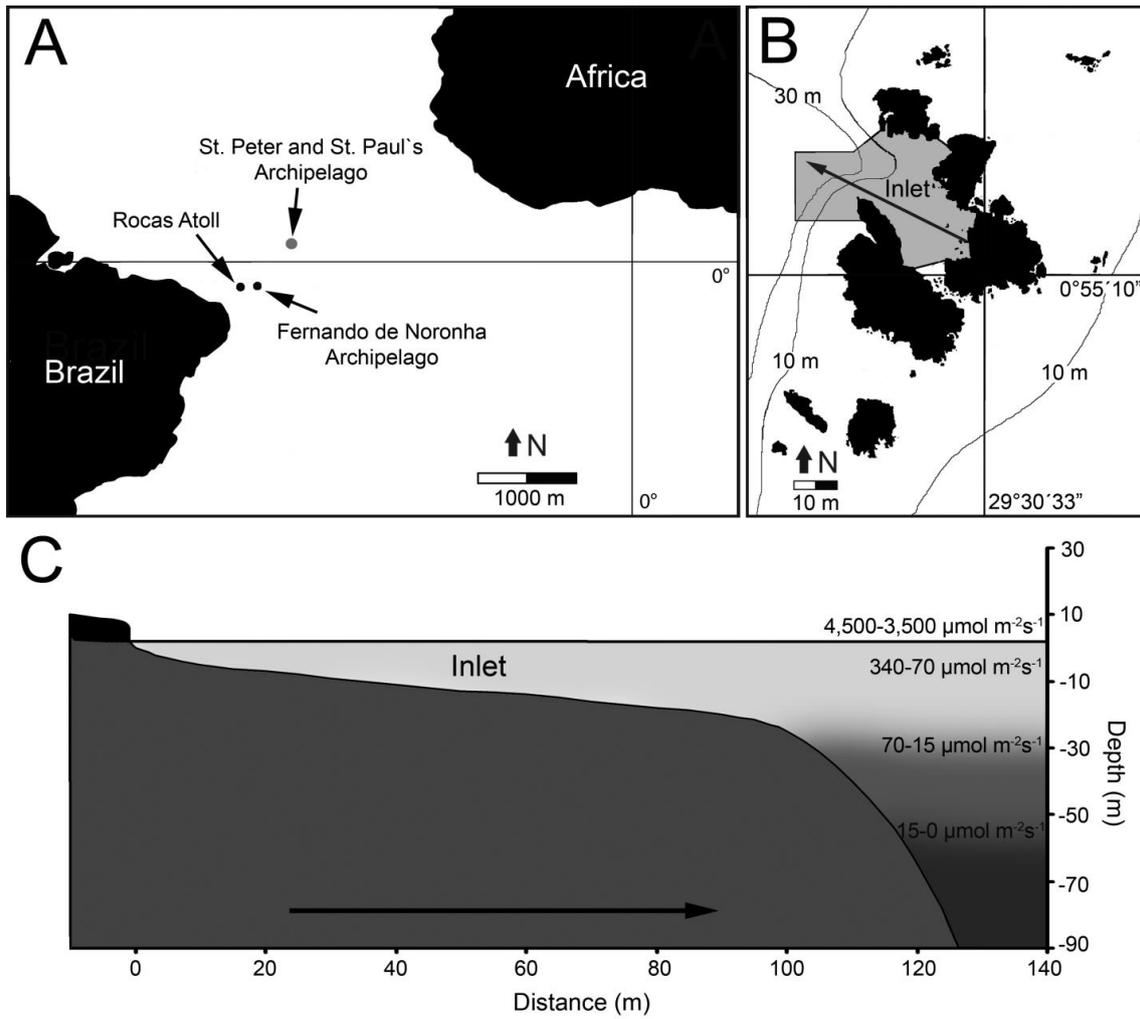


Figure 3 – 1.

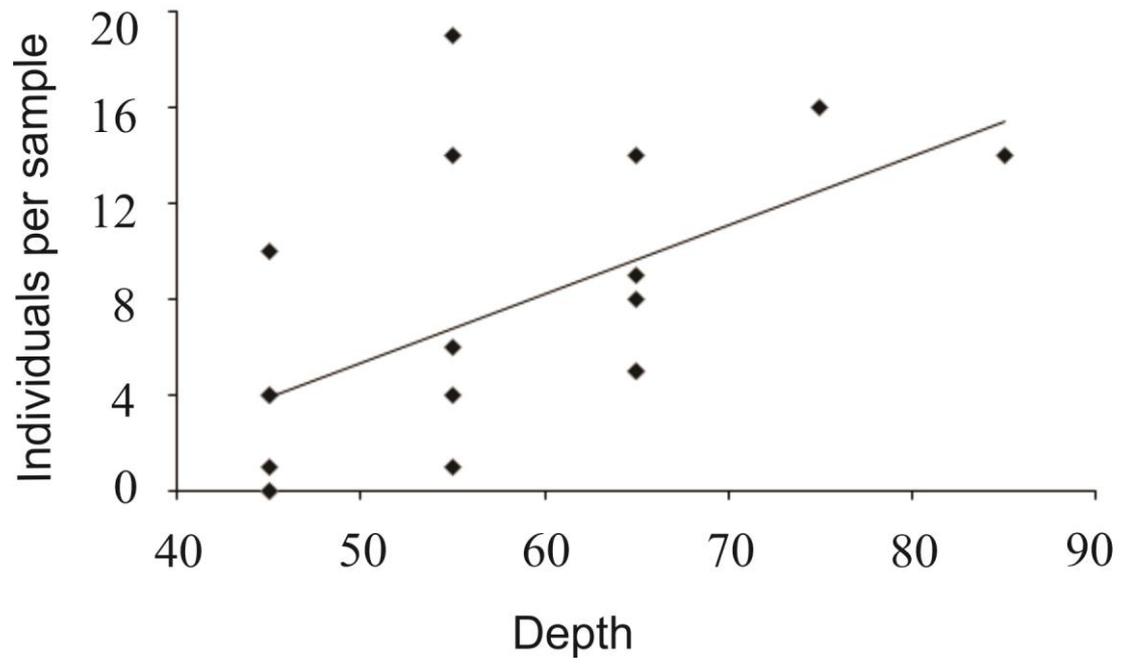


Figure 3 – 2.

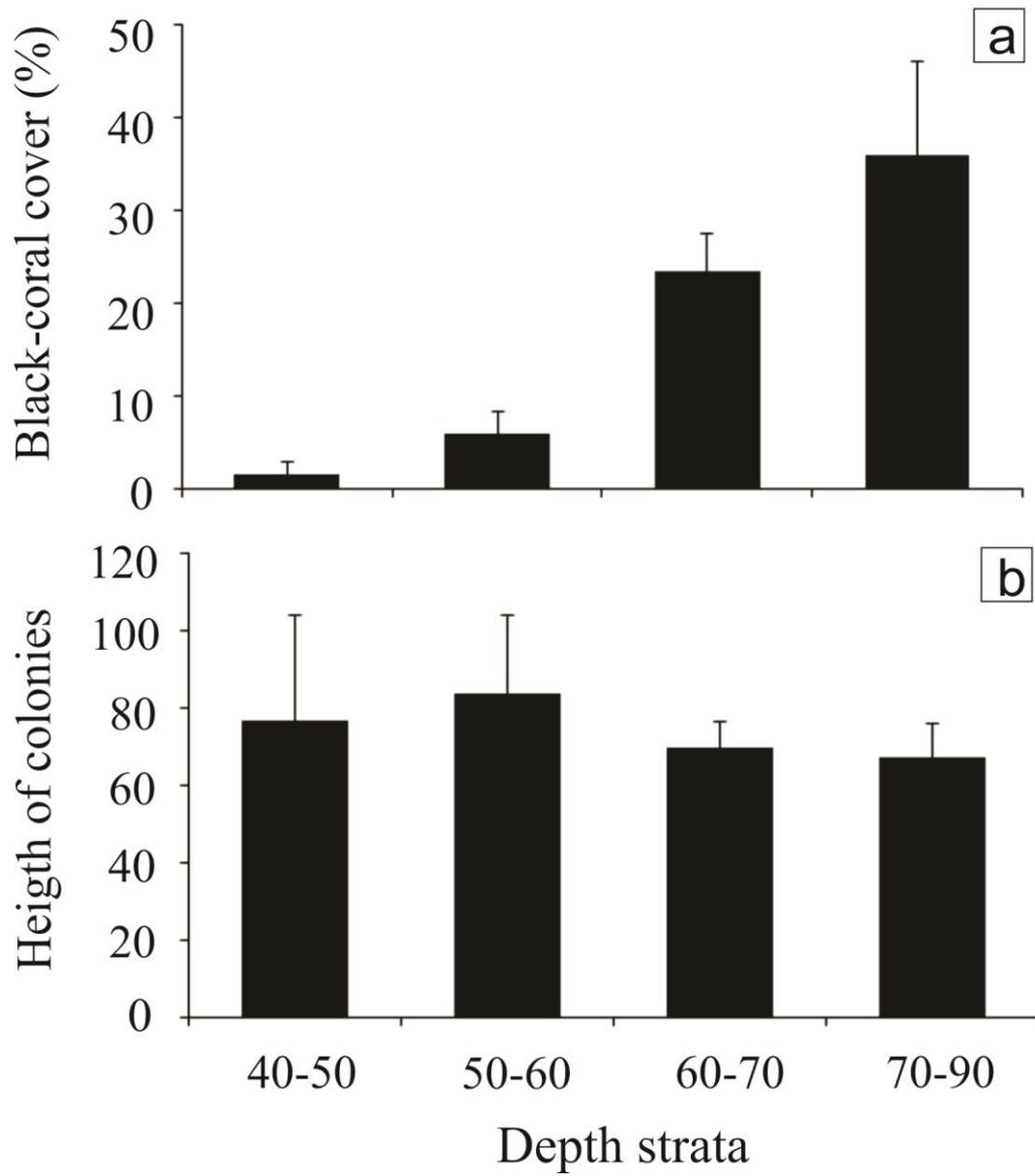


Figure 3 – 3.

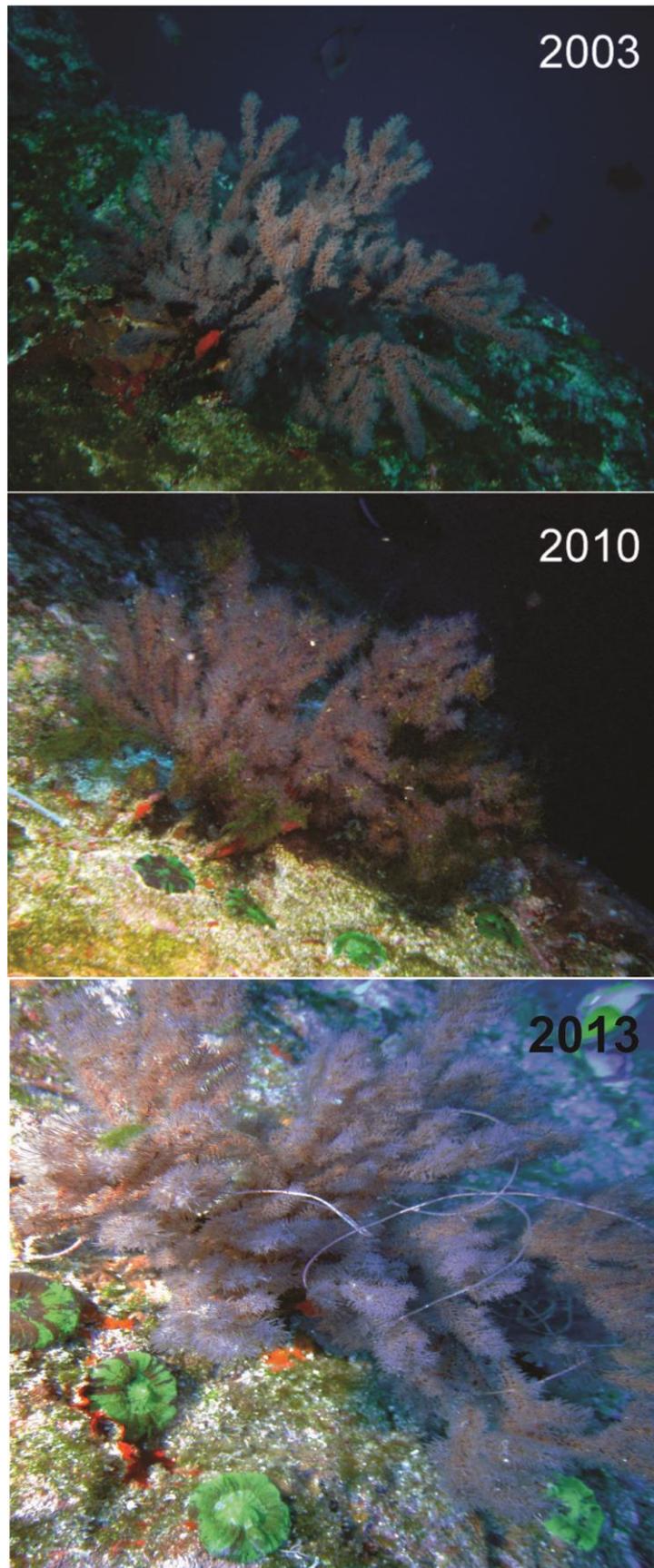


Figure 3 – 4.

Table 3 – 1. Number of colonies, density, length and relative cover of black-corals per depth strata. Values given are mean \pm standard error (SE).

| Depth | Height | | | |
|---------------|-----------------------|-----------------------------------|-----------------|---------------------------|
| strata | N° of colonies | Density ind.m⁻² | (cm) | Relative cover (%) |
| 40-50 | 3.1 \pm 1.5 | 0.063 \pm 0.016 | 76.6 \pm 27.2 | 1.6 \pm 1.3 |
| 50-60 | 8.8 \pm 3.3 | 0.175 \pm 0.066 | 84 \pm 19.9 | 5.9 \pm 2.4 |
| 60-70 | 8.2 \pm 1.6 | 0.163 \pm 0.032 | 69.8 \pm 6.8 | 23.5 \pm 3.9 |
| 70-90 | 15 \pm 1 | 0.231 \pm 0.019 | 64.6 \pm 9.1 | 35.9 \pm 10.0 |

Chapter 4

This chapter was prepared to be submitted for Marine Biology Research. The leading author is Marcos Rogerio Rosa. Erika Oliveira Cavalcanti Coni, Camilo Moitinho Ferreira, Diego Valverde Medeiros, Aline Alves, Ana Paula Moreira, Paulo Yukio Gomes Sumida, Fabiano Lopes Thompson, Gilberto Menezes Amado-Filho & Ronaldo Bastos Francini-Filho are co-authors.

Ecology of the bearded fireworm *Hermodice carunculata* (Pallas, 1766) (ANNELIDA: POLYCHAETA: AMPHINOMIDAE) in the remote St. Peter and St. Paul's Archipelago (Mid Atlantic Ridge, Brazil): A specialized mesophotic coral predator?

4.1. Abstract

The bearded fireworm *Hermodice carunculata* is widespread across the tropical and subtropical Atlantic Ocean on both, the coast and oceanic islands. Here we present data on the distribution, abundance and habitat use of *Hermodice carunculata* in the Saint Peter and Saint Paul Archipelago (SPSPA, Mid Atlantic Ridge, Brazil). Samples were collected in shallow (< 30 m depth) and mesophotic (30-90 m) reefs using SCUBA and a Remote Operated Vehicle (ROV), respectively. A total of 278 individuals of bearded fireworm were observed, with a significant difference in abundance between photic and mesophotic zones, and an abrupt increase in density with depth. Individuals were frequently observed grazing over the scleractinian coral *Madracis decactis* and over black-corals of genus *Tanacetipathes*. Abundance of *H. carunculata* was positively

correlated with depth and black-coral abundance, and negatively correlated with cover of bryozoans, turf algae, and several other benthic organisms. A multivariate analysis showed a direct association between *H. carunculata*, black-corals (*Tanacetipathes* spp.), the scleractinian *Madracis decactis* and depth. The high abundances of *H. carunculata* in depths > 50 m and its role as predator of scleractinians and black-corals, indicate it is a specialized predator of the mesophotic zone of the SPSPA, potentially exerting important roles in several community processes.

Key words: Benthic invertebrates, black-corals, corallivore, *Madracis decactis*, mesophotic and reef ecology.

4.2. Introduction

Mesophotic Reef Ecosystems (MREs) (30-150 m depth) are a direct extension of shallow reef areas (0-30 m depth), with physical and biological links between these zones (Lesser *et al.*, 2009). MREs are characterized by a mix of light-dependent and filter-feeding benthic communities dominated by corals, sponges and algae, which occur in relatively warm waters (Hinderstein *et al.*, 2010; Kahng *et al.*, 2010). The structure of mesophotic reef communities varies according to biotic (e.g. competition and predation) and abiotic factors (e.g. depth and substrate availability). The MREs are, therefore, considered as a biological transition between the shallow and deep reef communities (Lang, 1974; Ohlhorst and Liddell, 1988).

The mesophotic benthic communities has singular characteristics, formed especially by azooxanthellate organisms (Bridge and Guinote, 2013), including branching black-corals and gorgonians (Bo *et al.*, 2008; 2009). The former are key organisms on MREs due to their relatively large sizes and branching morphologies, thereby increasing benthic structural complexity. Shelter provided by gorgonians and black-corals are used by a diverse reef fauna that presents unique co-evolutionary strategies (Tazioli *et al.*, 2007; Bo *et al.*, 2008; 2009).

The bearded fireworm *Hermodice carunculata* (Polychaeta: Amphinomidae) is commonly found in tropical and subtropical waters in sandy and rocky bottoms and coral reefs (Kaplan, 1982; Kudenov, 1993; 1995; Lizama-Blanquet, 1975). Its populations are highly genetically connected on both sides of the tropical and subtropical Atlantic Ocean, where it is found in most coastlines and in oceanic islands (Barroso and Paiva 2007, Rivera and Vallejo 2011, Ahrens *et al.*, 2013). *Hermodice carunculata* is an important invertebrate predator, preying upon a wide range of sessile

and dead organisms, particularly cnidarians (Marsden, 1962; Vreeland and Lasker, 1989; Lewis and Crooks, 1996). The bearded fireworm live in holes and under rocks, coming out to feed during the early morning and late afternoon, on coastal sites of the Caribbean Sea (Marsden, 1960; 1962). The distribution of *Hermodice carunculata* is reported primarily for shallow sites (Ahrens *et al.*, 2013; Marsden, 1960; 1962), with no reports for the mesophotic zone.

The feeding habits of *H. carunculata* was initially studied by Marsden (1960; 1962; 1963a, b) and Glynn (1962), that showed this species exerts a strong top-down effect on the reef community in Caribbean. *H. carunculata* is omnivore, consuming zoanthids, anemones, scleractinian corals, hydrocorals, sponges, gorgonians and several dead organisms (Marsden, 1962; Witman, 1988; Vreeland and Lasker, 1989). It can limit the growth and distribution of several organisms in shallow reefs including fire-corals (*Millepora* spp.), scleractinians (e.g. *Acropora* spp.), octocorals (e.g. *Plexaura* spp.) and zoanthids (e.g. *Zoanthus*) and is selective when offered different prey types (Witman, 1988; Vreeland and Lasker, 1989). For instance, they have preference for coral polyps and juveniles less than three weeks old (Wolf and Nugues, 2012).

The bearded fireworm is a disease vector and pathogen reservoir in the Mediterranean, driving infection bleaching disease in the coral *Oculina patagonica* (Sussman *et al.*, 2003; Williams and Miller, 2005; Dalton and Godwin, 2006) and possibly in *Madracis decactis* in the Saint Peter and Saint Paul Archipelago (SPSPA), where it is extremely abundante (Moreira *et al.* 2014). In this context, information on the distribution, habitat preferences and predation rates of *H. carunculata* are essential to understand its importance to the ecology of MREs of the SPSPA.

The objective of this study was to quantitatively describe the bathymetric distribution, abundance and microhabitat use by the fireworm *Hermodice carunculata* in a depth gradient (0-90 m) in the isolated SPSPA. Our main hypothesis is that the fireworm aggregates to feed in mesophotic areas with highest coverages of *Madracis decactis* and black-corals.

4.3. Materials and methods

4.3.1. Study area

The SPSPA is a small group of five islets and rocks (total emerged area ~15,000 m²) located in the central equatorial Atlantic Ocean, just above the Mid Atlantic Ridge and about 1,000 km off the northeastern Brazilian coast of (Figure 4 – 1) (Edwards & Lubbock 1983a, b; Feitoza *et al.* 2003). The SPSPA is influenced by the South Equatorial Current, which flows westward, as well as by the Equatorial Undercurrent, which flows eastward below the surface, in depths between 40-150 m. The area of reefs <100 m depth is about 0.5 km² (Edwards & Lubbock 1983a, b). Shallow rocky reefs of the SPSPA are covered mainly by the zoanthid *Palythoa caribaeorum* and species of algae of the genera *Bryopsis*, *Caulerpa* and *Dictyota*. In depths > 30 m, most common organisms are the scleractinian corals *Madracis decactis* and *Scolymia wellsi*, crustose calcareous algae (CCA) and bryozoans. Sponges and black-corals of the genus *Tanacetipathes* are relatively abundant in depths > 40 m (Edwards & Lubbock 1983a, b; Feitoza *et al.* 2003; see chapter 3 in this thesis).

4.3.2. Sampling procedures

Samples were collected between September 2010 and June 2011, totaling 60 days of fieldwork. Shallow water sites (i.e. <30 m depth) were surveyed using SCUBA. Abundance of the bearded fireworm was estimated within a 4 m radius area using a stationary visual census protocol originally designed to estimate fish abundance (cf. Minte-Vera *et al.*, 2008). Benthic cover of different organisms was characterized using a photo-quadrat method (cf. Francini-Filho *et al.*, 2008), estimated through the identification of organisms (at the lowest possible taxonomic level) below 300 randomly distributed points per 0.7 m² quadrat using the Coral Point Count with Excel Extensions software (CPCe v. 4.1) (Kohler and Gill 2006). The benthic communities of the mesophotic zone were assessed using videos obtained with a Remotely Operated Vehicle (ROV) (VideoRay Explorer, equipped with lights and a laser scale). Benthic cover was quantified from 30 still frames obtained at 10 second intervals, a total of approximately 0.7 m² per sample. We also used the CPCe software to analyse the video still frames, using 10 randomly distributed points per frame (a total of 300 points per sampling unit). Fireworm abundance was estimated from the ROV video footages by considering the same area (4 m radius) and time (5-min) of stationary census used for the shallow zone. The substrate was classified as follows: bare rock, black-corals, *Caulerpa* spp., crustose calcareous algae, fleshy macroalgae (other than *Caulerpa* spp.), hydrozoans, live scleractinian corals, sediment, turf algae and zoanthids.

4.3.3. Data analyses

Possible differences in abundance of *Hermodice carunculata* between depth strata were tested using one-way analysis of variance (ANOVA), with values transformed to $\log(x + 1)$ to improve normality and homocedasticity, and a Student-Newman-Keuls

(SNK) multiple comparisons of means were performed as a post-hoc test (Zar 1999). A test t (Zar, 1995) was applied to evaluate possible differences in abundance of *Hermodice carunculata* between the euphotic (< 30 m depth) and the mesophotic (30-90 m) zones. A multiple regression analysis (Zar 1999) was performed to test the relationship between abundance of *Hermodice carunculata* and depth, benthic complexity and benthic cover.

4.4. Results

A total of 278 individuals of *Hermodice carunculata* were recorded. The abundance of *H. carunculata* varied significantly between depth strata (ANOVA) ($p < 0.001$), with densities in the 50-60 m stratum higher than in all other ones (Figure 4 – 2). A significant differences in abundance of *Hermodice carunculata* between photic and mesophotic zone was found ($p < 0.05$) (Figure 4 – 3). The multiple regression revealed a positive relationships ($p = 0.00017$) between *Hermodice carunculata* abundance and depth ($\beta = 0.27$, $p = 0.43$) and black-coral cover ($\beta = 0.12$, $p = 0.55$), and negative relationships with cover of bryozoans ($\beta = -0.49$, $p = 0.078$), turf algae ($\beta = -0.36$, $p = 0.36$), nude rocky ($\beta = -0.31$, $p = 0.56$), other corals ($\beta = -0.26$, $p = 0.21$), zoantids ($\beta = -0.25$, $p = 0.44$), *Caulerpa racemosa* ($\beta = -0.23$, $p = 0.47$), crustose coralline algae ($\beta = -0.19$, $p = 0.43$), sediment ($\beta = -0.16$, $p = 0.23$), octocorals ($\beta = -0.2$, $p = 0.79$) and sponges ($\beta = -0.1$, $p = 0.96$). A close relationship in the occurrence of black-corals and *Hermodice carunculata* across the depth gradient was noticed (figure 4 – 4).

The same pattern was seen in the PCA, which revealed the relationship between *H. carunculata*, black-coral and *M. decactis* and those with depth (Figure 4 – 5).

4.5. Discussion

Species of the family Amphinomidae are commonly found in shallow tropical and subtropical waters (Ott and Lewis, 1972; Kudenov, 1993), data of previous work on the bearded fireworm showed that they are more concentrated in shallow than deep areas (Marsden, 1962; Marsden, 1963a; b; Witman, 1988; Lewis and Crooks, 1996; Barroso and Paiva, 2007; Peres and Gomes, 2012; Wolf and Nugues, 2012). However, it is presented here for the first time the distribution of *H. carunculata* across a relatively large and steep depth gradient, showing that the abundance of this species increases with depth, thus plausibly playing more influential ecological roles in the mesophotic than in the euphotic zone. Ott and Lewis (1972) observed a decreasing density of *H. carunculata* with depth (until 25 m depth) in Barbados, which is opposite to the trend found in the present study. This suggests that previous studies on *H. carunculata* could have overlooked a major part of its population.

Few *H. carunculata* predators are known, including the anemone *Phyllactis flosculifera* (Sebens, 1982) and the wrasses (Labridae) *Thalassoma bifasciatum* and *Halichoeres garnoti* (Wolf, 2012). Predation of *H. carunculata* is highly dependent on the size of the individual, not occurring in adults with more than 4 cm length (Wolf, 2012).

Studies performed in shallow reefs (<30 m depth) indicate that the bearded fireworm is mainly associated with low light environments under rocks and corals, rising to feed on early morning and late afternoon, with peak activity during twilight periods (Marsden, 1962). Wrasses (Labridae: *Halichoeres*) are important fire-worm predators (Wolf, 2012). Although the wrasse *Halichoeres radiatus* is abundant in

shallow reefs of the SPSP (see Chapter 1), there are no records of predation of *H. carunculata* by *H. radiatus* (Randal 1967; Wolf, 2012). Thus, low light levels characteristic of mesophotic depths, associated with a low predation pressure may explain the high abundances of *H. carunculata* in the MREs of the SPSPA. *Hermodice carunculata* is a voracious coral predator (Ott and Lewis, 1972; Vreeland and Lasker, 1989; Wolf and Nugues, 2012) and can limit the distribution and growth of many marine organisms (Marsden, 1962, 1963; Endean, 1982; Vreeland and Lasker, 1989; Lewis and Crooks, 1996). Along with gastropods they are recognized as the most important invertebrate coralivores in the Caribbean (Wolf and Nugues 2012). Blooms in populations of coral predators can lead to irreversible damage to reef communities, such as the case of coral demise due to *Acanthaster planci* predation in the Indo-Pacific in the 80s (Endean, 1982). However, it remains unknown if the high abundances of *H. carunculata* in the MREs of the SPSPA pose a risk to populations of branching black-corals and scleractinians.

Hermodice carunculata can consume up to 12.9 cm² of organic matter per day (Ott and Lewis, 1972; Witman, 1988). Considering the abundance of the bearded fireworm in the mesophotic zone of the SPSPA of 4.5 individuals.m⁻² ± SE 0.10 they could consume up to 2915 cm² or 0.29 m² per day. Despite the threat of excessive coral predation, the role of decomposer is important for reef ecosystems (Baum *et al.* 2003) and further studies should focus on these questions, benefit of decomposition versus threat by intense predation.

In addition to coral predation, bearded fireworm can be a risk for the coral community by driving infection-bleaching disease (Sussman *et al.*, 2003, Kushmaro *et al.*, 1996; Sussman *et al.*, 2003, Miller and Williams, 2007). The bacterial community of the bearded fireworm in the SPSPA have being recently described (i.e *Vibrio shiloi*,

Vibrio communis, *Photobacterium* spp., *Bacillus*, among others). The same authors made a comparative survey of microbes associated with healthy and bleached *Madracis decactis* in the SPSPA (Moreira *et al.*, 2013). However, no relationship was found between the bacteria associated with the bearded fireworm and coral bleaching (Moreira *et al.*, 2013).

Although the bacterial fauna of bleached *M. decactis* in the SPSPA was not associated with *H. carunculata*, *Vibrio shiloi* accounted for 90% in *H. carunculata* tissue (Moreira *et al.*, 2013). *V. shiloi* is commonly found in corals (Bourne and Munn, 2005; Koren and Resenberg, 2006; Kushmaro *et al.*, 1996). Nevertheless, it is described as a principal pathogen of the scleractinian coral *Oculina patagonica* in the Mediterranean Sea (Kushmaro *et al.*, 1996; 1997; 2001) with *H. carunculata* as a principal reservoir of this vibrio during winter, working as vector during summer (Sussman *et al.*, 2003). The extension of possible damage that the bearded fireworm can cause to the coral community of SPSPA remains unknown, but future studies focusing on this theme are warranted.

Mesophotic zones were initially described as being free of impacts suffered by the shallow areas (e.g. Bak *et al.*, 2005; Hinderstein *et al.*, 2010; Bongaerts *et al.*, 2010) but with recent research it is now known that MREs may suffer some impacts, such as the ones caused by invasive species (Lesser and Slattery, 2011) and coral bleaching (Smith *et al.*, 2010). Here we highlight that the bearded fireworm, *H. carunculata*, a specialized coral predator a possible disease vector in the mesophotic zone of the SPSPA, may be also considered as an important threat to mesophotic communities.

Thus, other studies involving food preference, pathogens and behavior of *H. carunculata* as well as their distribution in deeper sites (mesophotic) in other regions of

the Atlantic, can elucidate the real impact of this fireworm on coral and benthic communities. It is, therefore, important to estimate the extension of damage caused by *H. carunculata* on the benthic community of euphotic and mesophotic reefs.

4.6. References

- Ahrens, J. B.; Borda, E.; Barroso, R.; Paiva, P. C.; Campbell, A. M.; Wolf, A.; Nugues, M. M.; Rouse, G. W.; Schulze, A. 2013. The curious case of *Hermodice carunculata* (Annelida: Amphinomidae): evidence for genetic homogeneity throughout the Atlantic Ocean and adjacent basins. *Molecular Ecology*, v. 22, p. 2280-2291.
- Bak, R. P. M.; Nieuwland, G.; Meesters, E. H. 2005. Coral reef crisis in deep and shallow reefs: 30 years of constancy and change in reefs of Curacao and Bonaire. *Coral Reefs*, v. 24, p. 475-479.
- Barroso, R.; Paiva, P.C. 2007. Amphinomidae (Annelida: Polychaeta) from Rocas Atoll, Northeastern Brazil. *Arquivos do Museu Nacional (ISSN: 0365-450)*, v. 65, 3, p. 357-362.
- Bo, M.; Tazioli, S.; Spanò, N.; Bavestrello, G. 2008. *Antipathella subpinnata* (Antipatharia, Myriopathidae) in Italian seas. *Italian Journal of Zoology*, v. 75, p. 185–195.
- Bo, M.; Bavestrello, G.; Canese, S.; Giusti, M.; Salvati, E.; Angiolillo, M.; Greco S. 2009. Characteristics of a black coral meadow in the twilight zone of the central Mediterranean Sea. *Marine Ecology Progress Series*, v. 397, p. 53–61.
- Bonatti, E. 1990. Subcontinental mantle exposed in the Atlantic Ocean on St Peter-Paul islets. *Nature*, v. 345, p. 800-802.
- Bongaerts, P.; Ridgeway, T.; Sampayo, E. M.; Hoegh-Guldberg, O. 2010. Assessing the ‘deep reef refugia’ hypothesis: focus on Caribbean reefs. *Coral Reefs*, v. 29, p. 309-327.

- Bridge, T.; Guinotte, J. 2013. Mesophotic coral reef ecosystems in the Great Barrier Reef world heritage area: their potential distribution and possible role as refugia from disturbance, Research Publication no.109, Great Barrier Reef Marine Park Authority, Townsville.
- Bourne, D. G.; Munn, C. B. 2005. Diversity of bacteria associated with the coral *Pocillopora damicornis* from the Great Barrier Reef. *Environ. Microbiol.*, v. 7, n. 8, p. 1162–1174.
- Dalton, S. J.; Godwin, S. 2006. Progressive coral tissue mortality following predation by a corallivorous nudibranch (*Phestilla* sp.). *Coral Reefs*, v. 25, p. 529-529.
- Edwards, A.; Lubbock, R. 1983. The ecology of Saint Paul's Rocks (Equatorial Atlantic). *J Zool.*, v. 200, p. 51-69.
- Endean, R. 1982. Crown-of-thorns starfish on the Great Barrier Reef. *Endeavour*, v. 6, p. 10-14.
- Francini-Filho, R. B.; Moura, R. L. 2008. Dynamics of fish assemblages on coral reefs subjected to different management regimes in the Abrolhos Bank, eastern Brazil. *Aquatic Conserv Mar Freshwater Ecosys.*, v. 18, n, 1166-1179.
- Glynn, P. W. 1962. *Hermodice carunculata* and *Mithraculus sculptus*, two hermatypic coral predators. Association of Island Marine Laboratories of the Caribbean, Fourteenth Meeting, Santo Domingo, v. 4, p. 16-17.
- Hinderstein, L. M.; Marr, J. C. A.; Martinez, F. A.; Dowgiallo, M. J.; Puglise, K. A.; Pyle, R. L.; Zawada, D. G.; Appeldoorn R. 2010. Introduction to mesophotic coral ecosystems: characterization, ecology, and management. *Coral Reefs*, v. 29, p. 247–251.

- Kahng, S. E.; Garcia-Sais, J. R.; Spalding, H. L.; Brokovich, E.; Wagner, D.; Weil E.; Hinderstein, L.; Toonen, R. J. 2010. Community ecology of mesophotic coral reef ecosystems. *Coral Reefs*, v. 29, p. 255-275.
- Kaplan, E. H. 1982. A field guide to the coral reefs of the Caribbean and Florida, including Bermuda and the Bahamas. Houghton Mifflin Co., Boston. (Peterson Field Guide series) ISBN 0-395-31661-8.
- Kohler, K. E.; Gill, S. M. 2006. Coral Point Count with Excel extensions (CPCe): A visual basic program for the determination of coral and substrate coverage using random point count methodology. *Comput Geosci*, v. 32, p. 1259-1269.
- Koren, O.; Rosenberg, E. 2006. Bacteria associated with mucus and tissues of the coral *Oculina patagonica* in summer and winter. *Appl Environ Microbiol.*, v. 72, n. 8, p. 5254–5259.
- Kudenov, J. D., 1993. Amphinomidae and Euphrosinidae (Annelida: Polychaeta) principally from Antarctica, the Southern Ocean, and Subantarctic regions. *Antarctic Research Series*, v. 58, p. 93-150.
- Kudenov, J. D. 1995. Family Amphinomidae Lamarck, 1818. In: J.A. Blake, B. Hilbig and P.H. Scott (eds.) *Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel*, Santa Barbara Museum of Natural History, California. pp. 207-215.
- Kushmaro, A.; Loya, Y.; Fine, M.; Rosenberg, E. 1996. Bacterial infection and coral bleaching. *Nature*, v. 380, p. 396.
- Kushmaro, A.; Rosenberg, E.; Fine, M.; Loya, L. 1997. Bleaching of the coral *Oculina patagonica* by *Vibrio* AK-1. *Mar Ecol Prog Series*, v. 147, p. 159–165.

- Kushmaro, A.; Banin, E.; Stackebrandt, E.; Rosenberg, E. 2001. *Vibrio shiloi* sp. nov. the causative agent of bleaching of the coral *Oculina patagonica*. *IJSEM* 51:1383–1388.
- Lang, J. C. 1974. Biological zonation at the base of a reef. *Am Sci.*, v. 62, p. 272–281.
- Legendre, P.; Legendre, L. 1998. *Numerical Ecology*. 2. ed. Elsevier, Amsterdam.
- Lesser, M. P.; Slattery, M.; Leichter, J. J. 2009. Ecology of mesophotic coral reefs. *J Exp Mar Biol Ecol.*, v. 375, n. 1-2, p. 1-8.
- Lesser, M. P.; Slattery, M. 2011. Invasive lionfish causes a phase shift to algal dominated communities at mesophotic depths on a Bahamian coral reef. *Biol Invasions*, v. 13, p. 1855-1868.
- Lewis, J. B.; Crooks, R.E. 1996. Foraging cycles of the amphinomid polychaete *Hermodice carunculata* preying on the calcareous hydrozoan *Millepora complanata*. *B. Mar. Sci.* v. 58, p. 853-857.
- Liddell, W. D.; Ohlhorst, S. L. 1988. Hard substrata community patterns, 1–120 M, North Jamaica. *Palaios*, v. 3, p. 413–423.
- Lizama, J.; Blanquet, R. S. 1975. Predation on sea anemones by the amphinomid polychaete, *Hermodice carunculata*. *B. Mar. Sci.*, v. 25, p. 442-443.
- Marsden, J. R. 1960. Polychaetous annelids from the shallow waters around Barbados and other islands of the West Indies, with notes on larval forms. *Can J Zool.*, v. 38, p. 989–1020.
- Marsden, J. R. 1962. A coral eating polychaete. *Nature*, v. 193, p. 598.

- Marsden, J. R. 1963a. A preliminary report on digestive enzymes of *Hermodice carunculata*. *Can. J. Zoolog.*, v. 41, p. 159-164.
- Marsden, J. R. 1963b. The digestive tract of *Hermodice carunculata* (Pallas) Polychaeta: Amphinomidae. *Can. J. Zoolog.* v. 41, p. 165-184.
- Miller, M. W.; Williams, D. E.; 2007. Coral disease outbreak at Navassa, a remote Caribbean island. *Coral Reefs*, v. 26, p 97-101.
- Minte-Vera, C. V.; Moura, R. L.; Francini-Filho, R. B. 2008. Nested sampling: an improved visual-census technique for studying reef fish assemblages. *Mar Ecol Prog Ser.*; 367:283-293.
- Ott, B.; Lewis, J.B. 1972. The importance of the gastropod *Coralliophila abbreviata* (Lamarck) and the polychaete *Hermodice carunculata* (Pallas) as coral reef predators. *Can. J. Zool.*, v. 50, p. 1651-1656.
- Perez, C. D.; Gomes, P. B. 2012. Primeiro registro do verme de fogo *Hermodice carunculata* (Annelida, Polychaeta) predando colônias do coral de fogo *Millepora alcicornis* (Cnidaria, Hydrozoa). *Biota Neotrop.*, v. 2012, n. 2, p. 12.
- Rivera, B.; Vallejo, S. I. 2011. Revision of *Hermodice* Kinberg, 1857 (Polychaeta: Amphinomidae). *Scientia Marina*, v. 75, n. 2, p. 262.
- Sebens, K. P. 1982. Inter-tidal distribution of zoanths on the Caribbean coast of Panama Effects of predation and desiccation. *Bull Mar Sci.*, v. 32, p. 316-335.
- Shantz, A. A.; Stier, A. C.; Idjadi, J. A. 2011. Coral density and predation affect growth of a reef-building coral. *Coral Reefs*, v. 30, p. 363–367.

- Smith, T. B.; Blondeau, J.; Nemeth, R. S.; Pittman, S. J.; Calnan, J. M.; Kadison, E.; Gass, J. 2010. Benthic structure and cryptic mortality in a Caribbean mesophotic coral reef bank system, the Hind Bank Marine Conservation District, U.S. Virgin Islands. *Coral Reefs*, v. 29, p.
- Sokal, R. R.; Rohlf, F. I. 1995. *Biometry: the principles and practice of statistics in biological research*. San Francisco: W.H. Freeman, 776 p.
- Souza, J. R. B.; Rodrigues, H. A.; Neves, B. M.; Pérez C. D. 2007. First report of bristleworm predator of the reef octocoral *Carijoa riisei*. *Coral Reef*, v. 26, p. 1033.
- Sussman, M.; Loya, Y.; Fine, M.; Rosenberg, E. 2003. The marine fireworm *Hermodice carunculata* is a winter reservoir and spring-summer vector for the coralbleaching pathogen *Vibrio shiloi*. *Environ Microbiol*, v. 5, p. 250–255.
- Tazioli, S.; Bo, M.; Boyer, M.; Rotinsulu, H.; Bavestrello, G. 2007. Ecology of some common antipatharians from the Marine Park of Bunaken (North Sulawesi, Indonesia). *ZoologicalStudies*, v. 46, p. 227–241.
- Vreeland, H. V.; Lasker, H. R. 1989. Selective feeding of the polychaete *Hermodice carunculata* Pallas on Caribbean gorgonians. *J Exp Mar Biol Ecol.*, v. 129, p. 265–277.
- Werner, E. E.; Gilliam, J. F. 1984. The ontogenetic niche and species interactions in sizestructured populations. *Annu Rev Ecol Syst*, v. 15, p. 393-425.
- Williams, D. E.; Miller, M. W. 2005. Coral disease outbreak: pattern, prevalence and transmission in *Acropora cervicornis*. *Mar Ecol-Prog Ser.*, v. 301, p. 119-128.

Witman, J. D. 1988. Effects of predation by the fireworm *Hermodice carunculata* on Milleporid hydrocorals. *B. Mar. Sci.*, v. 42, p. 446-458.

Wolf, A. 2012. The role of macroalgae and the corallivorous fireworm *Hermodice carunculata* on coral reef resilience in the Caribbean. PhD Thesis. Bremen, Germany.

Wolf, A. T.; Nugues, M. M. 2012. Predation on coral settlers by the corallivorous fireworm *Hermodice carunculata*. *Coral Reefs*, v. 32, n. 1, p 227-231.

4.7. Legends for figures

Figure 4 – 1. Map showing: A) the location of the St. Peter and St. Paul's Archipelago (SPSPA) and other Brazilian oceanic islands in the South Atlantic Ocean, as well as the coastal area of the Abrolhos Bank and B) Detail of the SPSPA showing the study area (light grey).

Figure 4 – 2. Bearded fireworm abundance by samples (mean + SE) across the depth gradient, with significant differences ($P < 0.001$). Homogeneous groups are identified by the same letters. Follow the total individual abundance by depth 0-10 (18), 10-20 (4), 20-30 (30), 30-40 (21), 40-50 (24), 50-90 (181).

Figure 4 – 3. Bearded fireworm abundance by samples (mean + SE) on photic and mesophotic zone, with significant differences ($P < 0.001$).

Figure 4 – 4. Abundance of black-coral and *Hermodice carunculata* overlaid. Colony of black-coral showed on bars, values are given on left axes and abundance of *Hermodice carunculata* showed on line, values are given on right axes.

Figure 4 – 5. Principal Component Analysis (PCA) with *H. carunculata* (HCAR) and (A) the six distinct depth strata, and (B) the benthic cover with the organism selected based on significance on the correlation analysis.

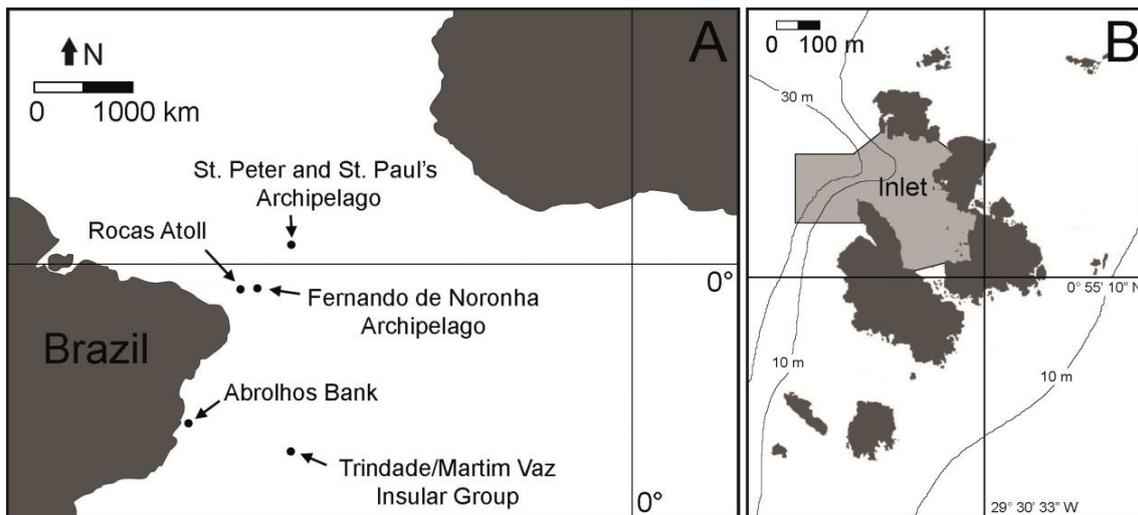


Figure 4 – 1.

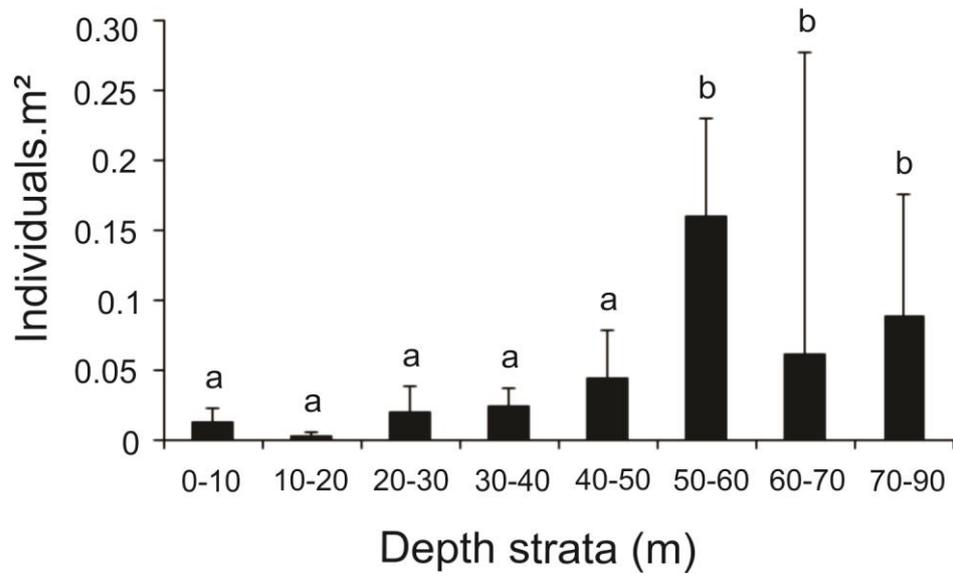


Figure 4 – 2.

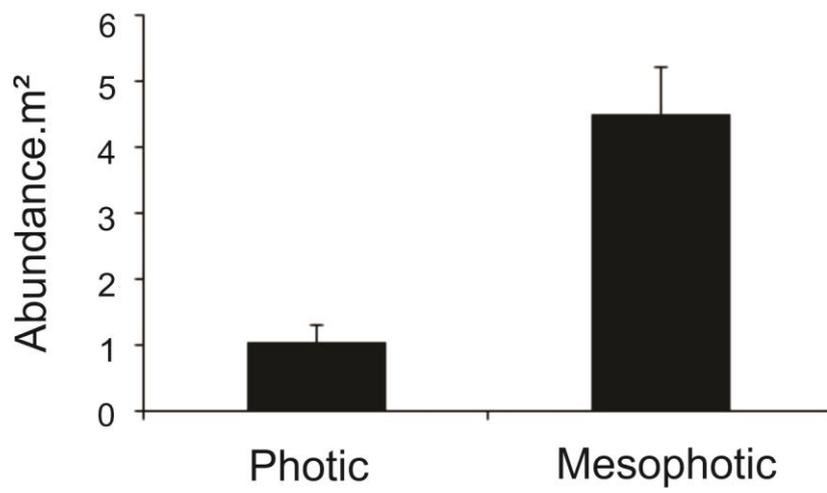


Figure 4 – 3.

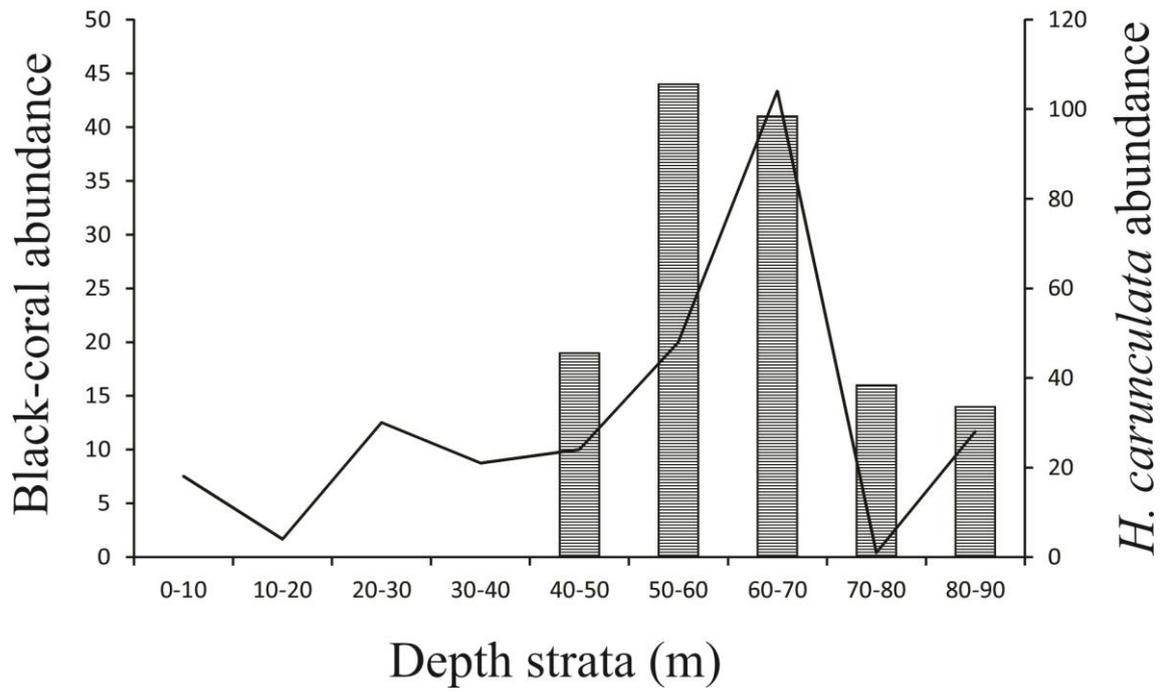


Figure 4 – 4.

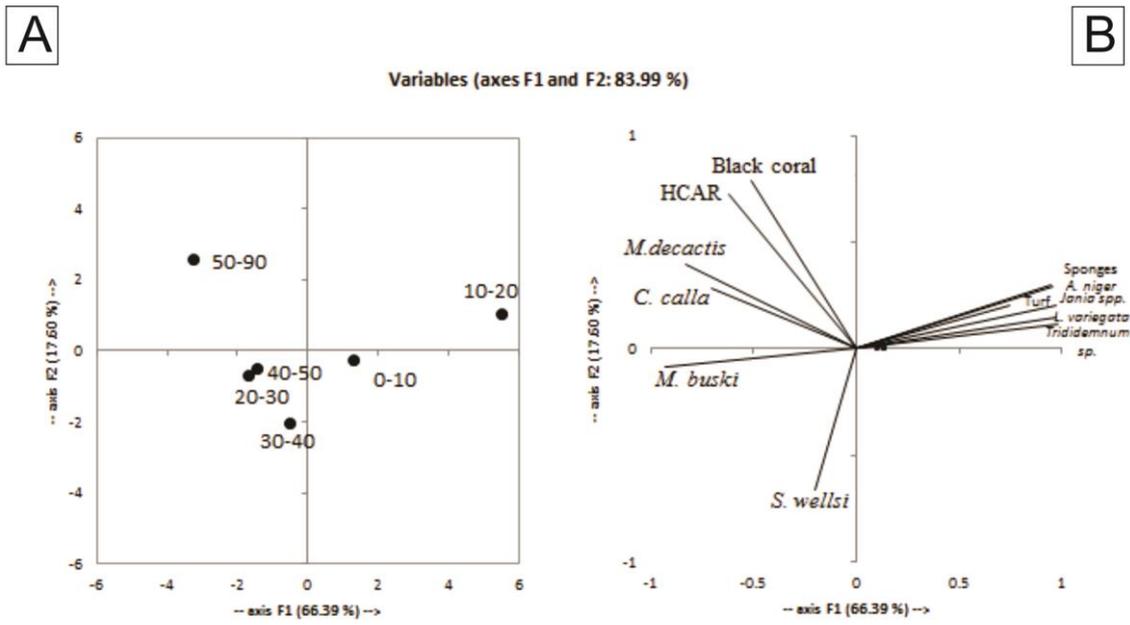


Figure 4 – 5.

5. Concluding remarks

A clear connectivity between shallow and mesophotic reefs (inferred by the wide bathymetric distribution of most species) is described, but genetic and demographic studies are needed to measure the connectivity between shallow (euphotic) and mesophotic systems.

The mesophotic zone of the SPSPA may work as a refuge for several species with broad depth distributions (through simultaneous transitions), while shallow water specialists may be more susceptible to extinction following global disturbances. Black-corals and depth were the most important factors affecting fish assemblages' structure. The relatively high biomass of mesopredator reef fish in the SPSPA in comparison with other Atlantic and Pacific reef systems, support the hypothesis of mesopredator release following the demise of the Galapagos shark, *Carcharhinus galapagensis*, due to overfishing. The area has no fishery regulations and a clear need of implementation of conservation measures is required.

Abiotic variables were the predictors of benthic community structure. Two distinct benthic communities were detected, a shallow one composed primarily by the zoanthid *Palythoa caribaeorum*, the fleshy alga *Caulerpa racemosa*, crustose coralline algae (CCA) and *Bryopsis* spp., and another deeper community dominated by CCA, bryozoans and scleractinian corals. The data on benthic cover presented do not support the hypothesis that substantial changes have occurred since the 70's. However, a long-term monitoring program is suggested.

Population of two black-coral species, *Tanacetipathes hirta* and *T. thamnea* was found one of the most important factors in structuring the reef fish community of the archipelago, with seven species of reef fish, particularly the endemics and threatened

species ones, intensively using them as microhabitat. Epibiosis by parasitic zoanthids (*Protopalycha* sp.), bryozoans and sponges decreased vitality (i.e. proportion of live tissue) of colonies. Overgrowth by algal detritus coming from the shallows and entanglement by fishing monofilament was another force driving the decreased of vitality. Because black-corals create important 3-dimensional microhabitats that serve as refuge and feeding grounds for several reef fish species (particularly threatened endemic species), urgent conservation measures, such as banning use of monofilament near the SPSPA, are suggested.

A direct association of *H. carunculata* with depth, black-corals and the scleractinian *Madracis decactis* was showed. Significant difference in abundance between photic and mesophotic zones exist, with an abrupt increase in density with depth, being highest at mesophotic depth, bellow 50 meters. *H. carunculata* was considered an important marine predator, describe here for the first time its specialization to mesophotic zone. Considering that the Mesophotic Reef Ecosystems play a fundamental role on the reef community structure, understanding the potential impacts of *H. carunculata* in this zone are a critical issue on the stability of reef community and in the conservation biota of SPSPA.