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NARA LINA OLIVEIRA

CRESCIMENTO E VITALIDADE DE UM CORAL CONSTRUTOR DE RECIFES (*Favia gravida* Verril, 1868) NO BANCO DOS ABROLHOS, BAHIA, BRASIL

ILHÉUS - BAHIA
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Dissertação apresentada, à Universidade Estadual de Santa Cruz para obtenção do titulo de Mestre em Ecologia e Conservação da Biodiversidade.

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Orientador: Prof. Dr. Rodrigo Leão de Moura
Co-orientador: Ronaldo Bastos Francini-Filho

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“An animal that is very abundant, before it gets extinct becomes rare. So you don't lose abundant animals. You always lose rare animals. Therefore, they're not perceived as a big loss (...) We transform the world, but we don't remember it. We adjust our baseline to the new level, and we don't recall what was there (...) You can have a succession of changes and at the end you want to sustain a miserable leftovers.”

Daniel Pauly
(The ocean’s shifting baseline)

CRESCIMENTO E VITALIDADE DE UM CORAL CONSTRUTOR DE RECIFES (*Favia gravida* Verril, 1868) NO BANCO DOS ABROLHOS, BAHIA, BRASIL

RESUMO

Os recifes de Abrolhos, no Sul da Bahia, abrigam as mais ricas comunidades coralíneas do Atlântico Sul. Assim como vem ocorrendo em outras regiões no mundo, estes recifes estão progressivamente perdendo cobertura de corais devido à interação entre "estressores" que operam em múltiplas escalas espaciais e temporais, tais como sobrepesca, aumento na sedimentação e eutrofização, anomalias térmicas e acidificação da água do mar. O estudo aqui apresentado explorou aspectos demográficos e biológicos de uma espécie de coral pertencente a um grupo funcional ainda pouco estudado, os "corais herbáceos" ou "weedy corals", o qual compreende espécies de crescimento rápido, alta fecundidade e baixa longevidade, buscando responder às seguintes perguntas: 1) Existe variação espacial e temporal na cobertura relativa, crescimento, tamanho das colônias e vitalidade do coral *F. gravida* no Banco dos Abrolhos? 2) Qual é a influencia relativa de fatores bióticos (substrato do entorno, cobertura relativa, biomassa de peixes herbívoros) e abióticos (turbidez, profundidade, níveis de proteção contra a pesca e distância da costa) sobre a abundância (cobertura relativa), longevidade (tamanho da colônia), crescimento, vitalidade (e.g. prevalência de branqueamento e doenças) e recrutamento do coral*?* Foram utilizadas imagens do substrato obtidas em 12 sítios, entre 2006 e 2009, abrangendo recifes próximos e afastados da costa, protegidos e desprotegidos contra a pesca. Foram realizadas medidas em 160 colônias, totalizando 487 observações sequenciais que também incluíram aspectos ligados à vitalidade e incidência de doenças. A cobertura, tamanho e vitalidade das colônias variaram espacialmente, com heterogeneidade marcante entre os arcos costeiro e externo. *Favia gravida* apresentou maior cobertura e maiores taxas de crescimento em recifes costeiros, sob níveis relativamente elevados de turbidez. Além disso, as taxas de crescimento mais elevadas foram associadas a colônias rodeadas por tufos de algas ("turf"). A cobertura de macroalgas apresentou relação negativa com a abundância e longevidade do coral, enquanto que a proteção contra a pesca esteve positivamente relacionada com o crescimento. O branqueamento crônico atingiu metade da população e a vitalidade das colônias foi positivamente influenciada pela distância da costa. Essas respostas de *F. gravida* às condições ambientais e regimes de manejo contrastantes são discutidas à luz do possível desempenho superior dos "weedy corals" nos recifes brasileiros.

Palavras-chave: Recifes coralíneos, vitalidade, branqueamento, doenças em corais, grupos funcionais, "corais herbáceos".

GROWTH AND VITALITY OF A REEF BUILDING CORAL (*Favia gravida* Verril, 1868) AT THE ABROLHOS BANK, BAHIA, BRAZIL

ABSTRACT

The Abrolhos Reefs, Southern Bahia state (Brazil), encompass the largest and richest coralline assemblages in the South Atlantic. As widely reported from reefs around the globe, this system is also steadily losing coral cover due to the interaction between "stressors" operating at multiple spatial and temporal scales, such as overfishing, increased sedimentation and eutrophication, temperature anomalies and seawater acidification. This study explored demographic and biological aspects of one coral species belonging to the “weedy” functional group, which comprise fast-growing, highly fecund and low-longevity species, seeking to answer the following questions: 1) Is there spatial and temporal variation in percentage cover, growth, colony size and vitality of *Favia gravida* in the Abrolhos Bank? 2) What is the relative influence of biotic (surrounding substrate, herbivorous fish biomass, relative benthic cover) and abiotic factors (turbidity, depth, distance from the coast and protection gradient) on the abundance (relative cover) growth, longevity (colony size), vitality (e.g. bleaching and disease prevalence) and recruitment of the coral? We used digital images of the substrate obtained between 2006 and 2009, from 12 sites that encompass reefs at different distances from the coast and contrasting management regimes. A total of 160 colonies were measured, totaling 487 sequential observations that also included vitality and disease incidence. Cover, colony size and vitality of *F. gravida* varied between sites, with significant heterogeneity among coastal and outer arc sites. *Favia gravida* presented higher cover and growth rates on coastal reefs under higher turbidity levels. Moreover, higher growth rates were associated with colonies surrounded by turf algae. Fleshy macroalgae cover was negatively correlated with *F. gravida* cover and colony size, while protection level was positively associated with its growth. Chronic bleaching affected half of the population studied and colony vitality was positively influenced by the distance offshore. Responses of *F. gravida* to contrasting environmental forcing and management regimes are discussed considering the potential superior performance of “weedy corals” in Brazilian reefs.

Key-words: Coralline reefs, vitality, bleaching, coral diseases, functional groups, “weedy corals”

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INTRODUÇÃO

Os corais representam um grupo chave em ecossistemas recifais, desempenhando papel fundamental em seu funcionamento, uma vez que são responsáveis por sua complexa arquitetura e provêem alimento e abrigo para as demais espécies (ALVAREZ-FILIP et al., 2009; BRUNO; BERTNESS, 2001). Os principais construtores dos recifes coralíneos são corais da ordem Sclecactinia (Cnidaria, Anthozoa), conhecidos comumente como corais pétreos, ou escleractíneos. Estes organismos são notáveis por sua capacidade de mineralizar formas estáveis de carbonato de cálcio ($CaCO_3$) em taxas superiores às dos processos erosivos físicos, químicos e biológicos, permitindo que construções recifais alcancem milhares de quilômetros de extensão e possam persistir ao longo de milhões de anos (KLEYPAS et al., 2001; KNOWLTON; JACKSON, 2001).

Os corais escleractínios são majoritariamente coloniais, vivendo em simbiose com uma complexa comunidade de microorganismos, especialmente bactérias e arqueias (GARCIA et al., 2013; ROSENBERG et al., 2007), juntamente com dinoflagelados fotossintetizantes do gênero *Symbiodinium*, conhecidos como zooxantelas, os quais fornecem a energia essencial para a biomineralização e outros processos metabólicos (ROWAN; POWERS, 1991; TITLYANOV; TITLYANOVA, 2002). Devido em parte a esta associação com as zooxantelas, a distribuição dos corais escleractíneos é limitada por fatores que estão diretamente relacionados com a disponibilidade de luz, tais como a turbidez e a profundidade (GLYNN, 1976; HOEGH-GULDBERG, 1999; KLEYPAS et al. 2001; PORTER, 1987; VERON, 2012). Em escala global, os recifes coralíneos se concentram nas zonas costeiras tropicais rasas e quentes, compondo o ecossistema mais rico e produtivo do planeta (ADEY, 2000; HOEGH-GULDBERG, 1999), contribuindo com a provisão de serviços ecológicos essenciais e com a subsistência de cerca de 500 milhões de pessoas (WILKINSON, 2008).

A cobertura de corais vem diminuindo aceleradamente em escala global, tendo atingido proporções críticas nas últimas três décadas (MUMBY; STENECK, 2008; WILKINSON, 2000). Metade dos recifes do mundo desapareceu nas últimas cinco décadas e 70% do restante está criticamente degradado (WILKINSON, 2008). Os principais estressores incluem a sobrepesca, anomalias térmicas e a eutrofização e acidificação da água do mar (e.g. HOEGH-GULDBERG, 1999; KLEYPAS et al., 2001), com destaque recente para as epizootias (WEIL et al., 2006). Em Abrolhos, principal conjunto recifal do Atlântico Sul, as doenças já representam uma das principais ameaças aos corais (FRANCINI-FILHO et al., 2008).

Variações espaciais e temporais marcantes na abundância e na distribuição dos organismos são frequentes em comunidades bentônicas marinhas (LEVIN, 1992; PANDOLFI et al., 2003). As comunidades recifais, devido à sua configuração naturalmente fragmentada e à predominância de espécies com ciclo de vida marcado por uma fase adulta com nenhuma ou pouca mobilidade e fases larvais com grande potencial dispersivo, apresentam forte estrutura metapopulacional e grande variabilidade (KRITZER; SALE, 2006). Tal dinâmica, manifestada em diferentes escalas espaciais e temporais, é influenciada pela interação entre fatores físicos (e.g. luminosidade, profundidade, temperatura), biológicos (e.g. competição, predação, doenças) e distúrbios antropogênicos (e.g. sobrepesca, poluição) (CONNELL, 1978; HUGHES et al., 2003).

Devido a limitações para acessar o *output* reprodutivo e a mortalidade na etapa larval, estudos ecológicos sobre comunidades recifais são geralmente baseados em informações sobre a dinâmica observada após o recrutamento (ROUGHGARDEN et al., 1985). No entanto, em função da escassez de séries temporais de dados com resolução suficiente, praticamente todos os componentes da dinâmica das comunidades coralíneas brasileiras (e.g., variabilidade no recrutamento, interações competitivas e de predação pós-recrutamento, taxas de crescimento e longevidade) ainda são insuficientemente conhecidos (FRANCINI-FILHO et al., 2013), dificultando a elaboração de estratégias de conservação e monitoramento, também deixando em aberto questões centrais relacionadas ao funcionamento desse conjunto recifal com características particulares, tanto em termos de composição (e.g. alto nível de endemismo e dominância de espécies relíquias do Neogeno) quanto de condições oceanográficas (e.g. elevados níveis de sedimentação e turbidez).

Mundialmente, tem sido observada uma tendência de ocupação do espaço recifal por organismos de crescimento rápido (e.g., algas filamentosas e frondosas), em detrimento dos organismos mais longevos e de crescimento lento (e.g., corais), acarretando em diminuição na complexidade estrutural do ecossistema e uma série de efeitos em cadeia (BELWOOD et al., 2004; SUCHANEK; GREEN, 1981). Mudanças de fase ("phase shifts") com perda na dominância de corais são eventos sucessionais de difícil reversão em ambientes recifais, tendo sido atribuídas à interação entre mudanças globais (anomalias térmicas e acidificação) e atividades humanas tais como a eutrofização e a sobrepesca de peixes herbívoros (BRUNO; SELIG, 2007; HUGHES, 1994; HUGHES et al., 2003). A crescente pressão da pesca tem causado o esgotamento dos estoques de peixes e eliminado, funcionalmente, os níveis tróficos superiores das cadeias tróficas marinhas (ESTES et al., 2011; PAULY et al., 2005). Em recifes coralíneos, na medida em que os consumidores de topo são esgotados, os peixes herbívoros de grande porte (e.g. famílias Acanthuridae e Labridae) tornam-se alvos principais da exploração pesqueira. Estes herbívoros desempenham funções críticas no ecossistema, controlando as macroalgas que, por sua vez, são as principais competidoras por espaço dos corais construtores. Na ausência de herbívoros, as algas podem se proliferar, especialmente quando há maior disponibilidade de nutrientes, determinando "mudanças de fase" que se manifestam por todo o ecossistema (BRUNO et al., 2009; DONE, 1992; HUGHES, 1994).

Anomalias térmicas extremas e o aumento na radiação solar têm aumentado o número de eventos de "branqueamento", durante os quais os corais perdem suas zooxantelas (BAKER et al., 2008) e podem apresentar mudanças agudas na comunidade de microorganismos a eles associados (KUSHMARO et al., 1996; ROSENBERG et al., 2008). Eventos extremos de branqueamento (i.e., eventos de longa duração ou grande intensidade e extensão), podem causar mortalidade em massa (GLYNN, 1984; BROWN, 1997; BAKER et al., 2008). Enquanto em escala global houve a perda de 16% dos corais apenas no ano de 1998 (WILKINSON, 2000), no Brasil os eventos de "branqueamento" ocorreram em menor intensidade e extensão, com baixa mortalidade, ou seja, com as espécies demonstrando resiliência relativamente elevada (CASTRO; PIRES, 1999; LEÃO et al., 2003). Entre 1998 e 2005, Leão et al. (2008) estimaram que 12% dos corais da Bahia apresentaram algum nível de "branqueamento", mas ainda não está clara qual a extensão da ameaça aos corais brasileiros em função desse fenômeno, que é uma importante causa de mortalidade e outros efeitos sub-letais em outras regiões (DE'ATH et al., 2013). A descoloração do tecido do coral é causada por stress oxidativo e colapso da interação alga-coral (LESSER, 2006), um processo atribuído à baixa densidade de *Symbiodinium* (POGGIO et al., 2009; HUEERKAMP et al., 2001), que são perdidos, expulsos ou sofrem redução de pigmentos (GLYNN, 1993; BROWN, 1997; FITT et al., 2001; MCCLANAHAN, 2004; BAKER et al., 2008; KNOWLTON; JACKSON, 2008), podendo também estar associado a infecções e proliferação de microorganismos (ROSENBERG et al., 2008). Estes distúrbios podem tornar os corais mais suscetíveis à doenças (RITCHIE, 2006), ou implicar em efeitos sub-letais que envolvem redução na taxa de alimentação, crescimento e reprodução, reduzindo a vitalidade dos indivíduos afetados

(HUGHES; CONNELL, 1999; BAKER et al., 2008).

Os esforços para a conservação dos recifes coralíneos têm se concentrado principalmente em medidas locais, especialmente na criação de áreas marinhas protegidas (AMPs) (MUMBY; STENECK, 2008; PANDOLFI et al., 2003). No entanto, nas AMPs não há possibilidade de controle dos estressores que operam em escala global (acidificação e anomalias térmicas) ou regional (sedimentação e eutrofização). Modelos recentes (KENNEDY et al., 2013) têm indicado que o manejo em escala local (controle da pesca) e regional (gestão adequada de bacias hidrográficas) pode retardar significativamente efeitos negativos associados a anomalias térmicas e acidificação, mas há carência de dados empíricos e experimentos para avaliar e aprimorar tais previsões. Além disso, apesar das evidências que as AMPs, especialmente as reservas marinhas (áreas sem pesca), podem contribuir para aumentar a biomassa de peixes recifais (FRANCINI-FILHO; MOURA, 2008a, b), ainda são mal conhecidos os seus efeitos na resistência e resiliência de organismos bentônicos (GRAHAM et al., 2011; KNOWLTON; JACKSON, 2008).

A gestão do quadro de degradação dos sistemas recifais depende, em boa parte, de um melhor entendimento do papel e da dinâmica de organismos-chave, bem como da extensão e magnitude de efeitos indiretos que se propagam através dos diferentes compartimentos do ecossistema (ALVAREZ-FILIP et al., 2011; HOEGH-GULDBERG et al., 2011; HOEY; BELWOOD, 2011). Por exemplo, tanto a definição de regras de uso de AMPS já existentes quanto o planejamento de novas áreas protegidas depende de uma compreensão que vá além dos efeitos já relativamente bem conhecidos, tais como a recuperação de populações de peixes após a proteção (GRAHAM et al., 2011) e a exportação de biomassa de peixes através de "spillover" (FRANCINIFILHO; MOURA, 2008b). Ações de mitigação endereçando as escalas regional e global (MUMBY; STENECK, 2008), assim como modelos preditivos que busquem subsidiar estratégias de adaptação (KENNEDY et al., 2013), também dependem de dados que abranjam vários compartimentos do ecossistema. Os dois trabalhos aqui apresentados abordam questões relacionadas a essa problemática, contribuindo para preencher lacunas críticas de conhecimento sobre a dinâmica de organismos bentônicos no principal conjunto recifal coralíneo do Atlântico Sul, o Banco dos Abrolhos (MOURA et al., 2013).

No primeiro trabalho (FRANCINI-FILHO et al., 2013) foi explorada a dinâmica de comunidades recifais bentônicas em uma malha amostral espacial e temporalmente abrangente (2003-8), incluindo áreas sob diferentes condicionantes ecológicas e regimes de manejo contrastantes. Trata-se do maior programa amostral em ambientes coralíneos do Atlântico Sul, envolvendo pesquisadores e instituições nacionais e estrangeiras com o objetivo de esclarecer as tendências temporais na cobertura dos recifes e os fatores que influenciam sua dinâmica (e.g. BRUCE et al., 2012), implementado no âmbito do Sistema Nacional de Pesquisa em Biodiversidade (SISBIOTA/Rede Abrolhos) e do Programa de Pesquisa Ecológica de Longa Duração (PELD-Abrolhos), iniciativas fomentadas pelo Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) e outras agências federais e estaduais. O segundo artigo (OLIVEIRA et al., submetido) representa a contribuição principal do projeto, tendo utilizado uma malha espacial mais reduzida, espacial e temporalmente (2006-9), na mesma área de estudo (Abrolhos). No entanto, apesar da malha ligeiramente reduzida, esse trabalho gerou informações de alta resolução sobre uma espécie de coral escleractíneo com características particulares, pertencente a um grupo funcional praticamente desconhecido nos recifes do Atlântico Sul. Nesse contexto, foram explorados os fatores que mais influenciam a cobertura, crescimento, longevidade, vitalidade e recrutamento de *Favia gravida, Verril, 1868*, uma espécie pertencente ao grupo funcional dos “corais herbáceos”, ou “weedy corals”, com o objetivo de explorar os aspectos mais centrais da dinâmica populacional de corais de crescimento rápido e ciclo de vida curto. Com a degradação crescente dos recifes, espécies mais “r-estrategistas” de corais tendem a dominar a cobertura bentônica (KNOWLTON, 2001; GREEN et al., 2008; ALVAREZ-FILIP et al., 2011), com implicações importantes tanto do ponto de vista da estrutura e funcionamento do sistema recifal quanto em relação a aspectos práticos ligados ao delineamento de estratégias de monitoramento e interpretação das tendências temporais.

ARTIGO 1

Dynamics of Coral Reef Benthic Assemblages of the Abrolhos Bank, Eastern Brazil: Inferences on Natural and Anthropogenic Drivers

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Abstract

The Abrolhos Bank (eastern Brazil) encompasses the largest and richest coral reefs of the South Atlantic. Coral reef benthic assemblages of the region were monitored from 2003 to 2008. Two habitats (pinnacles' tops and walls) were sampled per site with 3–10 sites sampled within different reef areas. Different methodologies were applied in two distinct sampling periods: 2003–2005 and 2006–2008. Spatial coverage and taxonomic resolution were lower in the former than in the latter period. Benthic assemblages differed markedly in the smallest spatial scale, with greater differences recorded between habitats. Management regimes and biomass of fish functional groups (roving and territorial herbivores) had minor influences on benthic assemblages. These results suggest that local environmental factors such as light, depth and substrate inclination exert a stronger influence on the structure of benthic assemblages than protection from fishing. Reef walls of unprotected coastal reefs showed highest coral cover values, with a major contribution of *Montastraea cavernosa* (a sediment resistant species that may benefit from low light levels). An overall negative relationship between fleshy macroalgae and slow-growing reef-building organisms (i.e. scleractinians and crustose calcareous algae) was recorded, suggesting competition between these organisms. The opposite trend (i.e. positive relationships) was recorded for turf algae and the two reef-building organisms, suggesting beneficial interactions and/or co-occurrence mediated by unexplored factors. Turf algae cover increased across the region between 2006 and 2008, while scleractinian cover showed no change. The need of a continued and standardized monitoring program, aimed at understanding drivers of change in community patterns, as well as to subsidize sound adaptive conservation and management measures, is highlighted.

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Introduction

Worldwide, reef ecosystems are declining rapidly due to multiple disturbances such as climate change, overfishing, emerging diseases, pollution and sedimentation, implying severe losses of biodiversity and ecosystem services [1]–[3]. Despite the general consensus on the decline of coral reefs, there is little information on the dynamics of coral assemblages and the current status of reefs in large and important areas with tropical reefs, such as the South Atlantic [4]–[8].

The balance between abundance of relatively slow-growing reef building organisms (mainly crustose calcareous algae and scleractinian corals) and fast-growing non-building organisms (mainly turf and fleshy macroalgae) is one of the most widely used metric to evaluate reef condition, with dominance of the former indicating a healthy ecosystem [2], [3], [9]–[11]. Coral bleaching and disease, both triggered primarily by elevated sea surfaces temperatures, are main drivers of mass coral death [12]–[14]. Local anthropogenic disturbances, particularly nutrient overload and the overfishing of herbivores, lead to decreased reef resilience (i.e. lower capacity to recover after disturbance) and proliferation and persistence of algae after coral loss. Knowledge about major processes affecting such shifts from coral- to algal-dominated states (the so called "phase shifts") is critical for the adequate conservation and management of coral reefs [3], [15]–[17].

The general perception of decline in coral cover is mostly based on long-term datasets and meta-analytical studies from the Caribbean and Indo-Pacific regions [2], [10]. However, even for these latter well studied regions, lack of historical baselines and long-term data obtained with standardized methodologies hampers accurate evaluations of reef conditions, leading to contrasting interpretations [11], [18], [19]. In addition, benthic coral reef assemblages vary greatly over several spatial and temporal scales, making it difficult to evaluate the relative importance of natural and anthropogenic drivers in assemblage patterns [20]–[22]. For example, high macroalgal cover may be determined by factors other than anthropogenic disturbances such as depth, nutrient and light availability, with shallow inshore sites generally showing higher fleshy macroalgal cover than deep offshore ones [23], [24].

Protection from fishing through establishment of no-take marine reserves may influence reef benthic assemblages via habitat protection and trophic cascading effects [25], [26]. For example, increased herbivory due to protection of populations of large roving reef fishes such as parrotfishes (Labridae) and surgeonfishes (Acanthuridae) may avoid macroalgal proliferation and thus facilitate coral recruitment and recovery after disturbance [25], [26]. Thus, it is not surprising that several studies have shown contrasting benthic communities between protected and unprotected reef sites [27], [28].

Brazilian coral reefs represent a priority area for biodiversity conservation in the Atlantic Ocean due to their relatively high endemism levels (about 25% for fishes and 30% for scleractinian corals) concentrated in a small reef area (5% of West Atlantic reefs) [6], [29]. Artisanal fisheries are largely unregulated and account for an estimated 70% of total fish landings in the Eastern Brazilian coast, where coral reefs are concentrated [4], [30]. Despite their importance, Brazilian reefs are under mounting anthropogenic disturbances, particularly overfishing, pollution and sedimentation [4], [31]–[33]. The recent proliferation of coral diseases in Brazil and the prognostic of mass death of a major endemic reef-building species (*Mussismilia braziliensis*) are of special concern [34].

This study aims to describe spatial and temporal patterns in reef benthic assemblages of the Abrolhos Bank, eastern Brazil, as well as to infer possible anthropogenic and natural processes/disturbances responsible for the observed patterns. The Abrolhos region encompasses the largest and richest coral reef complex in the South Atlantic Ocean and the oldest among the few networks of marine protected areas in the country [4].

Materials and Methods

Study region

The Abrolhos Bank (16°40′,19°40′S–39°10′, 37°20′W) is a wide portion of the continental shelf (46 000 km^2), with depths rarely exceeding 30 m and a shelf edge at about 70 m. Reefs and rhodolith beds are the most prominent benthic features in the region [5]. Most reef structures display a characteristic form of mushroom-shaped pinnacles, which attain 5 to 25 m in height and 20 to 300 m across their tops [4]. Two main habitats can be distinguished in the reef pinnacles: tops (horizontal inclination; 2–6 m depth) and walls (vertical inclination; 3–15 m depth). About 20 scleractinian species are recorded for the region, at least six of them being endemic to Brazil [35].

Main rivers influencing the Abrolhos Bank are in its northern and southern extremes (River Jequitinhonha and River Doce, respectively). A large estuary formed by River Caravelas and River Peruípe is a remarkable feature of the coastline in the central portion of the Bank, near the main reefs [36]. Terrigenous sediments transported from land by river discharge predominate on coastal reefs, while biogenic carbonatic sediments predominate on mid- and outer-shelf reefs [37], [38]. Sedimentation regimes vary during the year, with higher sedimentation rates in winter-spring [33], [38], [39]. In summer, the rainfall is relatively high, leading to an increase in sediment transport to reefs via river discharge, while in winter resuspension of sediments is commonly caused by polar front winds [39].

Sampling design and field measurements

The long-term monitoring program of coral reef benthic assemblages of the Abrolhos Bank started in 2003, through engagement of scientists and members of governmental and non-governmental organizations related to coastal management. Surveys were always carried out in the summer (January–March), thus avoiding seasonal artifacts. Each site was about 300 m in diameter and composed by 1–3 interconnected reef pinnacles, except for the rocky reefs of the Abrolhos Archipelago (see below). Spatial coverage and sampling methodologies varied through time, with two main periods. From 2003 to 2005 point-intercept lines (10 m length and 100 points; n = 4 per site) [40] were haphazardly placed on the pinnacle's tops, and groups of four quadrats (50×50 cm; 25 intercepts) equally distributed within 10 m lines were haphazardly placed on the pinnacle's walls. Each group of quadrats was considered as a single sample (n = 4 per site). Organisms immediately below each point were recorded *in situ* and classified as follows: turf algae, crustose calcareous algae, fire-corals (milleporids), fleshy macroalgae, live corals, octocorals and zoanthids. The "live coral" category includes only scleractinians, with no species distinction. During this first period, monitoring was performed in four areas (Fig. 1), as follows: **Area 1) No-take reserve of Timbebas Reef** (three sampling sites) – Located within the National Marine Park of Abrolhos (NMPA). Created by the Brazilian government in 1983, the NMPA comprises two discontinuous portions, one closer to the coast and poorly enforced (Timbebas Reef), and another farther from the coast and more intensively enforced (Abrolhos Archipelago and Parcel dos Abrolhos Reef). **Areas 2 and 3) Multiple-use and no-take zones of Itacolomis Reef –** Itacolomis Reef is the largest reef complex (~50 km^2) within the Marine Extractive Reserve of Corumbau (MERC) [41], [42]. It is divided into two main zones: multiple-use (Area 2; seven sampling sites) and no-take (Area 3; three sampling sites). **Area 4) Unprotected coastal reefs** (five sampling sites) – It encompasses the Parcel das Paredes Reef and Sebastião Gomes Reef, both subjected to the highest fishing pressure in the region [4] (Fig. 1).

Between 2006 and 2008 benthic assemblages were characterized using fixed photo-quadrats [34] in both, reef tops and walls (n = 10 per site). Each sample was composed by a mosaic of 15 high-resolution digital images totaling 0.7 m^2. Quadrats were permanently delimited by fixed metal pins and set at haphazardly distances along 20–50 m axes. Relative cover of different benthic organisms was estimated through the identification of organisms (lowest taxonomic level possible) below 300 randomly distributed points per quadrat (i.e., 20 points per photograph) using the Coral Point Count with Excel Extensions Software [43]. Besides sampling the same sites within the abovementioned areas, two additional areas were sampled between 2006 and 2008, the Abrolhos Archipelago (five sampling sites) and Parcel dos Abrolhos

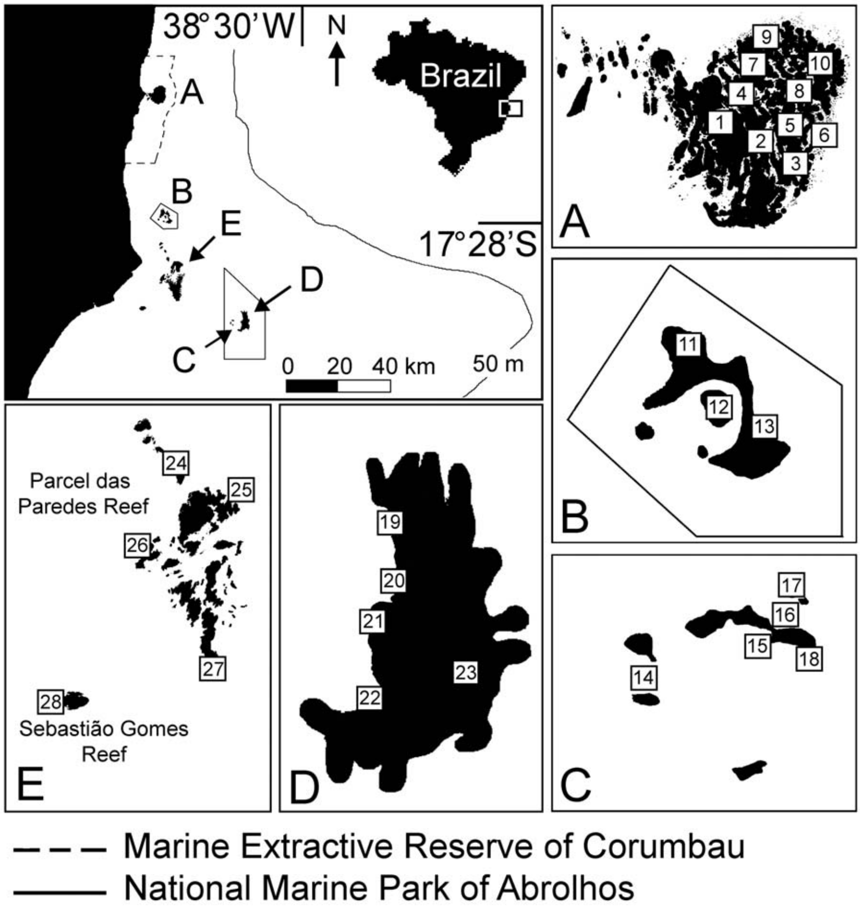

Figure 1. Map of the Abrolhos Bank, eastern Brazil, showing study sites and marine protected areas. A - Itacolomis Reef (no-take zone: sites 1–3; multiple-use zone: sites 4–10), B - Timbebas Reef, C - Abrolhos Archipelago, D - Parcel dos Abrolhos Reef, E – Unprotected coastal reefs. doi:10.1371/journal.pone.0054260.g001

Reef (five sampling sites), both within the NMPA portion that is farther from the coast (Fig. 1). The Abrolhos Archipelago is a rocky reef with no clear distinction between reef tops and walls, thus a single habitat (the reef front) was sampled. In total, 27 sites were sampled and 448 photo-quadrats were obtained per year between 2006 and 2008. A summary of the environmental characteristics of each sampling site is shown in Table S1.

Logistical support and research permits were provided by Parque Nacional Marinho de Abrolhos and Reserva Extrativista Marinha de Corumbau/ICMBio (through J.R.S. Neto, R. Jerolisky and R. Oliveira). Data from this work was made available for public access through the Dryad platform (http://datadryad.org/).

Data analyses

Detailed analyses were performed for the period between 2006 and 2008 ("short-term comparisons"), in which data was obtained with a higher taxonomic resolution and a greater spatial coverage (see above). Inferences for the entire sampling period (2003–2008, "long-term comparisons") were performed by making separate analyses for the two sampling periods: 2003–2005 and 2006–2008, and by considering only the same sampling sites and benthic categories (i.e. by standardizing data obtained in the two sampling periods). Long-term changes were taken into account only when similar trends were recorded for both sampling periods.

Some metal pins marking the fixed photo-quadrats were lost during the sampling period. These samples were excluded from the analyses in order to assure that exactly the same photo-quadrats were used for the temporal comparisons. Final sample size ranged between 7–10 quadrats per habitat per site per year. Three common genera of fleshy macroalgae (*Canistrocarpus* spp., *Dictyota* spp. and *Dictyopteris* spp.) were difficult to distinguish in the images, thus being pooled into a single category (hereafter called "other fleshy macroalgae"). All scleractinians were identified to the species level, except for *Siderastrea* spp., a genus for which three morphologically similar species are recorded for Brazil (*S. stellata*, *S. siderea* and *S. radians*) [44]. Data was also pooled for two morphologically similar fire-coral species (*Millepora brasiliensis* and *M. alcicornis*), but treated separately for the small-sized and conspicuous *Millepora nitida*.

Analysis of variance (ANOVA) was used to evaluate spatial and temporal variations in benthic cover. Two separate groups of ANOVA were calculated, the first one focusing on differences between tops and walls (considering reef pinnacles only) and the second one focusing on differences between reefs while ignoring between-habitat variability, this latter including the shallow rocky reefs of the Abrolhos Archipelago (which has no distinction between tops and walls). Because data could not be collected in the tops of three reefs (see Table S1), between-site variability was ignored in the ANOVA models, thus avoiding missing observations and the need of application of a less robust ANOVA model.

In order to satisfy ANOVA assumptions of normality and homocedasticity, benthic cover percentages were converted to arcsin $\sqrt{x}$. Student-Newman-Keuls (SNK) multiple comparisons of means were performed as a *post-hoc* test [45].

Non-metric multidimensional scaling (MDS) ordination was used to summarize spatial and temporal similarities (Bray-Curtis) on the structure of benthic assemblages, and separate one-way analyses of similarities (ANOSIM) were used to evaluate significant differences according to reef areas, habitats and years [46].

Canonical correspondence analysis [47] was used to evaluate the influence of ecological and environmental explanatory variables on the structure (i.e. composition and relative cover) of benthic assemblages. Three fish functional groups are likely to exert strong influence on the benthos: 1) Large-bodied scrapers and grazers (Labridae: Scarinae), 2) Large-bodied browsers (Labridae: Sparisomatinae) and 3) Small-bodied territorial damselfish (Pomacentridae) [24], [48]–[50]. Biomass estimates for these three functional groups, together with depth, latitude, distance offshore and levels of protection were used as explanatory variables in the canonical correspondence analysis. Data on fish biomass was obtained from previous surveys [4], [41]. A forward selection procedure was used to include only the most important independent variables in the model, 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 model. Reef areas were dummy-coded for levels of protection from fishing, as follows: 1) open-access reefs, 2) Itacolomis Reef (multiple-use portion), 3) Itacolomis Reefs (young no-take reserve), 4) Timbebas Reef (old and poorly enforced no-take reserve) and 5) Abrolhos Archipelago and Parcel dos Abrolhos Reef (old and well enforced no-take reserve) (see [4] for detailed information on protection levels of these areas; see Table S1).

Multiple linear regression analyses [45] were used to evaluate the relative influence of major non-building organisms (i.e. turf algae, fleshy macroalgae and *Palythoa caribaeorum*) on the abundance of key reef-building organisms (scleractinians and crustose calcareous algae). Percentage cover data are compositional and thus subjected to constant sum constraint. Because this may mask true relationships among variables, analyses were performed using the centered log-ratio transformation [51].

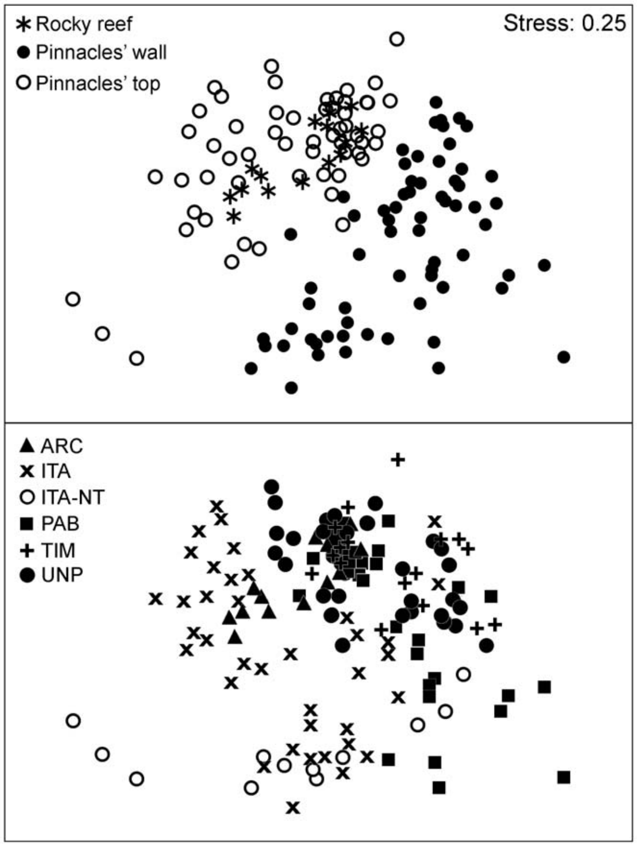

Figure 2. Multidimensional scaling (MDS) of benthic assemblages (i.e. relative cover of different organisms) based on Bray–Curtis similarities. Top panel: samples classified according to habitat; Bottom panel: samples classified according to reef areas. Reef areas: ARC – Archipelago, ITA-NT – Itacolomis Reef (no-take), ITA – Itacolomis Reef (multiple-use), PAB – Parcel dos Abrolhos (no-take), TIM – Timbebas Reef (no-take) and UNP – Unprotected coastal reefs.
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Results

Short-term comparisons

The top five most abundant benthic organisms in the Abrolhos Bank, considering all sampling sites and years (2006–2008), belonged to different functional groups. Turf algae were by far the most abundant benthic organisms (56.1%), followed by crustose calcareous algae (12.1%), the zoanthid *Palythoa caribaeorum* (6.6%), the scleractinian coral *Monstastrea cavernosa* (4.1%) and the category composed by the fleshy macroalgae *Canistrocarpus* spp., *Dictyota* spp. and *Dictyopteris* spp. (2.9%) (Fig. S1). In ANOSIM analyses, values of global R were higher for contrasts between habitats (R = 0.26; P = 0.001) than reefs (R = 0.10; P = 0.003). The two-dimensional MDS ordination diagrams showed a much clearer distinction between habitats than between reefs, with samples from shallow rocky reefs of the Abrolhos Archipelago clustering together with samples from pinnacles' tops (Fig. 2). Benthic assemblages of both, pinnacles' tops and rocky reefs of the Abrolhos Archipelago, were characterized by relatively high covers of the scleractinian corals *Agaricia humilis*, *Favia gravida*, *Mussismilia braziliensis* and *Siderastrea* spp., articulated calcareous algae, as well as fleshy macroalgae of genus *Sargassum* (Figs. 3 and 4; Tables S2 and S3). Benthic assemblages of reef walls were characterized by high covers of the corals *Agaricia fragilis*, *Madracis decactis*, *M. cavernosa*, *Mussismilia hispida* and *Scolymia wellsi*, octocorals, sponges, ascidians, bryozoans, crustose calcareous algae, macroalgae of genus *Caulerpa* and cyanobacteria (Figs. 3 and 4; Tables S2 and S3).

Highest coral cover values were recorded at the walls of both protected (Timbebas Reef) and unprotected coastal reefs, with major contributions of *Montastraea cavernosa* and *Mussismilia hispida*. The reef coral *Mussismilia harttii*, octocorals, the algae *Halimeda* spp. and zoanthids of genus *Zoanthus* were also common at Timbebas, while the fire-coral *Millepora nitida* was also abundant at unprotected coastal reefs. The colonial zoanthid *P. caribaeorum* showed highest cover values at coastal reefs (both protected and unprotected) and at the mid-shelf fully-protected reefs of Parcel dos Abrolhos. Turf algae and fleshy macroalgae, particularly *Sargassum* spp., were more prevalent in the no-take and multiple-use zones of Itacolomis Reef (Figs. 3 and 4; Tables S2 and S3). Benthic assemblages of the Abrolhos Archipelago were dominated by the reef corals *Favia gravida*, *M. braziliensis* and *Siderastrea* spp., articulated calcareous algae and *Sargassum* spp. (Figs. 3 and 4; Table S4).

No significant between-years variation was detected on the structure of benthic assemblages (R = 0.008; P = 0.8). However,

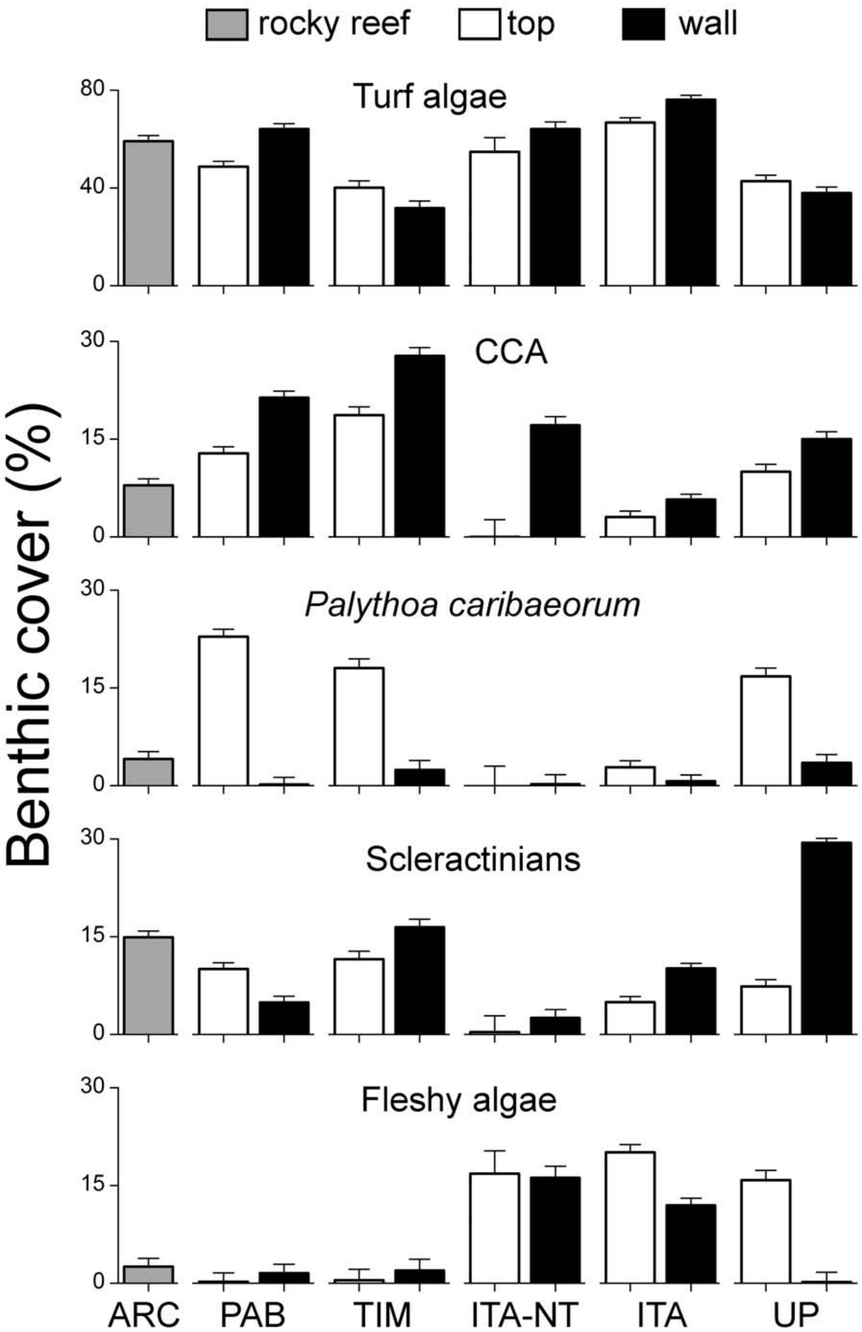

Figure 3. Benthic cover (mean + SE) of the top five most abundant organisms in the Abrolhos Bank.
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significant variations were recorded for several individual organisms/categories. Most noticeable was the increase in turf algae cover in most reef areas between 2006 and 2008 (Fig. 5; Tables S2 and S3). Crustose calcareous algae declined sharply on reef tops of unprotected coastal reefs. Temporal dynamics of *Caulerpa* spp. and cyanobacteria was not consistent among reef areas, with significant interactions being recorded (Fig. 5; Tables S2 and S3).

The multiple regression models explained a much higher variance for scleractinian corals ($r^2 = 0.57$) than for crustose calcareous algae ($r^2 = 0.13$). Negative relationships were recorded between fleshy macroalgae and reef-building organisms, the opposite trend (i.e. positive relationships) being recorded between turf algae and reef-building organisms. The zoanthid *P. caribaeorum* showed a negative effect on the cover of crustose calcareous algae and a weak yet significant positive effect on the cover of scleractinian corals (Table S5).

Depth, latitude, distance offshore and protection levels were, in decreasing order (i.e. order of entrance in the model), the four most important variables affecting the structure of benthic assemblages. Latitude and distance offshore were positively correlated with each other, with southern reefs (Parcel dos Abrolhos Reef) more distant from the coast than northern ones (Itacolomis Reef), making difficult to disentangle the effect of these two explanatory variables. The first two axes explained 75.3% of

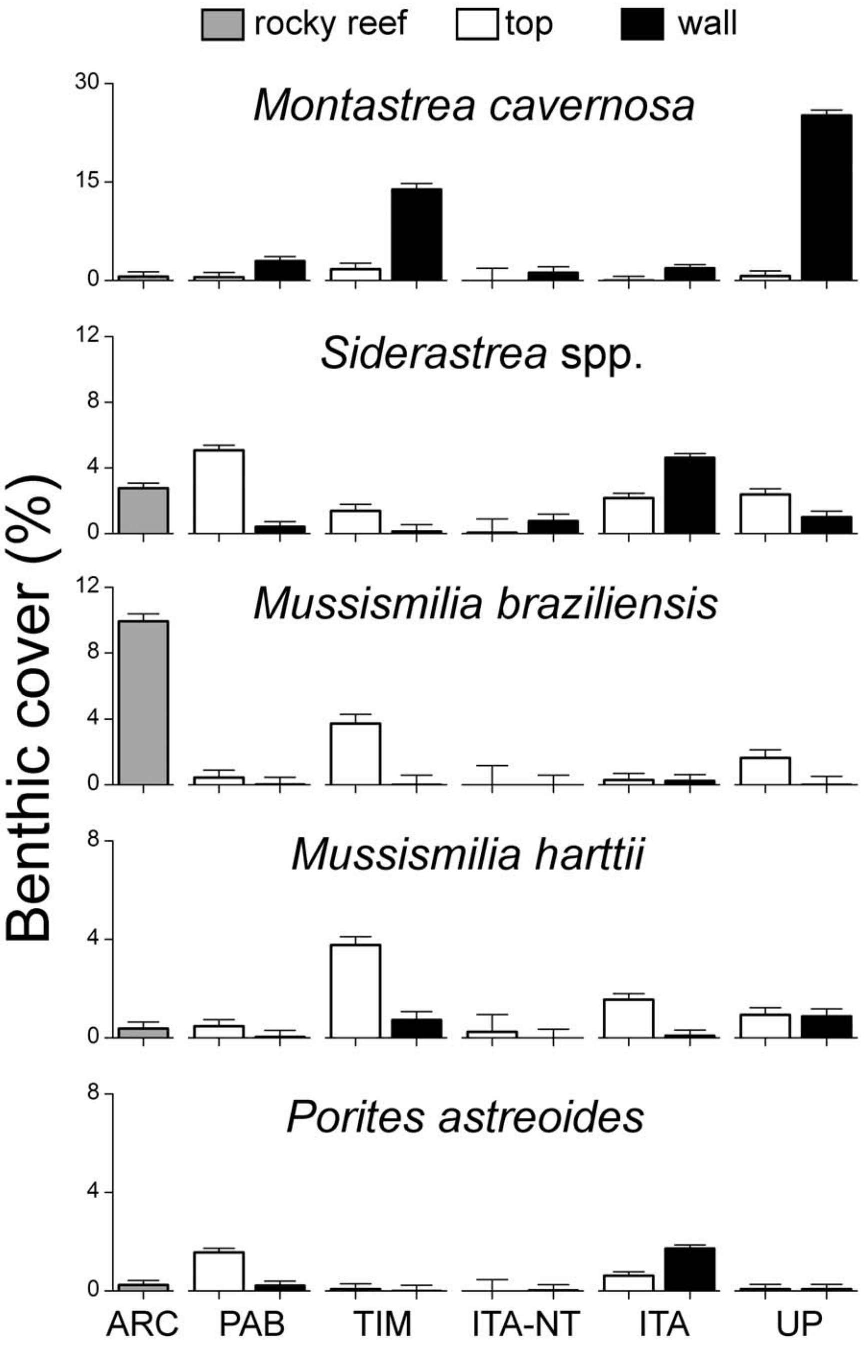

Figure 4. Benthic cover (mean + SE) of the top five most abundant reef corals (secleractinians) in the Abrolhos Bank.
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the relationship between environmental characteristics and benthic assemblages' structure. Inclusion of the remaining three explanatory variables (i.e. biomass of scrapers, grazers and territorial herbivores) increased the power of explanation of the model by less than 1%. Most importantly, these latter three variables were not significant ($P > 0.05$) according to the Monte Carlo test. There was a clear distinction of samples obtained in different habitats and reef areas in the two-dimensional ordination diagram (Fig. 6). Four main reef benthic assemblages were recorded: 1) Reef tops of northern/inshore reefs, 2) Reef tops of southern/offshore reefs, 3) Reef walls of northern/inshore reefs and 4) Reef walls of southern/offshore reefs (Fig. 6).

Long-term comparisons

When considering data pooled for all habitats and sites, temporal variations between 2003 and 2008 (i.e. for both sampling periods) were recorded for CCA only, with no clear overall trend of increase or decrease through time (Fig. 7). A significant increase in turf algae cover was recorded for the entire Abrolhos Bank in the second period of the study (2006–2008) (Fig. 7). All interactions were significant in this latter case, with increases recorded for most habitats/reefs, except for reef walls of the no-take zone of Itacolomis Reef (Fig. 8; Table S6). Octocoral cover declined on reef tops of the unprotected coastal reefs between 2003 and 2005

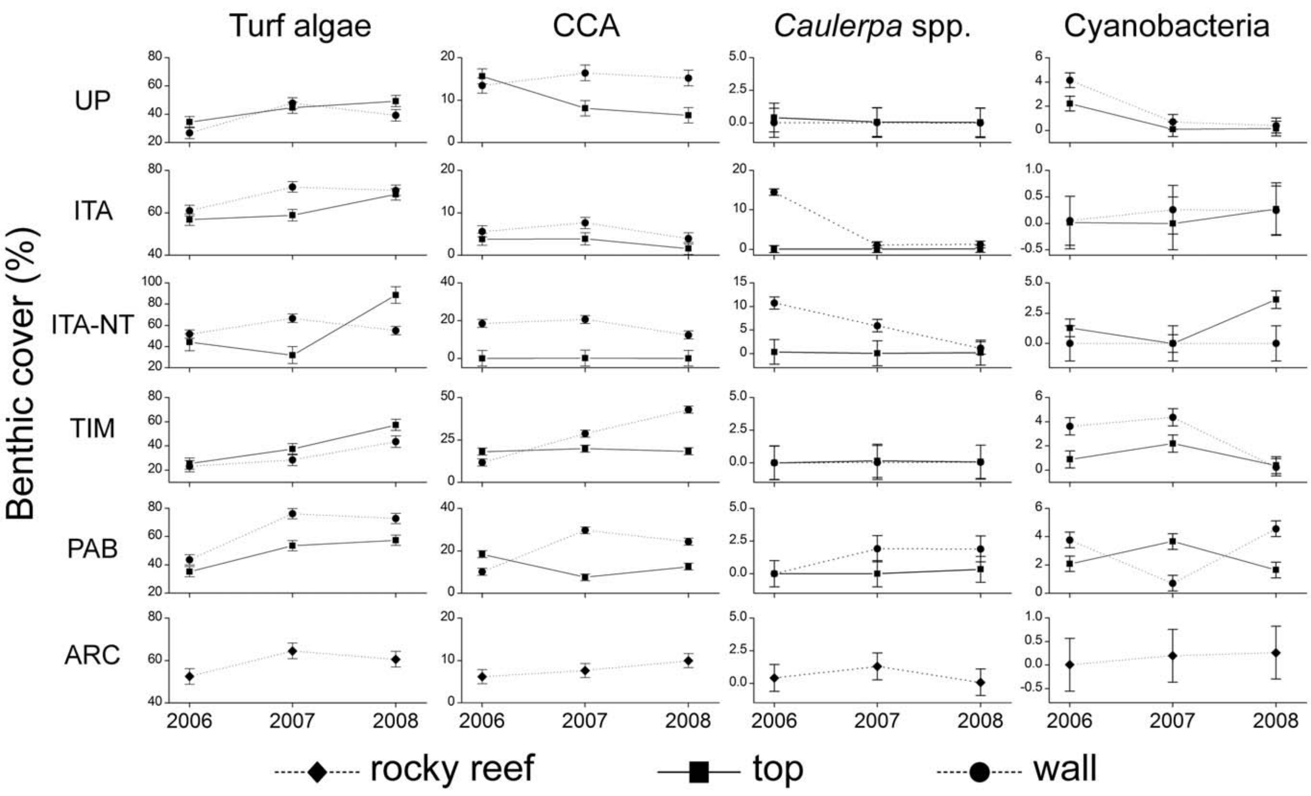

Figure 5. Temporal dynamics in cover (mean ± SE) of benthic organisms in the Abrolhos Bank between 2006 and 2008. Only organisms for which significant temporal variations were recorded are shown.
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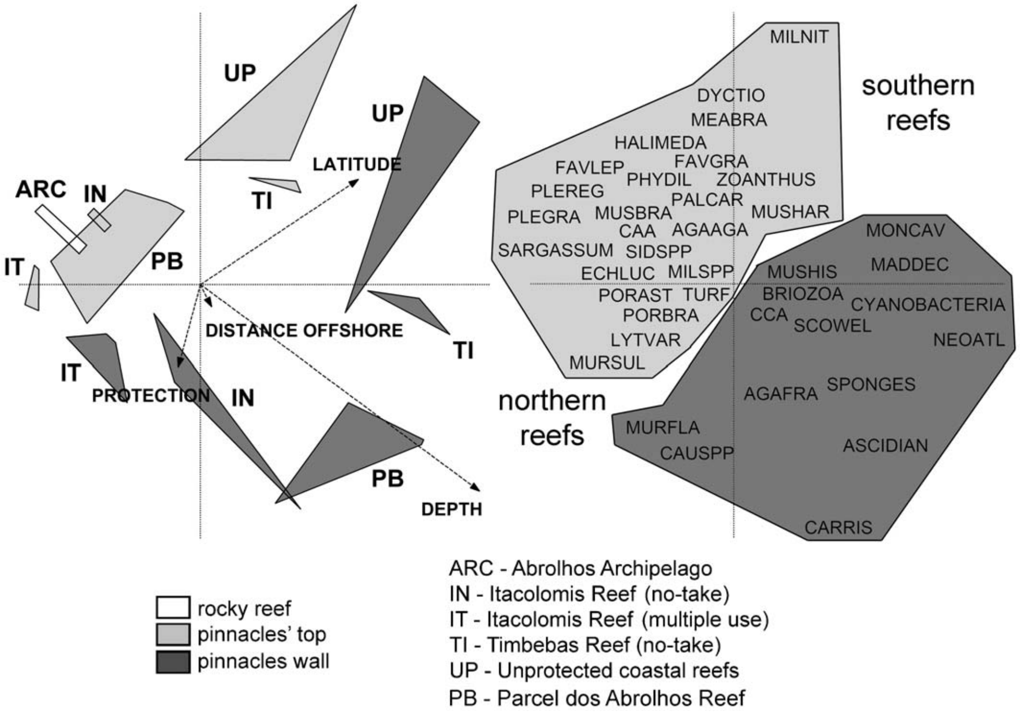

Figure 6. Canonical correspondence analysis plot showing: (left) relationship between independent variables (arrows) and reef areas and (right) distribution of benthic organisms in the two-dimensional ordination space.
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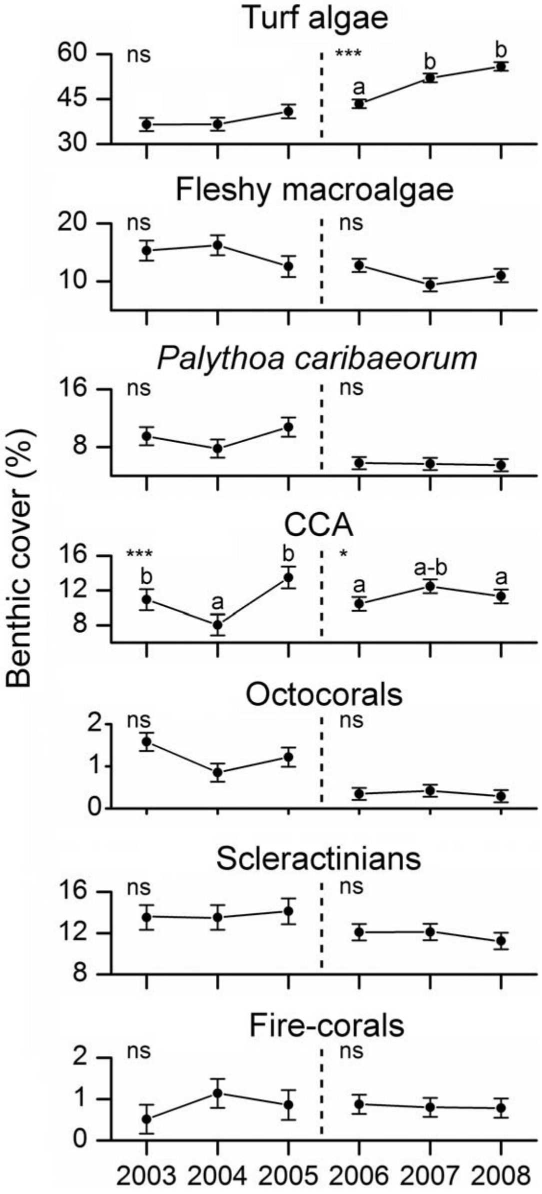

Figure 7. Temporal dynamics in cover (mean ± SE) of benthic organisms in the Abrolhos Bank between 2003 and 2008. The dashed line separates the two sampling periods in which different methodologies were used (see Materials and Methods). Analyses of Variance (ANOVA) results: $^*P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$. Homogeneous groups are identified by equal letters.
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(Fig. 9; Table S6). No other significant temporal variations were recorded (Figs. 7, 8 and 9; Table S6).

Discussion

This is one of the most comprehensive characterizations of shallow coral reef benthic assemblages of the Abrolhos Bank performed to date and one of the few studies focusing on a relatively long temporal scale [8], [52]. The first study focusing on coral cover in the region was performed by [53]. Unfortunately, direct comparisons between data from [53] and data obtained here are not possible, as in the former study no absolute coral cover values were given, only species percentages in relation to total coral cover. Other relevant studies in the Abrolhos Bank were performed with no clear specification of site location [54], by using different methodologies [55], [56] and/or by applying different metrics [52], [55]. Thus, caution is needed when performing between-studies comparisons (see below).

In the present study, highest coral cover values (with a major contribution of *Montastraea cavernosa*) were recorded in reef walls of unprotected coastal reefs (Fig. 10). It is important to note that most previous studies focusing on coral reef benthic assemblages of the Abrolhos Bank have sampled reef tops only, but see [52], thus underestimating the relevance of coastal reefs in terms of coral cover [8], [33], [53], [54]. For example, [8] stated that "Because the lateral walls of these pinnacles are mostly inhabited by small coral colonies (such as *Agaricia fragilis*, *Scolymia wellsi*, *Meandrina braziliensis*) that do not have great importance as reef builders, they were not assessed". This limitation in the sampling design of previous studies is particularly important considering the results obtained here showing that differences between habitats are more important than differences between reefs. Results from this study indicate that *M. cavernosa* is a major reef-building species in SW Atlantic coral reefs, highlighting the importance of studies focusing particularly on the healthy and dynamics of this species. In the Caribbean, habitats dominated by *Montastraea* spp. have the highest biodiversity and support the largest number of ecosystem processes and services [57]. Other scleractinians characteristics of reef walls commonly recorded here (*Agaricia fragilis*, *Mussismilia hispida* and *Scolymia wellsi*) may have also been underestimated in previous studies, but see [52]. Only one previous study conducted in the Abrolhos region has also sampled reef tops and wall [52]. Results from this latter study (based on semi-quantitative and presence-absence data obtained in 42 sites), also indicated significant differences in the structure of coral assemblages (hidrocorals, octocorals, scleractinians and *P. caribaeorum*) between tops and walls.

The high coverage of *M. cavernosa* on walls of inshore unprotected reefs is not surprising. *Montastraea cavernosa* is recognized as a sediment resistant species with a high capacity for sediment removal, being a major component of the "sediment resistant coral fauna" in the West Atlantic [58]. *Montastraea cavernosa* is also abundant in sediment-free mesophotic (30–150 m) reef communities [59], [60], which suggests that this species benefits from low light levels. The same pattern (i.e. occurrence in shallow turbid reefs and mesophotic clear water reefs) was recently recorded for *A. fragilis*, *M. hispida* and *S. wellsi* [60]. Another possible explanation for the high coverage of *M. cavernosa* on inshore reefs of the Abrolhos Bank is the relatively high availability of nutrients in inshore reefs, which may lead to high coral growth rates and reproductive output [61], [62].

The strong between-habitat differences recorded here suggest that factors such as light, depth and bottom inclination are the main drivers of benthic assemblages' structure in the Abrolhos region. Other studies performed elsewhere have highlighted the importance of such environmental variables for coral reef benthic assemblages [63]–[65]. Due to the peculiar growth form of reef pinnacles in the Abrolhos region, depth, inclination and light levels vary sharply in a scale of just a few meters, accounting for the extreme variability recorded here. In this study, only weak relationships were recorded between protection levels and the structure of benthic assemblages. In particular, no relationship between biomass of herbivorous fish and the structure of benthic assemblages were recorded. Thus, although previous studies have shown that protection afforded by no-take reserves within the Abrolhos Bank lead to increased fish biomass, including large herbivorous fish [4], [24], [41], it is suggested here that fish

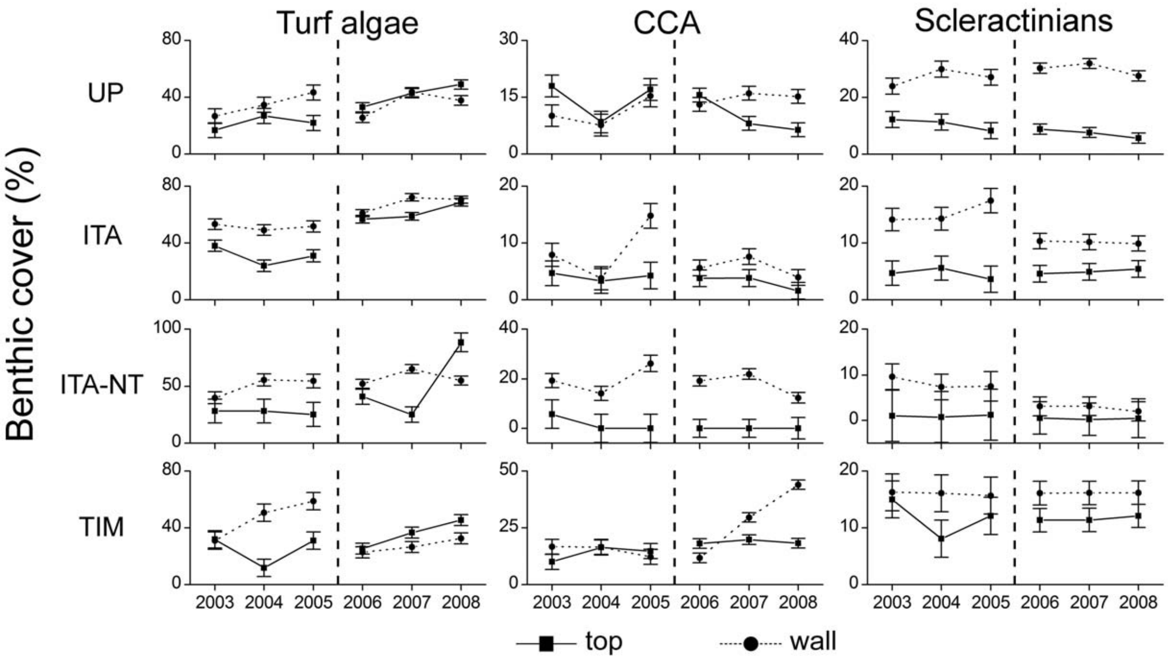

Figure 8. Temporal dynamics in cover (mean ± SE) of benthic organisms in the Abrolhos Bank between 2003 and 2008 considering different reef areas and habitats. Reef areas: ITA-NT – Itacolomis Reef (no-take), ITA – Itacolomis Reef (multiple-use), TIM – Timbebas Reef (no-take) and UNP – Unprotected coastal reefs. The dashed line separates the two sampling periods in which different methodologies were used (see Materials and Methods).
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recoveries are still incipient to promote noticeable changes in benthic assemblages [66], [67]. Depending on the degree of reef degradation, up to 10 years of effective protection may be necessary for detecting changes in benthic assemblages [68]. The Brazilian-endemic brain coral *Mussismilia braziliensis* was an exception to the abovementioned pattern, as this species was relatively more abundant inside no-take zones (Timbebas Reefs and the Abrolhos Archipelago) (see Fig. 4). [52] also recorded higher cover values of *M. braziliensis* inside no-take zones within the Abrolhos Bank (Parcel dos Abrolhos Reef and Timbebas Reefs). A recent study [28] has shown that no-take zones of the Abrolhos Bank may promote coral reef health, with noticeable positive

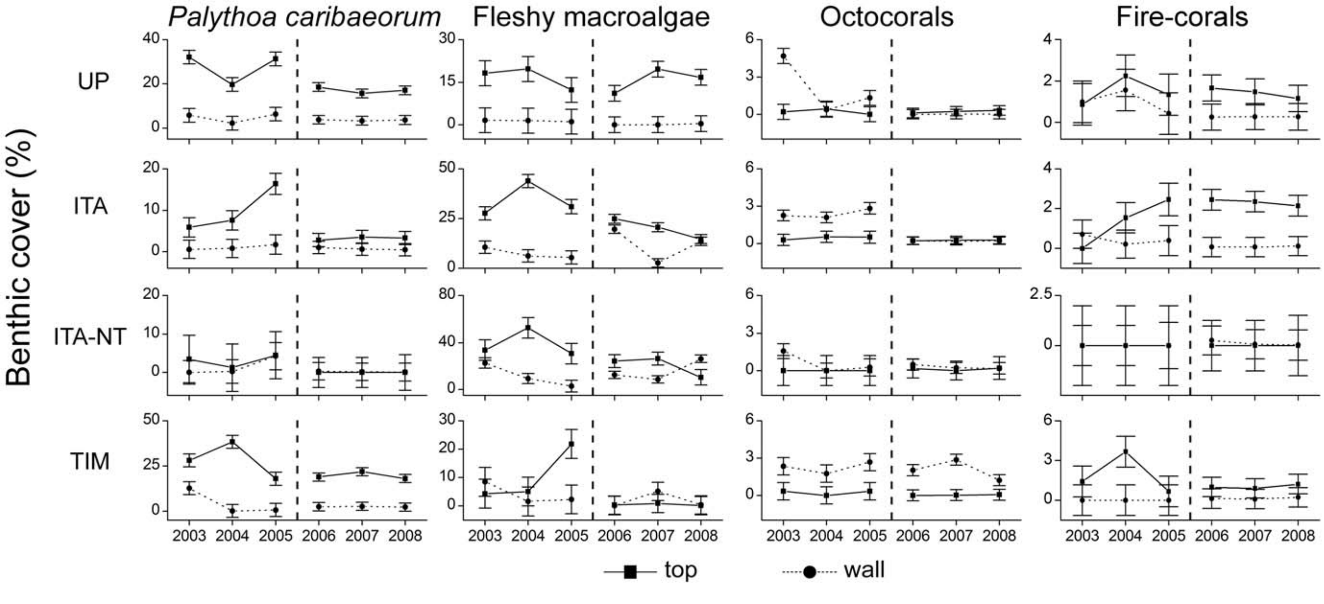

Figure 9. Temporal dynamics in cover (mean ± SE) of benthic organisms in the Abrolhos Bank between 2003 and 2008 considering different reef areas and habitats. Reef areas: ITA-NT – Itacolomis Reef (no-take), ITA – Itacolomis Reef (multiple-use), TIM – Timbebas Reef (no-take) and UNP – Unprotected coastal reefs. The dashed line separates the two sampling periods in which different methodologies were used (see Materials and Methods).
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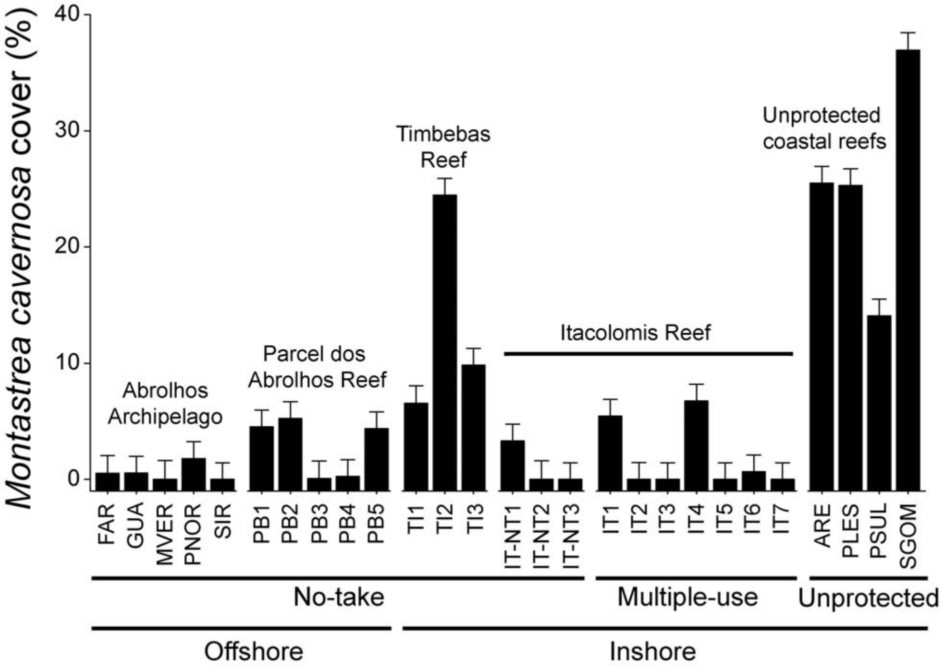

Figure 10. Cover (mean + SE) of the reef coral *Montastraea cavernosa* in reef walls of the Abrolhos Bank (data pooled for samples obtained between 2006 and 2008).
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effects on microbial, benthic and fish assemblages. However, the sampling design of this latter study was limited to the spatial comparison of reef tops of four sampling sites only, with no formal evaluation of the relative influence of different factors (e.g. habitat characteristics and protection levels).

The relatively high cover of the zoanthid *Palythoa caribaeorum* in the Abrolhos Bank is noteworthy (up to 25% in some sites). This species is an aggressive competitor for space, killing or inhibiting the growth of nearly all other sessile reef invertebrates, including corals [69], thus playing important roles in reef community processes [70]. The negative relationship between cover of *P. caribaeorum* and that of crustose calcareous algae suggests competition between these organisms. [38] sampled three sites also included in this study (Pedra de Leste, Ponta Sul and Parcel dos Abrolhos) and found a negative relationship between distance offshore and *P. caribaeorum* cover, the opposite trend being recorded for scleractinians. Such a pattern was not recorded here, with highest values of *P. caribaeorum* cover recorded in tops of both inshore unprotected coastal reefs and tops of mid-shelf fully-protected reefs (Parcel dos Abrolhos Reef). [38] suggested that sedimentation levels may mediate competition between *P. caribaeorum* and scleractinians, with high sedimentation levels favoring the former. Sedimentation, desiccation and predation levels are some of the environmental and ecological drivers that may influence *P. caribaeorum* abundance [70]–[72], but detailed experimental studies are still needed in order to understand factors affecting abundance and competitive capabilities of *P. caribaeorum* in the Abrolhos Bank and elsewhere.

A moderate increase in turf algae cover was recorded across the Abrolhos Bank between 2006 and 2008. The lack of relationship between biomass of herbivorous fish and algae abundance reported here indicate that other factors, such as coral mortality *per se* due to diseases [34] and nutrient enrichment [28] are more important than herbivory levels for controlling turf algae abundance in the Abrolhos Bank. The lack of temporal variation for most benthic organisms/categories recorded here suggests that longer-term data may be necessary in order to detect possible shifts in coral reef benthic assemblages of the Abrolhos region and to better understand the underlying processes.

Results from the multiple regression models obtained here indicate that competition with fleshy macroalgae is important for both scleractinian corals and crustose calcareous algae. Negative effects of fleshy macroalgae on corals have been widely reported [73]–[75]. The strong positive relationship between turf algae cover and scleractinian cover recorded here was surprising, as turf algae may also cause deleterious effects to scleractinians [76]–[78]. However, some coral species may suffer no effects or even be competitively superior to turf algae. The variation in the outcomes of interactions between scleractinians and turf algae may be related to several factors. For example, relatively large and massive coral colonies may be competitively superior to turf algae than small branching ones [79], [80]. Algal identity is also important, with different species showing negative or null effects on scleractinians [81]. In some particular cases, turf algae may exert positive effects by providing species-specific settlement cues for scleractinians [82].

The lack of historical ecological data impedes the understanding of processes underlying community-level dynamics and the evaluation of the actual degree of conservation/degradation of reef communities [11], [83]. In this regard, large spatial and temporal scale monitoring programs such as the present one may provide key data for understanding drivers of change in community patterns and for creating sound adaptive conservation and management measures [83], [84]. As more long-term monitoring results are made available, more comprehensive qualitative [85] and meta-analytical studies using data from different geographical regions will be made possible [2], [10], [84]. Data from Brazil may be of particular interest when testing hypotheses related to the effects of functional diversity on assemblage resistance/resilience, given the low species richness and functional redundancy of Brazilian reefs.

Supporting Information

Figure S1 Decreasing order of abundance of benthic organisms in the Abrolhos Bank. Species codes: First three letters of genus name followed by first three letters of specific epithet (see full names in Table S2).
(TIF)

Table S1 Summary of environmental characteristics of sampling reefs and sites.
(DOC)

Table S2 Analyses of Variance (ANOVA) testing the effect of reef areas (R), habitats (H) and years (Y) in cover of different benthic organisms with data obtained between 2006 and 2008. The Abrolhos Archipelago area (rocky reef) was excluded from these analyses in order to allow a more comprehensive comparison between pinnacles' tops and walls (see Material and Methods).
(DOC)

Table S3 Significant differences in benthic cover according to reef areas (R), habitats (H) and years (Y), as determined by Student-Newman-Keuls (SNK) *post-hoc* comparisons. Reefs arranged in decreasing order of benthic cover, with homogeneous groups linked by an equal sign. Reef areas: IN – Itacolomis Reef (no-take), IT – Itacolomis Reef (multiple-use), PB – Parcel dos Abrolhos (no-take), TI – Timbebas Reef (no-take), UP – Unprotected coastal reefs. Habitats: TP – tops and WA – walls. Years: 2006–2008. The Abrolhos Archipelago area (shallow rocky reef) was excluded from these analyses in order to allow a more comprehensive comparison between pinnacles' tops and walls (see Material and Methods).
(DOC)

Table S4 Analyses of Variance (ANOVA) testing the effect of reef areas (R) and years (Y) in cover of different benthic organisms with data obtained between 2006 and 2008. Reef areas: AR – Abrolhos Archipelago, IN – Itacolomis Reef (no-take), IT – Itacolomis Reef (multiple-use), PB – Parcel dos Abrolhos (no-take), TI – Timbebas Reef (no-take), UP – Unprotected coastal reefs.
(DOC)

Table S5 Multiple regression results showing the relative influence of fast growing non-reef building organisms (turf alga, fleshy algae and *Palythoa caribaeorum*) on abundance of key reef-building organisms (scleractinians and crustose calcareous algae). Levels of significance for full model and partial r^2: * $P<0.05$; ** $P<0.01$; *** $P<0.001$.
(DOC)

Table S6 Analyses of Variance (ANOVA) testing the effect of reef areas, habitats and years in cover of different benthic organisms for the two sampling periods (2003–2005/2005–2008).
(DOC)

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Author Contributions

Conceived and designed the experiments: RBFF RLM. Performed the experiments: RBFF EOCC PMM DPA CMF RLM. Analyzed the data: RBFF. Contributed reagents/materials/analysis tools: RBFF GMAF FLT ACB PYGS RLM. Wrote the paper: RBFF EOCC PMM GMAF FLT GHPF ACB DPA CMF FG AZG PYGS NLO LK CVM RLM.

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ARTIGO 2

Growth and vitality of the South Atlantic “weedy” coral *Favia gravida* Verril, 1868: Effects of cross-shelf gradients, protection levels and surrounding substrate

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Abstract

Coral reefs are steadily losing coral cover due to the interaction between stressors operating at multiple spatial and temporal scales. The decline of reef ecosystems is commonly associated with changes in water chemistry and quality, temperature anomalies and poor fisheries management. Besides the widely reported coral-to-macroalgal phase shifts, deterioration of reefs may involve the replacement of large and slow-growing coral species by faster-growing “weedy” or “stress-tolerant” corals. During a relatively long-term study (4 years) in the Abrolhos Reefs, Brazil, we assessed selected aspects of the population dynamics of an allegedly “weedy” coral species (*F. gravida* Verril, 1868) along a cross shelf gradient of potential stressors (turbidity) and under different management regimes (open and closed to fishing, with contrasting herbivorous fish biomass). We also explored the influence of the immediate surrounding substrate on colony size, growth and vitality. *Favia gravida* presents higher cover and growth rates on coastal reefs under relatively high turbidity levels. Moreover, higher growth rates were associated with colonies surrounded by turf algae than by other substrate types that are generally considered more positive to corals (e.g. crustose calcareous algae). Fleshy macroalgae cover was negatively correlated with *F. gravida* cover and colony size, while a higher protection level was positively associated with its growth and negatively associated with colony size. Bleaching affected half of the studied population and colony vitality was primarily influenced by the distance from the coast. Potential consequences of better performance of "weedy" corals species in the long-term dynamics of Brazilian coral reefs are discussed.

Keywords: Functional groups, coral growth, bleaching, Abrolhos

Introduction

Coral cover and diversity are rapidly declining globally (Carpenter et al. 2008; Wilkinson 2008), challenging scientists and managers to assess and model its direct and indirect effects (Hoegh-Guldberg et al. 2011; Hoey and Belwood 2011), and highlighting the urgent need of finding new ways to conserve and manage reef ecosystems (Mumby and Steneck 2008). Drivers of the ongoing coral decline, including overfishing, thermal anomalies, changes in water chemistry, and emerging multifactorial diseases, operate at different temporal and spatial scales (Kleypas et al. 2001; Knowlton 2001; Rosenberg and Loya 2004). Besides the widely reported coral-to-macroalgal phase shifts (Hughes 1994; Bruno and Selig 2007; Norström et al. 2009), coral decline may be less evident when large and slow-growing species are replaced by small faster-growing ones (Green et al. 2008; Alvarez-Filip et al. 2011).

However, the dynamics of corals with different life histories/ecological traits is still poorly known, making it difficult to understand the relative importance of species' replacements in the dynamics of coral assemblages (Darling et al. 2012).

The small (~5% of Atlantic reefs) Southwest Atlantic reefs are remarkable for their low species richness and relatively high endemism levels (Moura 2002; Nunes et al. 2011). Brazilian scleractinian reef assemblages lack branching forms and encompass "weedy", "generalist" and "stress-tolerant" forms living under high sedimentation levels (Leão et al. 2003; Francini-Filho et al. 2013). Due to their small size, high endemism levels and escalating threats, Brazilian reefs may be the current frontlines of extinction in the Atlantic (Moura 2002; Francini-Filho et al. 2008a). The main coral framework-builders in the South Atlantic include slow-growing "generalists" belonging to the endemic genus *Mussismilia*, a Neogene relict widely reported in the fossil record of the Caribbean and the Mediterranean (Jackson et al. 1996). A 3-4 fold decline of *Mussismilia* cover occurred in the last 6 ky in the tropical coast of Brazil (Leão and Kikuchi 2005), and these longer term trends were recently aggravated by white plague-like disease, which may reduce ~60% of its cover in the next 50 years if current trends are maintained (Francini-Filho et al. 2008a). In contrast to large, long-lived and slow-growing corals, small "weedy" species (i.e. fast-growing and higher population turnover species) provide relatively rapid responses that can be associated with both, long timeframe environmental processes and short-term acute disturbances (Bak and Meesters 1998, 1999)(Darling et al 2012). However, detailed time series including information on coral abundance, growth, vitality and mortality are still lacking for Brazilian reefs, especially for "weedy" species (Francini-Filho et al. 2013).

Even for relatively well-studied regions, the lack of long-term datasets obtained with high-resolution methods hampers accurate evaluations about the relative importance of natural and anthropogenic drivers on reef dynamics, leading to contrasting interpretations (Sweatman et al. 2011; Francini-Filho et al. 2013). Scale issues are also critical, as they imply in perceptual biases that complicate the interpretation of the relative importance of regional/global level and local stressors (Levin 1992). The scale at which several facilitation and competition process operate (e.g. allelopathy, overgrowth, abrasion) is frequently ignored in coral reef dynamics studies (Barott 2009, 2011; Ortiz 2009; Vermeij 2010).

During four years we assessed the vitality and selected demographic aspects of the Brazilian-endemic coral *Favia gravida* Verril, 1868, a small (< 10 cm in diameter) coral typical of early successional stages that presents traits of "weedy" or “stress tolerant” species (Knowlton 2001; Darling et al. 2012). *Favia gravida* is hermaphroditic, with brooding reproduction and monthly release of short-lived larvae (~ 6 days) with settlement preferences in shallow (< 10 m) reef areas (Calderon et al. 2000; Conceição et al. 2006). With use of high-resolution sequential images of 160 colonies of *F. gravida* under contrasting ecological settings, the relative influence of the land-proximity gradient of turbidity and management regimes (areas with contrasting herbivorous fish biomass) on coral abundance, size, growth, vitality, as well as density of recruits was explored. The sampling design also incorporated the effects of the immediate substrate surrounding the colonies, a scale that has been largely neglected in most studies focusing on coral dynamics (but see Ortiz et al. 2009). Besides adding more elements to the functional categorization of *F. gravida* as a “weedy” coral, we provide insights on the relative role of turf and crustose calcareous algae as competitors or facilitators of abundance and health of scleractinian corals.

Material and Methods

Study Area

Samples were taken at 12 sites (Fig. 1; Table 1) across the central portion of the Abrolhos Bank, eastern Brazil (16° 40' - 19° 40' S, 39° 10'- 37° 20' W). The region harbors the largest and richest coral reefs in the South Atlantic (Laborel 1969; Dutra et al. 2005), presenting unusual structures that resemble giant mushroom-shaped pinnacles (with 5-25 m heights and 5-300 diameters across their tops) (Leão et al. 2003, FranciniFilho et al. 2013). Reefs are distributed in two arcs and around the small volcanic islands of the Abrolhos Archipelago. The coastal arc presents higher turbidity and higher fishing pressure, although there is a N-S gradient of decreasing turbidity and sedimentation levels (Dutra et al. 2003), and the northernmost coastal reefs (Timbebas) are within a poorly enforced no-take zone (but with significantly higher herbivorous fish biomass than adjacent unprotected reefs, Francini-Filho and Moura 2008a). In the coastal arc, most pinnacles are coalesced and form larger bank reefs (Laborel 1969). The Abrolhos Archipelago and the outer arc present lower turbidity, lower terrestrial influence, and significantly higher biomass of large roving herbivorous fish. The best-implemented MPA encompasses the entire mid-shelf stratum, complicating the disentanglement of cross-shelf versus protection effects (Francini-Filho and Moura 2008a, b; Bruce et al. 2012; Francini-Filho et al. 2013).

Field sampling and image processing

Data were collected during the summers (Jannuary-March) of four consecutive years (2006 – 2009) in two habitats: pinnacles’ tops (1 - 8 m depth, horizontal inclination) and walls (4 - 20 m, vertical). At each of the 12 sampling sites (seven in the coastal and five in the outer arc; Fig. 1), ten quadrats with 75 x 66 cm were randomly placed in each habitat, totaling 4.9 m^2 of surveyed area per habitat per site per year. Permanent metal pins fixed in the initial position of the photo quadrats (15 images per quadrat) allowed acquisition of data from the exact same places during the sampling period. Details of the benthic sampling methodology are provided by Francini-Filho et al. (2013).

The trajectories of 160 colonies of *F. gravida* (115 colonies in 2006, 144 in 2007, 127 in 2008 and 101 in 2009) were tracked, totaling 487 sequential observations, with and average of three observations per colony (Table 1). Differences in the number of colonies sampled in each year were due to death and recruitment of new individuals. For each observation total colony area (hereafter "colony size") and healthy tissue area, as well the colony perimeter were measured using the *Image J* software (Schneider et al. 2012). Colony size was calculated from planar areas (Bak and Meesters 1998) and growth was estimated by subtracting colony size from one year to another (Allemand et al. 2011). Surrounding substrates were assessed by measuring the relative perimeter of colonies in contact with the following organisms or surfaces (Ortiz et al. 2009): turf algae (multispecific and heterogeneous assemblages of filamentous algae and cyanobacteria, with less than 1 cm height), fleshy macroalgae, calcareous crustose algae (CCA), *Palythoa caribaeorum*, *Zoanthus* spp., *F. gravida*, other scleractinians, sand,(all these categories together represented 92% of average perimeter), and "others". This latter category included reef edges, shades, PVC frame, and other organisms averaging less than 0.4% of contact perimeter with colonies,

Vitality refers to the proportion of healthy tissue in relation to the total colony area. Levels of bleaching were visually recorded and classified as light, moderate and intense. To ensure that moderate and high bleaching levels were indeed related to vitality, photosynthetic activity was measured in the summer of 2012 with the Pulse Amplitude Modulated method (PAM). We used a red light Diving PAM (Walz, Germany) to obtain and compare initial (F_0) and maximum fluorescence (F_m) of moderately bleached and non-bleached colonies (5 - 10 measurements per colony, depending on colony size). Measurements were conducted in the afternoon (3 moderately bleached and 4 visually healthy colonies) and at night (5 moderately bleached and 11 healthy colonies). Diseases were recorded and classified following Francini-Filho et al. (2008a). Mortality was assigned when the whole colony was clearly devoid of live tissue or completely overgrown by other organisms. The annual mortality rates of colonies were calculated by dividing the total number of deaths by the total number of colonies recorded alive in the previous year. In addition, the proportion of surviving colonies was calculated for each site considering the whole sampling period. Between 2007 and 2009 the number of *F. gravida* recruits and their prevalent surrounding substrates (i.e. more than 50 % of the recruits' perimeter) were recorded. Annual influx of recruits was estimated from 15 images within each of the 12 sites, totaling 0.5 m^2.site.yr^{-1}.

Benthic cover, herbivorous fish biomass and abiotic data

Benthic cover data from all sites was acquired from 2006-2008 (data available from Francini-Filho et al., 2013; downloadable at http://datadryad.org/). Relative cover of different benthic organisms was estimated on top habitats through the identification of organisms below 300 randomly distributed points per quadrat using the Coral Point Count with Excel Extensions Software (Kohler and Gill 2006) in the following categories (>90% of the total benthic cover): turf algae, CCA, scleractinians other than *F. gravida* (*see* Francini-Filho et al. 2013), the zoanthid *Palythoa caribaeorum*, fleshy macroalgae, sand, and *F. gravida.* Relative benthic cover was pooled at the site level (10 quadrats/site) and at the quadrat level, this latter comprising the relative benthic cover only from the quadrats where *F. gravida* colonies were measured.

Biomass of large roving herbivorous fish (Labridae: Scarinae and Sparisomatinae - five species and Acanthuridae - three species) was obtained from stationary census surveys on reef top habitats at the same sites and periods (15 samples per site) using the methodology described by Minte-Vera et al. (2008).

Annual means of the diffuse light attenuation coefficient at 490nm (Kd490) were used as a proxy for seawater turbidity. Values of Kd490 (hereafter "turbidity") with 4 km^2 spatial resolution were obtained from the MODIS-Ocean platform (http://oceancolor.gsfc.nasa.gov/) using the Giovanni online data system (http://disc.sci.gsfc.nasa.gov/giovanni). Distance offshore was estimated using digital nautical charts and depth was measured in the field. Protection levels were dummy coded as follows (see Fig. 1 for site codes): 1) unprotected coastal arc reefs (SGOM, PA2, PLEST, ARENG); 2) protected coastal arc reefs (TIM1, TIM2, TIM3); 3) protected outer reefs (GUA, MV, PNORT, PAB2, PAB3).

Statistical Analyses

Spatial and temporal dynamics in cover of *F. gravida*

A t-test for independent groups was used to evaluate differences in cover of *F. gravida* between habitats (pinnacles' tops and walls) with data pooled for all sites and years. Three sites within the Abrolhos Archipelago, where no habitat distinction can be noticed, where excluded from this latter analysis. Spatial and temporal variations in *F. gravida* cover, size, growth and vitality were evaluated using two-way analyses of variance (ANOVA) with years and sites as fixed factors. Quadrats were used as replicates for estimates of coral cover and colonies were used as replicates for estimates of size, growth and vitality. Additional one-way ANOVA were used to clarify temporal variation within each site. Student Newman Keuls (SNK) was used as a *post hoc* test to detect homogeneous groups. The spatial heterogeneity between coastal and outer arc reefs was explored by comparing the coefficients of variation (CV) of mean values of the demographic parameters at the site level (cf. Bak and Meesters 1998). In order to satisfy assumptions of normality and homoscedasticity, cover and vitality data were transformed to *arcsine* $\sqrt{x}$ and colony size to $log\ (x+1)$ (Zar 1999). The photosynthetic activity between healthy and bleached colonies was compared with t-tests using day and night measurement as replicates. Initial (F_0) and Maximum fluorescence (F_m) data were transformed to $log\ x$.

Factors affecting cover, colony size, growth, vitality and recruitment of *F. gravida*

Multiple linear regressions using the forward stepwise selection procedure were performed to assess the relative influence of abiotic and biotic variables on *F. gravida* cover, colony size, growth, vitality and recruitment. With the expansion of our analysis to include several regional variables, the likelihood of introducing highly correlated terms and generating erroneous estimates of regression coefficients due to multicollinearity increased. Benthic cover was incorporated into these models at different scales: for evaluating *F. gravida* cover and recruits' density relative benthic cover data were used at the site level, and for evaluating growth, estimates of colony size and vitality, with data pooled at the quadrat level, were used. Relative surrounding substrate perimeters included only organisms or substrate representing > 0.49% of average colony perimeter (Table 5). A correlation analysis of all variables was previously conducted to evaluate covariation patterns to avoid multicollinearity in multiple regression models.

Abiotic variables, relative benthic cover and biomass of herbivores (independent variables) were regressed against *F. gravida cover* (dependent variable) (N=36) using the average.yr^{-1}.site values of the dependent and independent variables in the first model. Abiotic variables, relative benthic cover at the quadrat level, biomass of herbivores and relative surrounding substrate perimeters (independent variables) were regressed against colony size (dependent variable) in the second model. A third multiple regression was performed using the same independent variables against vitality (dependent variable) (N=160) but excluding herbivorous fish biomass from the independent variables' list. The same procedure was performed for colony vitality (dependent variable) but including colony vitality with other independent variables (N=160). Herbivorous fish biomass was excluded as predictors in the two last models because no direct link with vitality and growth were thought to be possible, as there were no evidences of bites on the colonies. For these latter three regressions the average of biotic and abiotic variables were calculated considering the period during which each colony was alive. As growth rate was correlated to colony size, a preliminary linear regression between growth and colony size was performed and the resultant residuals were used as dependent variable in the multiple linear regression model of growth. In the last model, abiotic variables, relative benthic cover, mean values of vitality of *F. gravida* colonies and herbivorous fish biomass (independent variables) were regressed against mean recruit's density.site (dependent variable) (N=36).

Relative benthic cover at the site level was transformed to the centered log-ratio in the first model, aiming to remove the effect of covariance and constant-sum constraints typical of compositional data (Kucera and Malmgren 1998; Pawlowski-Glahn and Buccianti 2012) as *F. gravida* cover was the dependent variable. For all other models, abiotic variables, herbivorous fish biomass and colony size data were transformed to *log* (x +1)*,* while vitality, relative benthic cover at quadrat and site level and surrounding substrates were transformed to *arcsine* √x. Data of mean recruit's density.0.033m^2.yr^{-1} was transformed to *log* (x +1) in order to satisfy assumptions of normality.

Results

Coral cover

Favia gravida is a ubiquitous coral in the Abrolhos reefs. It was recorded in 40% of the quadrats in the tops of the pinnacles (35.7% and 46.5% of quadrats in the coastal and outer arc, respectively). It presents a strong habitat preference, with higher cover on the pinnacles' tops than walls (t-test, $p<0.001$). On pinnacles' tops and fringing reefs *F. gravida* was the eighth most abundant coral, averaging 0.24 ± SE 0.02 % of the benthic cover, against 0.04 ± SE 0.01 % on reef walls. Due to such differences, the following results concern only data from tops and the Abrolhos Archipelago fringing reefs.

Significant spatial variation of *F. gravida* cover was recorded among sites ($F_{11,354}= 3.15$, $p<0.0001$), but not years ($p>0.05$). A strong interaction between these two factors was recorded ($F_{22,354}= 2.34$, $p<0.0001$) indicating that spatial patterns were not consistent trough time (Table 2; Fig 2). One-way ANOVA indicated that temporal variation in cover was significant at two sites only, with a decrease recorded at PLEST ($F_{2,30}=10.36$, $p<0.001$) and an increase at PNORT ($F_{2,30}= 3.54$, $p< 0.04$) (Table 3; Fig 2). Coral cover presented a remarkably higher variation among sites in the coastal arc (CV=69.9) than among sites in the outer arc (CV=20.05), with the highest mean cover recorded at PLEST and the lowest at the neighboring, but slightly deeper ARENG (both within the coastal arc). In the multiple regression model, turbidity and biomass of roving herbivores were the most important variables positively affecting *F. gravida* cover, while fleshy macroalgae showed the opposite effect ($R^2=0.51$, $F_{5,30}=6.13$, $p<0.001$) (Table 4; Fig 3).

Colony size

Favia gravida is a small-sized coral, with a mean colony area of 1.79 ± SE 0.11 cm^2. Colonies grouped into size classes of 1 cm^2 showed a right-skewed distribution, with 70% of the population falling within the two smallest size classes, and only two coastal sites (PA2 and TIM 3) showing a more homogeneous size distribution (Fig. 4). Mean colony size differed significantly between sites ($F_{11,487}=5.4$, $p< 0.01$) (Fig. 5), but not between years ($p>0.05$). TIM3 presented the largest colonies, while TIM2 and MV presented the smaller ones. Spatial variation in colony size was two times higher at sites within the coastal arc than those within the outer arc (CV=45.82 and 22.42, respectively). Colony size was negatively related to protection level and to the cover of fleshy macroalgae, and positively related to the cover of *F. gravida* and CCA at the quadrat level ($R^2= 0.29$, $F_{7, 152}= 8.75$, $p<0.001$) (Table 4).

Growth rates and mortality

Considering all 160 colonies monitored for at least two years, mean growth of *F. gravida* was negative (i.e. area loss; -0.18 ± SE 0.07 $cm^2.yr^{-1}$). When considering only positive values (i.e. area gains) an average value of 0.71 ± SE 0.04 $cm^2.yr^{-1}$ was obtained. Significant temporal variation in growth was recorded for the whole study area ($F_{2, 415}=7.72$, $p<0.001$). Mean growth rate of 0.24 ± SE 0.09 $cm^2.yr^{-1}$ was recorded from 2006 to 2007, decreasing to -0.29 ± SE 0.13 $cm^2.yr^{-1}$ in 2008 and to -0.46 ± SE 0.11 $cm^2.yr^{-1}$ in 2009 (Fig. 6). No spatial variation in growth rates was recorded, but there was a significant interaction between sites and years ($F_{22, 415}=2.48$, $p<0.001$). Significant negative growth rates were recorded at TIM3 ($F_{2, 16}=4.53$, $p<0.05$), PLEST ($F_{2, 72}=$, $p<0.01$), PNORT ($F_{2, 42}=16.92$, $p<0.001$) and GUA ($F_{2, 73}=4.39$, $p<0.05$) (Table 3). Greater variation was observed among coastal arc sites (CV=-130.6) than among outer arc sites (CV=-69.95) (Fig 5). Colony growth was positively influenced by turbidity, turf algae perimeter, CCA perimeter, turf cover at the quadrat level, protection, and the surrounding perimeter of sand and *Zoanthus* spp. (R^2=0.33, $F_{14, 145}$=5.15, p<0.001) (Table 4).

Annual mortality of *F. gravida* averaged 6.2% in 2007, 12% in 2008 and 21.5% in 2009 (Fig. 8). During the entire study period total mortality was 33.75% ranging between 0 and 57% of the colonies across sites and years (Fig. 9). When mean annual mortality was pooled by reef, we observed that coastal reefs presented earlier mortality compared to outer reefs (Fig. 8).

Vitality

Significant lower photosynthetic activity was detected in colonies visually recorded as presenting moderate bleaching, with consistently lower F_0 and F_m (daytime F_0: T-test, p<0.01; daytime F_m: T-test, p<0.05; nighttime F_0: T-test, p<0.01; nighttime F_m: T-test, p<0.001). Bleaching was widespread and chronic: seventy-four colonies (46%) were moderately or intensely bleached in at least one observation, and the frequency of bleached colonies was relative constant (49-59% between 2006-2009). All nine colonies (5.6%) affected by white-plague like disease died after one year, except one colony that died after two years.

Vitality varied significantly between sites ($F_{11,487}$=6.92 p<0.001) (Fig. 7), with a significant interaction between years and sites ($F_{33,487}$=1.85, p<0.01) (Table 2). Significant temporal changes in vitality were recorded only in TIM3 ($F_{3,19}$=5.28, p<0.05) (Table 3), where mean vitality of colonies increased from 49% in 2006 to 98% in 2007. Coastal arc sites presented a slightly higher variation in average vitality (57-96%) when compared to outer arc sites (84-97%). The multiple regression explained 17% of the variability in *F. gravida* vitality, with distance from the coast and turbidity being the most important predictors positively associated with it ($R^2 = 0.17$, $F_{6,153}=5.36$, $p<0.001$) (Table 4).

Recruitment

Density of recruits for the whole study region between 2007 and 2009 averaged 3.36 ± SE 0.43 recruits.0.5m^2.yr^{-1}. Density of recruits was evenly distributed across reefs and protection levels (Fig. 10). We failed to detect significant predictors of recruitment in the multiple regression models (Table 4). Turf was the most frequent perimeter (62%) surrounding the 121 recruits observed during the study period, followed by CCA (27.3%), fleshy algae (4.96%), *Zoanthus* spp. (2.48%), other corals, sand or sediment (1.65% each).

Discussion

The rapid decline of coral cover in the last five decades is a worldwide trend, owing to the interaction between multiple anthropogenic and natural stressors (Gardner et al. 2003; Fabricius et al. 2005). While general patterns of coral decline are being increasingly well understood from larger time series (e.g. Wilkinson 2008; De'ath et al. 2012) and regional meta-analyses (Côté et al. 2005; Bruno and Selig 2007), the relative importance of different drivers in different regions and the varying responses of different functional groups (Darling et al. 2012) remain as critical knowledge gaps to a more complete understanding of the ongoing coral reef crisis. Using a high-resolution sampling technique (fixed photoquadrats) and a relatively long time series of data (4 years) we showed that *F. gravida*, a small and ubiquitous Brazilian-endemic "weedy" coral, presented low inter-annual variation in a reef system where the main building corals (*Mussismilia* spp.) are declining more sharply, mainly from disease outbreaks (Francini-Filho et al. 2008a, 2013). Our results add to recent literature from turbid zone reefs highlighting that coral cover, growth, and mortality may not always be directly related to water quality gradients (Lirman and Fong 2007; Browne et al. 2012).

Favia gravida showed a relatively high performance under typically stressful conditions of increased turbidity (see Fig. 3). Indeed, the largest colonies were found in the coastal arc, turbidity was the most important variable associated not only with *F. gravida* cover, but also with its growth (Table 4; Figs. 4 and 5). Faster growth rates and higher cover of “weedy” and “stress-tolerant” corals (*Porites astreoides* and *Siderastraea siderea*, respectively) were also documented on coastal reefs of Florida (Lirman and Fong 2007). Positive responses to turbidity have also been recorded for the two most important framework builders on coastal reefs of Abrolhos, which show higher cover (Francini Filho et al. 2013) or higher reproductive effort (Pires et al. 2010) in reefs within in the inner arc.

Growth rates comprise an important process that determines coral cover, but its measurement depends on temporal series of data that are not readily available for most areas and species (Pandolfi et al. 2003; Côté et al. 2005). From 2007-2009 we recorded a significant negative growth rate of *F. gravida* across the study region. The main environmental variable positively influencing growth rates were turbidity, followed by other local scale factors and higher protection levels (Table 4). Higher nearshore growth rates may be associated with specific tolerances and heterotrophic feeding capabilities (Lewis 1974; Anthony et al. 2000; Anthony and Frabricius 2000). Remarkably, growth rates of *F. gravida* were not significantly higher in colonies with higher photosynthetic potential (i.e., those not showing bleaching signals), and the proportion of mortality of bleached colonies was even lower than non-bleached colonies. Vitality was also dependent on distance offshore (Table 4), adding to the idea that heterotrophic feeding may play an important role in *F. gravida* nutrition (Grottoli et al. 2006), and also that its photosynthetic potential may be related to the level of heterotrophic feeding. Heterotrophy may allow for the chronic partial-bleaching state that affects nearly half of the studied population. Indeed, the bleaching levels that recorded here for *F. gravida* are similar to those recorded for this same species (~57% in frequency) during a severe bleaching event that affected several other species in 1998 (Leão et al. 2003). Nevertheless, evidences that Abrolhos coastal reef system is under increasing eutrophication (Bruce et al. 2012) also support the positive association between vitality of *F. gravida* and distance from the coast. One of the reasons is that elevated nutrient concentrations can reduce resistance of corals to temperature anomalies and increase their susceptibility to bleaching (Wooldridge 2009; Wiedenmann et al. 2012, Fabricius et al. 2013).

Besides the positive relationship with turbidity, *F. gravida* cover was also positively associated with high herbivorous fish biomass and negatively associated with high fleshy macroalgae cover (Fig. 3). A consistent decrease in the proportion of *F. gravida* cover was recorded along the studied period in unprotected coastal reefs. Therefore, despite its ability to thrive in turbid waters, *F. gravida* and other “weedy” and “stress-tolerant” coral species may suffer from the indirect effects of overfishing. By preferentially consuming fast-growing turf algae, large roving herbivorous reef fish tend to interrupt benthic succession and avoid fleshy macroalgae proliferation by keeping the system in a turf and CCA-dominated state. However, macroalgae can become rapidly dominant when these fishes are overexploited or under high nutrient concentration (Hughes et al. 2007; Francini-Filho et al. 2009; Vermeij et al. 2010). Thus, turbid zone reefs, although hosting an assemblage of dominated by “stress-tolerant” and “weedy” species, may be more vulnerable to overfishing and to nutrient enrichment than reefs where algal growth is more limited by nutrient availability.

The large roving herbivorous parrotfish, *Scarus trispinosus*, which comprises the largest proportion of fish biomass in the Abrolhos region (Francini-Filho and Moura 2008a), allocates 0.8% of its bites to live corals (Francini-Filho et al. 2008b). However, in the present study a single bite mark was recorded on the monitored colonies, supporting the idea that parrotfishes' role on the control of fleshy macroalgae cover seems to compensate from the losses from corallivory.

Although macroalgal canopy may sometimes reduce predation of juvenile corals by parrotfishes (Venera-Ponton et al. 2011), it can negatively influence growth of small-sized coral species (Ferrari et al. 2012). In the Caribbean, Box and Mumby (2007) reported that juveniles of small "weedy" corals (*Agaricia* spp.) in contact with fleshy algae (*Dictyota*) presented severe growth inhibition (99% inhibition when shaded and 31% when in peripheral contact). Indeed, *Dictyota* spp. and *Dictyopteris* spp. were the most abundant fleshy algae recorded in the Abrolhos reefs, with the highest cover at PLEST. At this coastal and unprotected site we recorded an increase of fleshy algae cover from 38.7 ± SE 2.7 to 57 ± SE 5.2 % between 2006 and 2008, and a corresponding abrupt decrease of *F. gravida* cover from 1.04 ± SE 0.25 to 0.07 ± SE 0.07 % (Fig. 2).

In addition to factors that operate at the cross-shelf strata or site levels (e.g. turbidity, management regime), competition and facilitation processes operating near the colonies may also be important coral demography drivers (Tanner 1995; River and Edmunds 2001; Vermeij et al. 2010). Turf algae was the most common substrate at all sites and scales, also representing the predominant perimeter of *F. gravida* colonies. Besides being primarily associated with higher turbidity (cross-shelf strata scale), growth rates of *F. gravida* were also positively associated with the amount of both turf algae and CCA surrounding the colonies (Table 5). While contacts with CCA are considered facilitators of coral growth, interfaces between corals and fleshy or turf algae can be abrasive and are frequently hypoxic due to microbial respiration, being generally harmful to the corals (Barott 2009, 2011). Fleshy and turf algae may also host coral pathogens (Nugues et al. 2004). Under high nutrient loads (Vermeij et al. 2010) or when released from herbivory (Lewis and Wainwright 1985), turf algae are capable of overgrowing, reducing fitness, or even killing corals (Barott 2009, 2011). However, under some specific circumstances, such as limited canopy height and without being associated with fleshy macroalgae, coral-turf interactions may exert mutual competitive effects and not be detrimental to coral growth (McCook 2001; Vermeij et al. 2010; Venera-Ponton 2011). Turf cover may also show positive association with coral cover (Francini-Filho et al. 2013) or even provide a positive substrate for settlement (Suzuki et al. 2010) and growth for some species of coral, as recorded herein. Turf algae are a dominant benthic functional group in reefs, both degraded and pristine (Barott 2009), being particularly abundant on coastal, turbid zone reefs (Gorgula and Connell 2004; Sandin et al. 2008). As recently documented for Abrolhos (Francini-Filho et al. 2013), turf algae abundance seems to be increasing worldwide (Gorgula and Connel 2004; Sandin et al. 2008), and its role in coral reef degradation tends to increase due to increasing nutrient loads and thermal anomalies (Vermeij et al. 2010). Another important remark is the fact that turf algae is a generic denomination to heterogeneous and diverse consortia of small algae, invertebrates and microorganisms (Steneck and Dethier 1994). Thus, turf algae can respond differently to changing environmental forcing, explaining the variable outcomes of both observational and manipulative experiments (Birrell et al. 2005; Vermeij et al. 2010; Venera-Ponton 2011; Francini-Filho et al. 2013.

Contacts between *F. gravida* and *P. caribaeorum* were less common than the relative cover of the latter (Table 5), indicating that the corals avoid recruiting in *Palythoa* zones, or are killed by this aggressive space competitor (Suchanek and Green 1981). *Palythoa caribaeorum* can occupy up to 25% of the tops of both coastal and mid-shelf pinnacles in Abrolhos (Francini-Filho et al. 2013). On the other hand, *Zoanthus* spp. was more frequent in the colonies' perimeter than in the reef (Table 5), being positively associated with *F. gravida* growth rates (Table 4). Besides CCA and turf, *Zoanthus* seems to have a positive interaction with the corals, but potential facilitation mechanisms and the circumstances in which they operate are unclear. The positive coral-CCA interaction can be related to the selective ability of larvae to distinguish suitable substrates to settle and grow (Ritson-Wiliams et al. 2009), possibly related to the more stable and non-hypoxic environment provided by CCA, which also seems to be an inferior competitor in eutrophic conditions (Vermeij et al. 2010). A positive relationship between the proportion of sand surrounding coral colonies and bleaching susceptibility has been recorded for massive corals by Ortiz et al. (2009), highlighting the importance of other type of smaller scale processes in coral reef dynamics. We failed to detect effects from the amount of sand surrounding the colonies, which is greater than the amount of sand over the reef (Table 5). Indeed, only regional factors (distance offshore and turbidity; Table 4) had a significant association with *F. gravida* vitality.

Although prevalence of diseases has increased in Abrolhos since 2005 (Francini-Filho et al. 2008a), causing greater impact on long-lived species with a few seasonal spawning events such as *Mussismilia braziliensis*, it may not be affecting small and short-lived species in a similar extent. While we recorded 100% of mortality in *F. gravida* colonies affected by white plague-like disease, its prevalence is still relatively low (5.6%). Despite methodological differences, recruits' density of *F. gravida* in Abrolhos (3.4 individuals.0.5m^2) was 19 times higher than that of *F. fragum* (0.43 individuals.1.25 m^2) in the same depth range in Curacao (Vermeij et al. 2011). As expected for a short-lived species, negative growth and percentage of mortality increased over the years (Fig. 8), which together with a relatively high recruitment rate contributed to the highly right-skewed size distribution of the population (Meesters et al. 2001) with 70% of the individuals within the two smallest size classes (Fig. 4).

The robust Plio-Pleistocene (5 Myr) fossil record from the Caribbean is the textbook example of how severe environmental shifts (e.g. water temperature, circulation) and area reduction can drive mass extinctions of corals, providing important insights about the unequal vulnerability of different species (van Woesik et al. 2011, 2012). Although "weedy" corals may benefit from frequently disturbed environments (Loya et al. 2001; Aronson et al. 2004, 2005; Green et al. 2008; Alvarez-Filip et al. 2011; Woesik et al. 2011), a number of short-term losers, generally considered as "endangered" species (e.g. *Acropora* spp. and *Mussimillia* spp.), may turn out as long-term winners due to their more ubiquitous distribution (van Woesick et al. 2011, 2012), and less variable mortality, which can be advantageous under acute stressful periods with successive recruitment failures, for example. Apparently, the brooding reproductive mode and faster growth rates coupled with high post-settlement survivorship, typical of "weedy" species contribute to the relative success of *F. gravida* under conditions that affect *Mussimilia* spp. (e.g. disease outbreaks). However, besides suffering from indirect effects of overfishing, *Favia* and other smaller sized "weedy" coral species do not substitute *Mussismilia* spp. as framework builders.

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Tables

Table 1. Environmental conditions of sites surveyed in the Abrolhos Bank and sampling effort of growth, colony size and vitality

		Name of sites	**Depth on reef top (m)**	**Distance from the coast (km)**	**Protection level**	**Number of monitored colonies**				**Total individual colonies per site**
						2006	**2007**	**2008**	**2009**	
Unprotected coastal reefs	**Coastal arc**	**Paredes and S.Gomes Reefs**								
		Sebastião Gomes (SGOM)	3.2	13.7	1	2	2	10	10	10
		Ponta Sul (PA2)	4.4	31.4	1	6	7	5	3	7
		Pedra de Leste (PLEST)	2.3	14.3	1	21	27	15	14	28
		Arenguera (ARENG)	5.2	15	1	10	11	8	7	13
Protected coastal reefs		**Timbebas Reefs**								
		Timbebas 1 (TIM1)	4.7	19	2	9	14	12	12	14
		Timbebas 2 (TIM2)	6	17.4	2	3	10	12	11	13
		Timbebas 3 (TIM3)	5.6	17	2	6	5	5	3	6
Protected outer reefs	**Outer arc**	**Abrolhos Archipelago Reefs**								
		Guarita (GUA)	5.4	58.1	3	25	26	21	17	26
		Mato Verde (MV)	4.1	58.1	3	10	11	9	4	11
		Portinho Norte (PNORT)	5.4	58.1	3	11	14	14	10	14
		Parcel dos Abrolhos Reefs								
		Parcel dos Abrolhos 2 (PAB2)	7.3	61.4	3	7	10	9	8	11
		Parcel dos Abrolhos 3 (PAB3)	6.9	61.7	3	5	7	7	2	7

Table 2. Results of Factorial ANOVA testing the effect of sites (S) and years (Y) in cover, colony size, growth, and vitality of *Favia gravida:* *P<0.05; **P<0.01; ***P<0.001; NS: not significant.

	Factorial ANOVA		
Source of variation	**df**	**F**	**P**
Cover (S)	11	3.15	***
Cover (Y)	2	1.39	ns
Cover (S x Y)	22	2.34	***
Colony Size (S)	11	5.43	**
Colony Size (Y)	3	1.15	ns
Colony Size (S x Y)	33	0.69	ns
Growth (S)	11	1.29	ns
Growth (Y)	2	7.72	***
Growth (S x Y)	22	2.48	***
Vitality (S)	11	6.92	***
Vitality (Y)	3	1.75	ns
Vitality (S x Y)	33	1.85	**

Table 3. Results of One-way ANOVA testing the effect of years in cover, colony size, growth and vitality of *Favia gravida* in each site: *P<0.05; **P<0.01; ***P<0.001; NS: not significant.

	One -way ANOVA											
SITES	**Cover**			**Colony Size**			**Growth**			**Vitality**		
	df	**P**	**F**	**df**	**P**	**F**	**df**	**P**	**F**	**df**	**P**	**F**
SGOM	2	ns	0.05	3	ns	1.32	2	ns	1.73	3	ns	0.88
PA2	2	ns	1.92	3	ns	0.63	2	ns	1.64	3	ns	1.72
PLEST	2	***	10.36	3	ns	0.53	2	**	6.69	3	ns	2.24
ARENG	2	ns	1.83	3	ns	0.55	2	ns	0.07	3	ns	2.88
TIM1	2	ns	0.28	3	ns	0.47	2	ns	1.07	3	ns	1.67
TIM2	2	ns	1.48	3	ns	1.13	2	ns	0.70	3	ns	1.73
TIM3	2	ns	0.19	3	ns	0.32	2	*	4.53	3	*	5.28
GUA	2	ns	0.59	3	ns	0.62	2	*	4.39	3	ns	1.06
MV	2	ns	1.36	3	ns	0.17	2	ns	0.09	3	ns	1.86
PNORT	2	*	3.54	3	ns	0.50	2	***	16.92	3	ns	2.71
PAB2	2	ns	1.23	3	ns	0.17	2	ns	2.22	3	ns	1.72
PAB3	2	ns	1.06	3	ns	1.10	2	ns	0.21	3	ns	0.37

Table 4. Multiple linear regressions' results showing the relative influence of biotic and abiotic factors on population traits and vitality of *Favia gravida* in the Abrolhos Bank, Brazil. Levels of significance for full model and partial r2: *P<0.05; **P<0.01; ***P<0.001; NS: not significant. (S) Site, (Q) Quadrat, (P) Perimeter.

Population traits	**R^2**	**P**	**Partial R^2 and (P-value)**												
Relative cover			**Turbidity**	**Biomass of roving herbivores**	**Fleshy algae (S)**	***P. caribaeorum* (S)**	**Crustose calcareous algae (S)**								
	0.51	***	0.85 (***)	0.74 (***)	- 0.45 (*)	- 0.29 (ns)	0.27 (ns)								
Colony size			**Protection**	**Fleshy algae (Q)**	***Favia gravida* (Q)**	**Crustose calcareous algae (Q)**	**Biomass of roving herbivores**	**Crustose calcareous algae (P)**	**Fleshy algae (P)**						
	0.29	***	- 0.38 (**)	- 0.35 (***)	0.30 (***)	0.28 (***)	0.20 (ns)	- 0.13 (ns)	0.11 (ns)						
Growth			**Turbidity**	**Turf algae (P)**	**Crustose calcareous algae (P)**	**Turf algae (Q)**	**Protection**	**Sand (P)**	***Zoanthus spp.* (P)**	**Depth**	***P. caribaeorum* (Q)**	**Crustose calcareous algae (Q)**	**Scleractinians (Q)**	**Fleshy algae (P)**	**Scleractinians (P)**
	0.33	***	0.81 (***)	0.60 (***)	0.38 (**)	0.27 (**)	0.35 (**)	0.23 (*)	0.20 (**)	0.27 (ns)	0.24 (ns)	0.20 (ns)	0.16 (ns)	0.10 (ns)	0.10 (ns)
Vitality			**Distance from the coast**	**Turbidity**	**Protection**	**Coral (Q)**	**Sand (Q)**	**Crustose calcareous algae (Q)**							
	0.17	***	0.55 (**)	0.38 (**)	- 0.20 (ns)	0.13 (ns)	0.11 (ns)	- 0.06 (ns)							
Recruitment			**Vitality**	**Crustose calcareous algae (S)**											
	0.12	ns	0.25 (ns)	-0.19 (ns)											

Table 5. Mean (±SE) of perimeter of *Favia gravida* (%), mean (±SE) of relative cover (%) of most abundant organisms/substrate at the quadrat and site levels between 2006 and 2008

Organisms or substrate	**Relative perimeter (%)**	**Relative cover at quadrat level (%)**	**Relative cover at site level (%)**
Turf algae	65.63 (±2.12)	47.8 (±1.43)	44.60 (±1.06)
Calcareous crustose algae	16.35 (±1.51)	11.84 (±0.99)	12.50 (±0.62)
Zoanthus spp.	3.14 (±0.74)	0.53 (±0.10)	0.6 0 (±0.07)
Fleshy algae	3.03 (±0.95)	6.57 (±1.13)	6.60 (±0.83)
Other scleractinians	2.52 (±0.73)	13.17 (±0.96)	12.20 (±0.65)
Sand or sediments	1.82 (±0.78)	1.57 (±0.53)	1.50 (±0.33)
Palythoa caribaeorum	0.49 (±0.26)	10.13 (±1.33)	12.40 (±1.02)

Figures

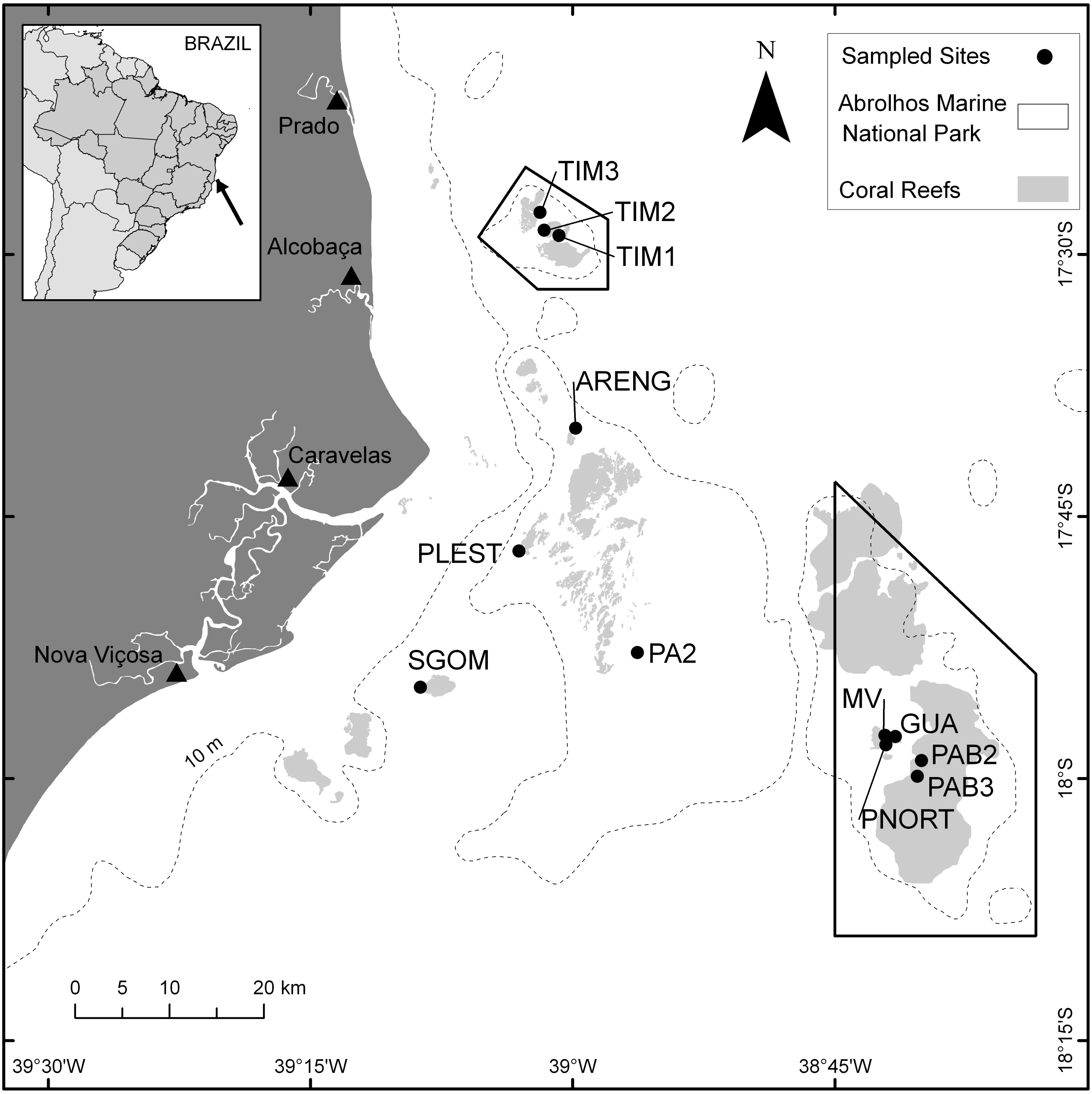

Fig. 1 Map of the study area showing the studied sites: **Coastal arc- Unprotected Coastal Reefs**: SGOM, PA2, PLEST, ARENG; **Protected Coastal Reefs**: TIM1, TIM2, TIM3; **Outer arc**- **Protected Outer Reefs**: GUA, MV, PNORT, PAB2 and PAB3

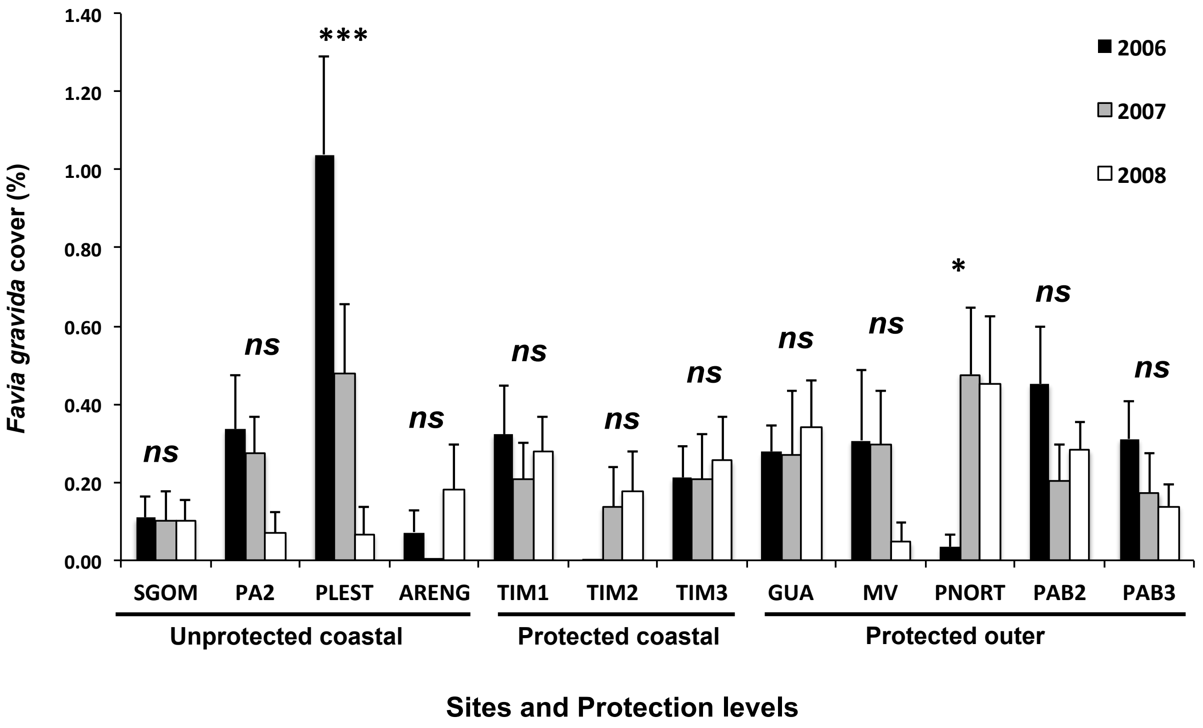

Fig. 2 Mean (± SE) relative cover of *F. gravida* in the Abrolhos Bank, Brazil

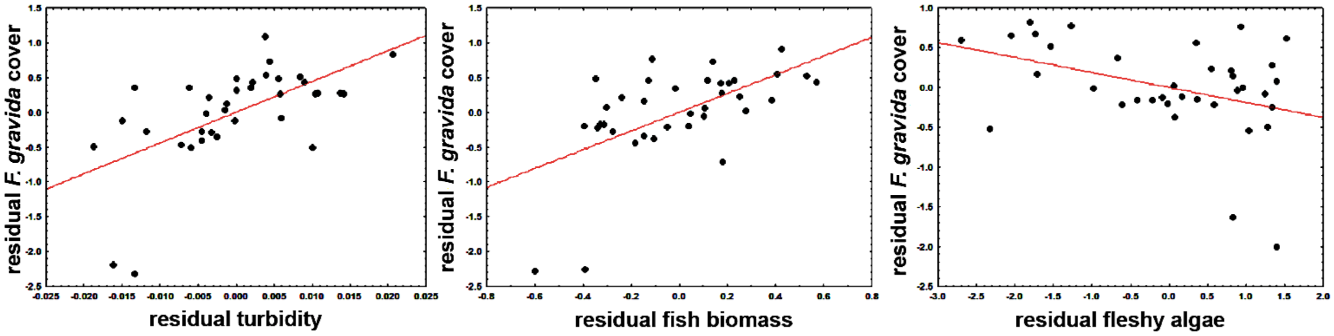

Fig .3 Partial regressions plots showing the effects of turbidity, herbivorous fish biomass and fleshy algae on *F. gravida* relative cover in the Abrolhos Bank, Brazil

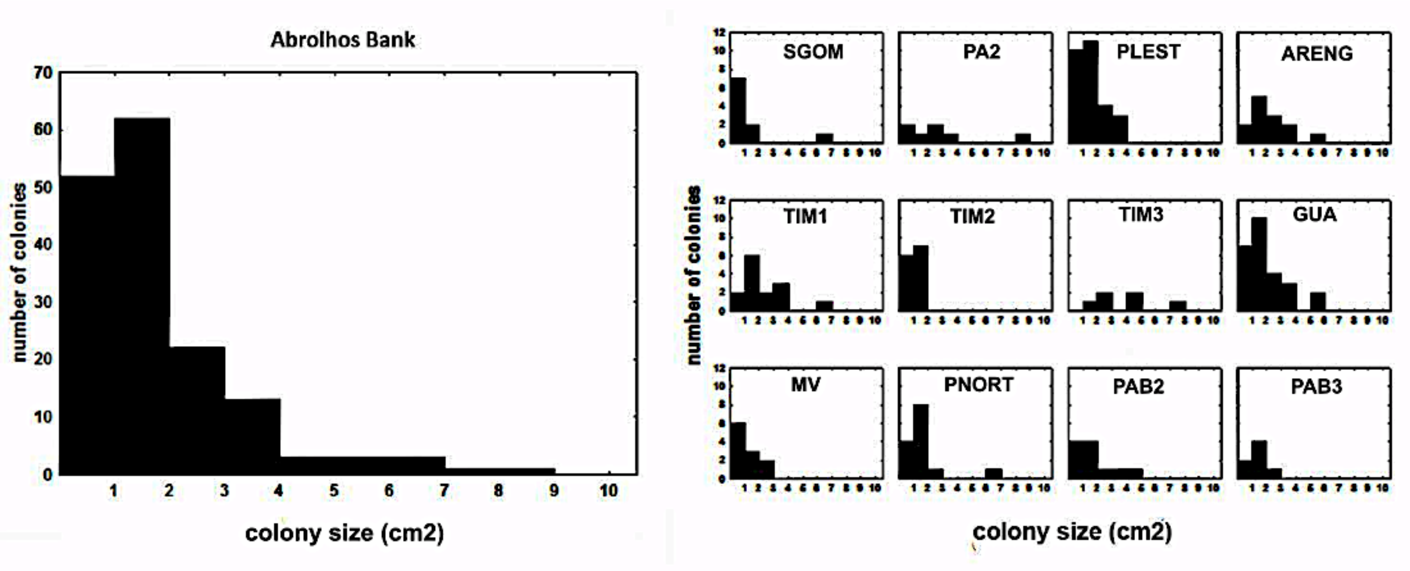

Fig. 4 Size frequency distributions of *F. gravida* colonies in the Abrolhos Bank, Brazil

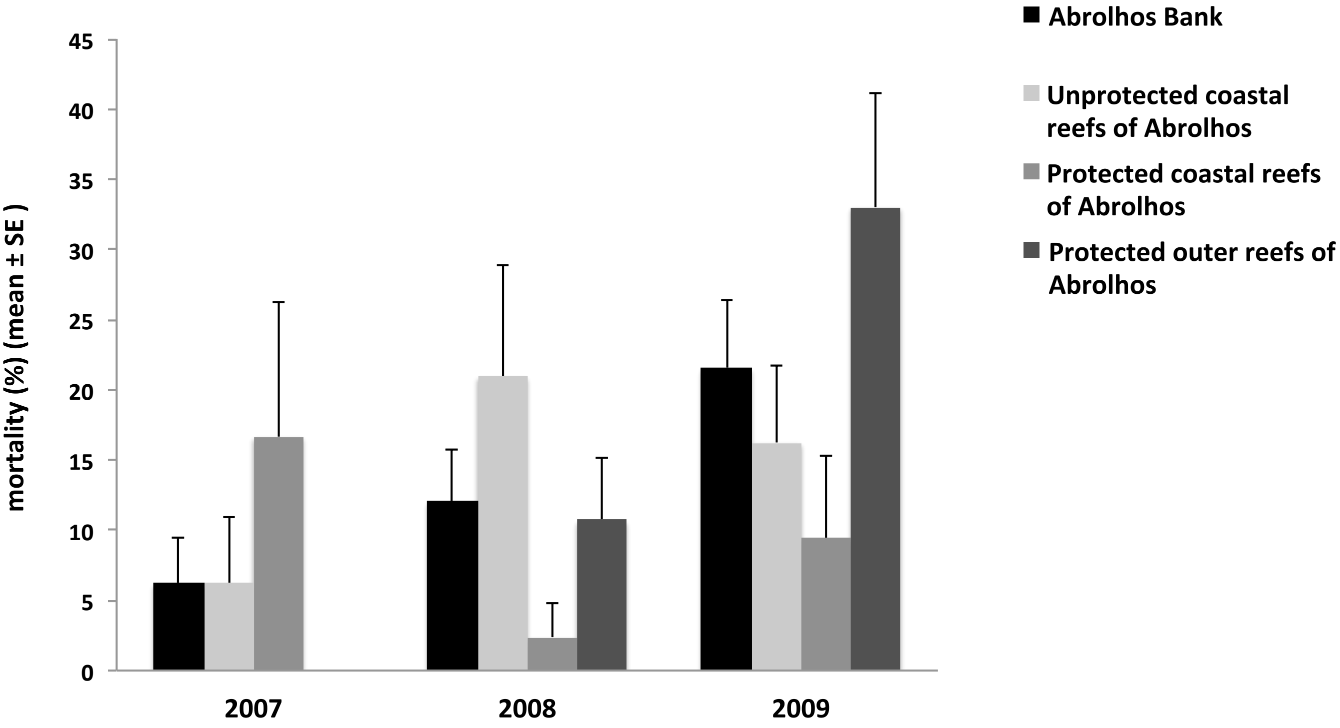

Fig.8 Mean (± SE) annual mortality of *Favia gravida* colonies from 2007-2009 in the Abrolhos Bank, Brazil

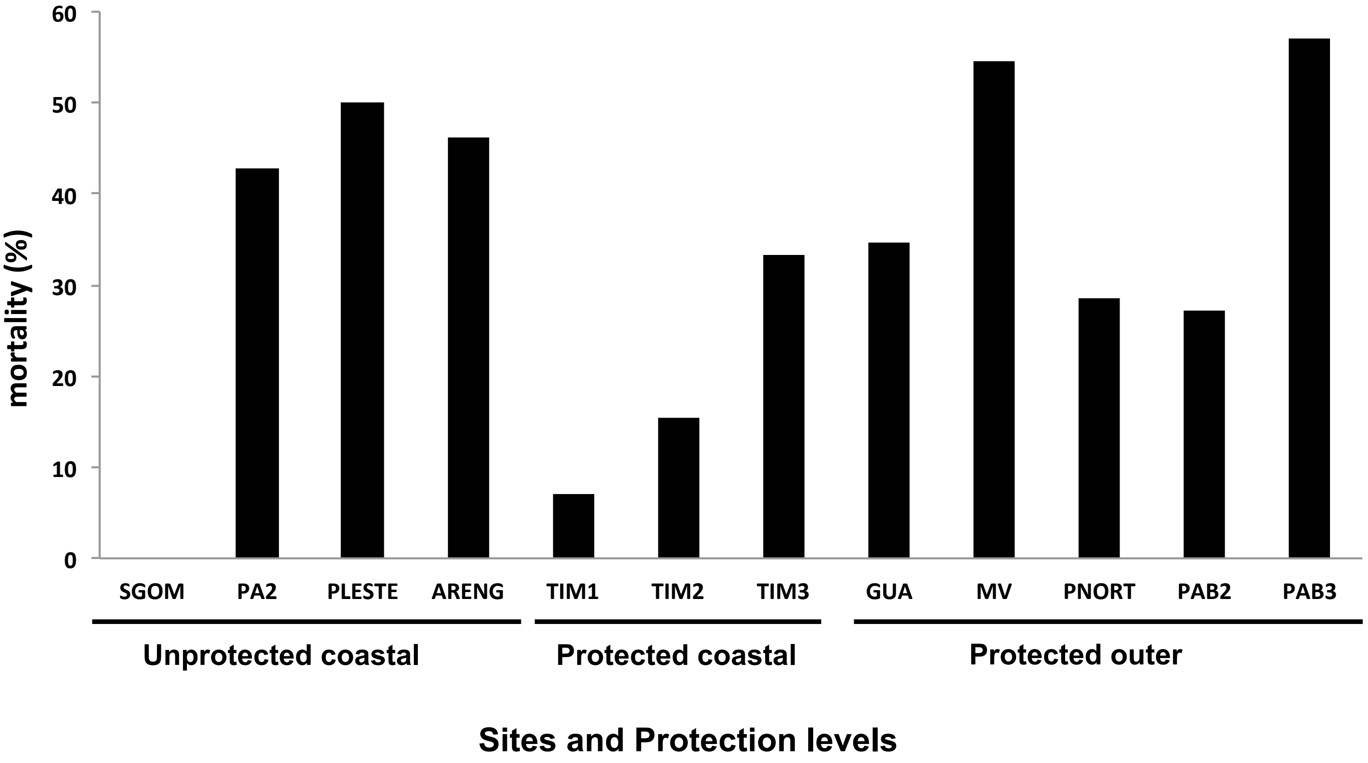

Fig. 9 Percent mortality of *Favia gravida* between 2007-2009 in the Abrolhos Bank, Brazil

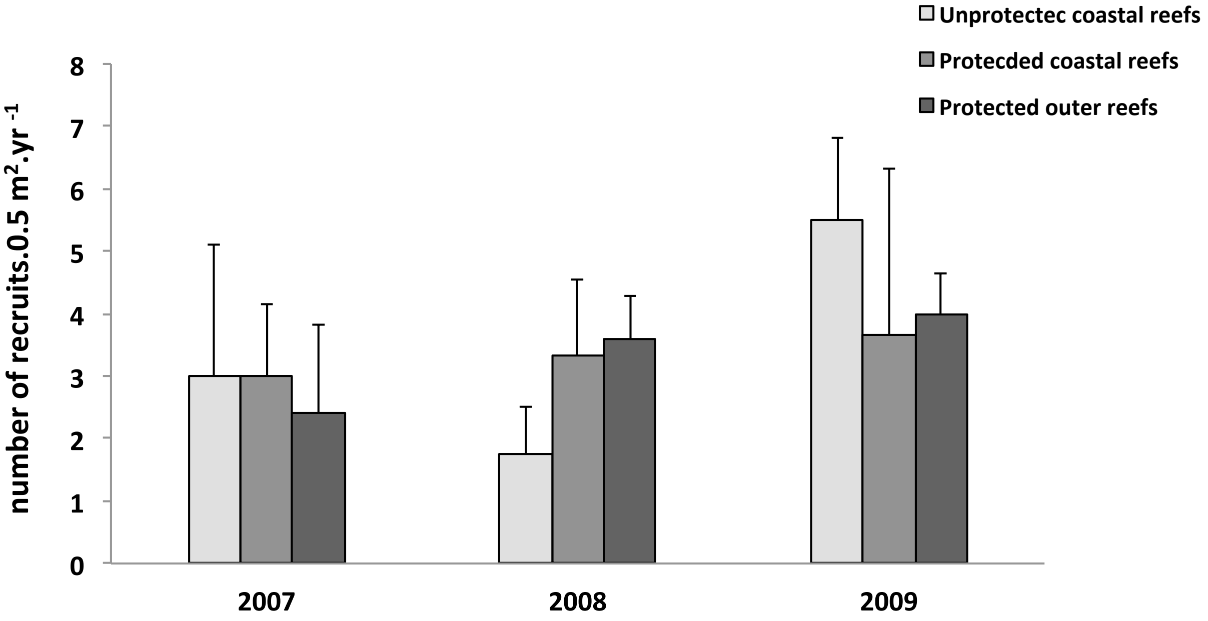

Fig. 10 Mean (± SE) density of *F. gravida* recruits between 2007-2009 in the Abrolhos Bank, Brazil

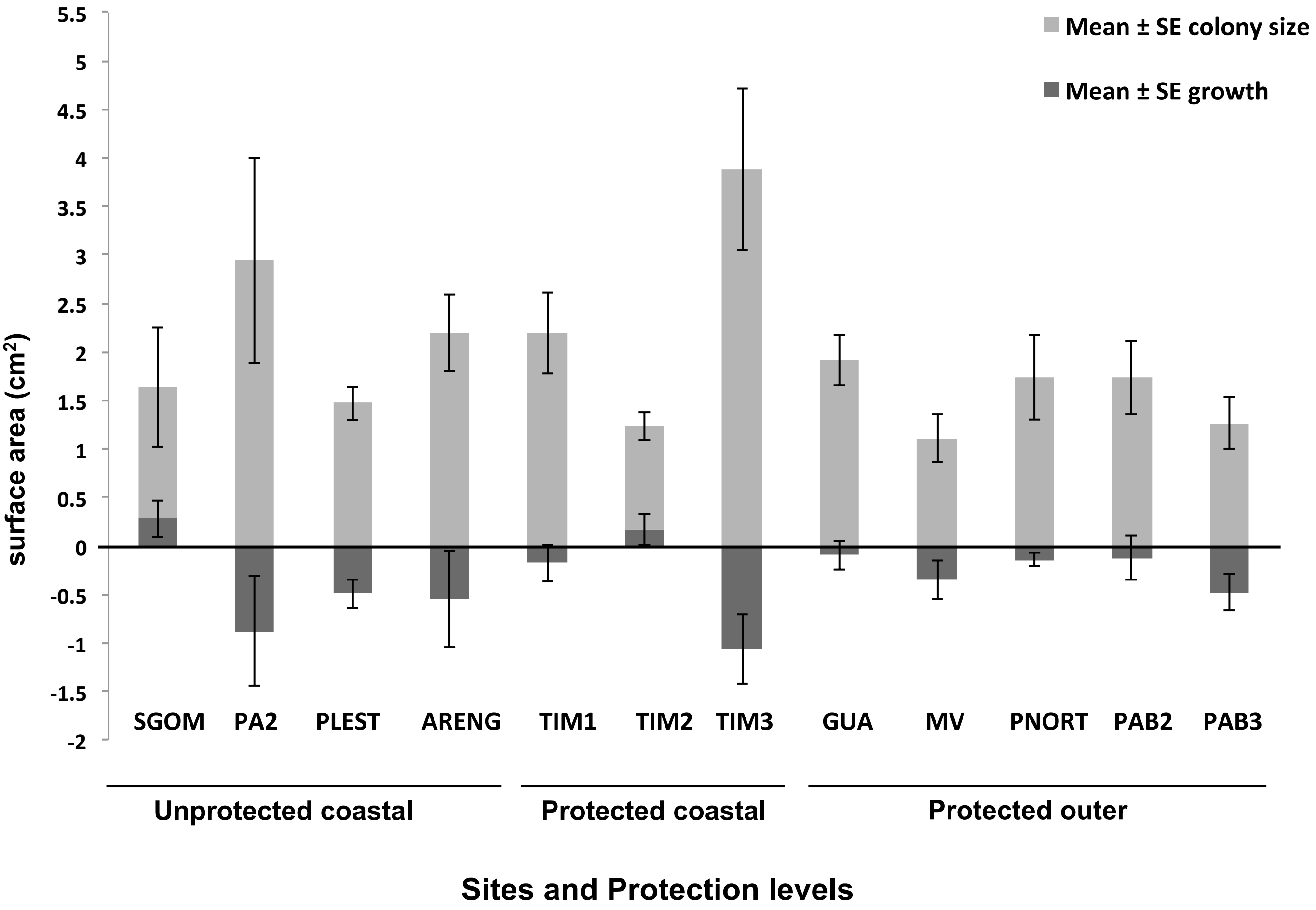

Fig. 5 Mean (± SE) colony size and growth of *F gravida* in the Abrolhos Bank, Brazil

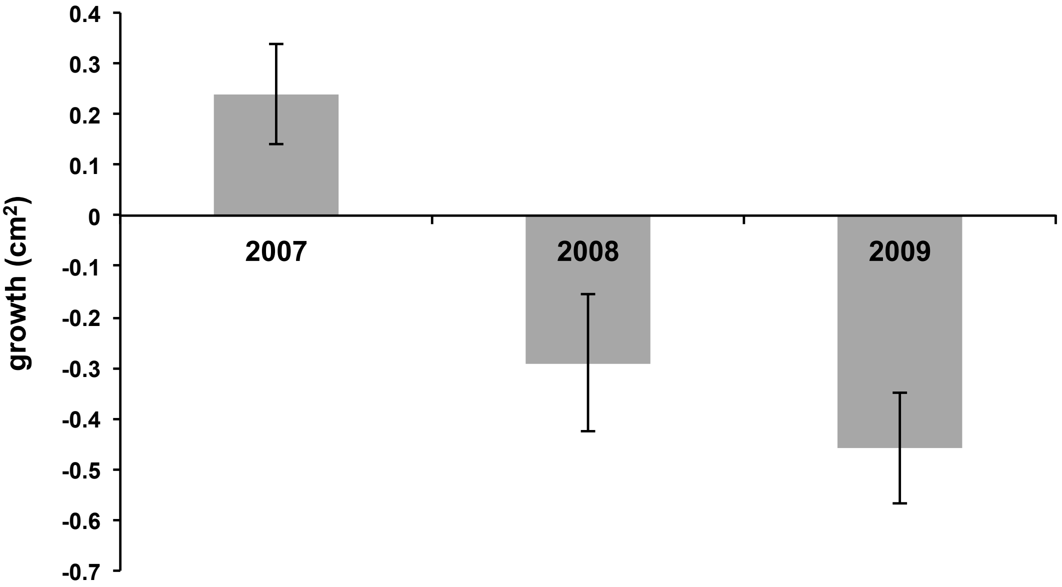

Fig. 6 Mean (± SE) growth of *F. gravida* colonies between 2007-2009 in the Abrolhos Bank, Brazil

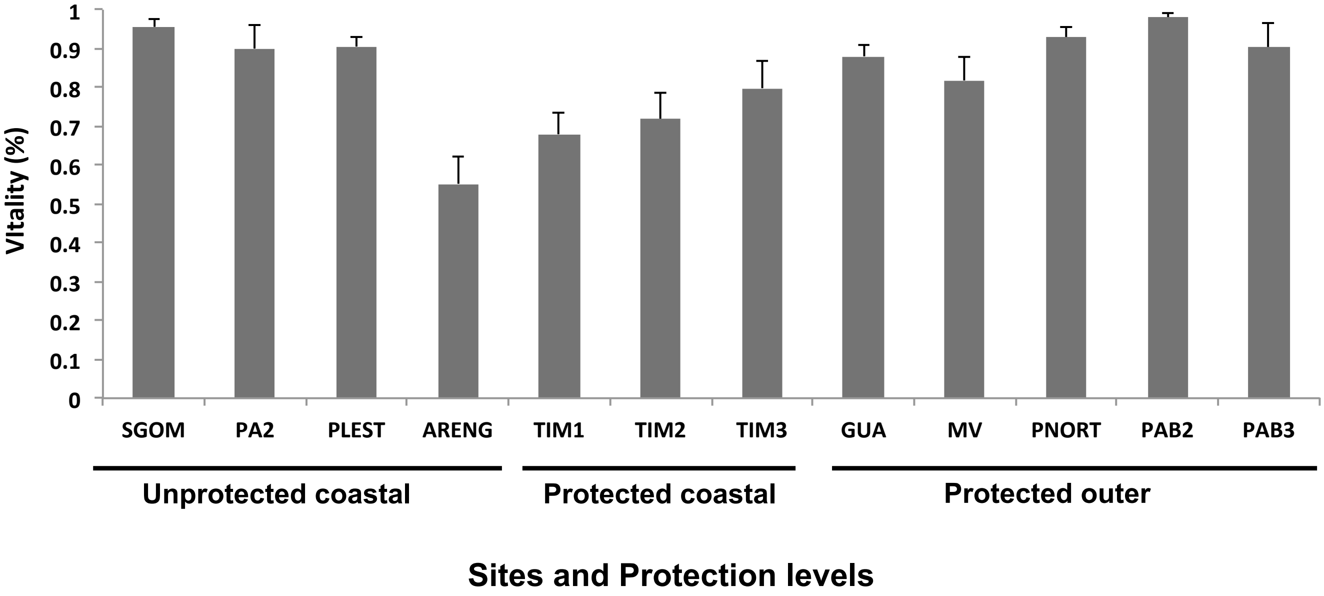

Fig. 7 Mean (± SE) vitality (i.e. proportion of healthy tissue) of *F. gravida* colonies between 2006-2009 in the Abrolhos Bank, Brazil

Supplementary Material

Tables

Table 1S Latitude and Longitude of sampled sites

sites	Latitude [a]	Longitude [a]
Sebastião Gomes (SGOM)	-17.913	-39.145
Ponta Sul (PA2)	-17.880	-38.938
Pedra de Leste (PLEST)	-17.783	-39.051
Arenguera (ARENG)	-17.666	-38.997
Timbebas 1 (TIM1)	-17.482	-39.013
Timbebas 2 (TIM2)	-17.477	-39.027
Timbebas 3 (TIM3)	-17.460	-39.031
Guarita (GUA)	-17.960	-38.692
Mato verde (MV)	-17.959	-38.702
Portinho Norte (PNORT)	-17.968	-38.701
Parcel dos Abrolhos 2 (PAB2)	-17.983	-38.667
Parcel dos Abrolhos 3 (PAB3)	-17.998	-38.671

[a] Datum: WGS84

Figures

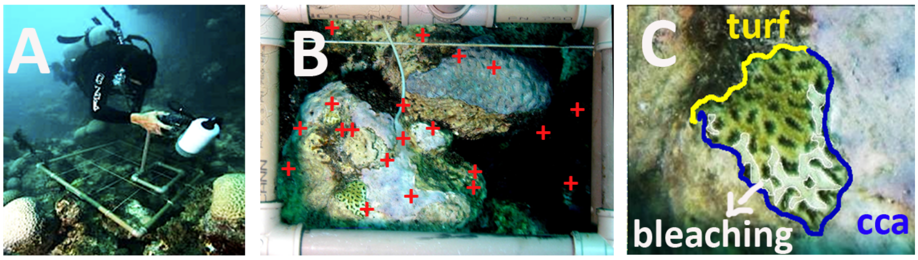

Fig. 1S Sequence of sampling: (A) and (B) Assessing relative benthic cover at quadrat level (C) Assessing colony size, colony growth, colony vitality and relative perimeter with other organisms.

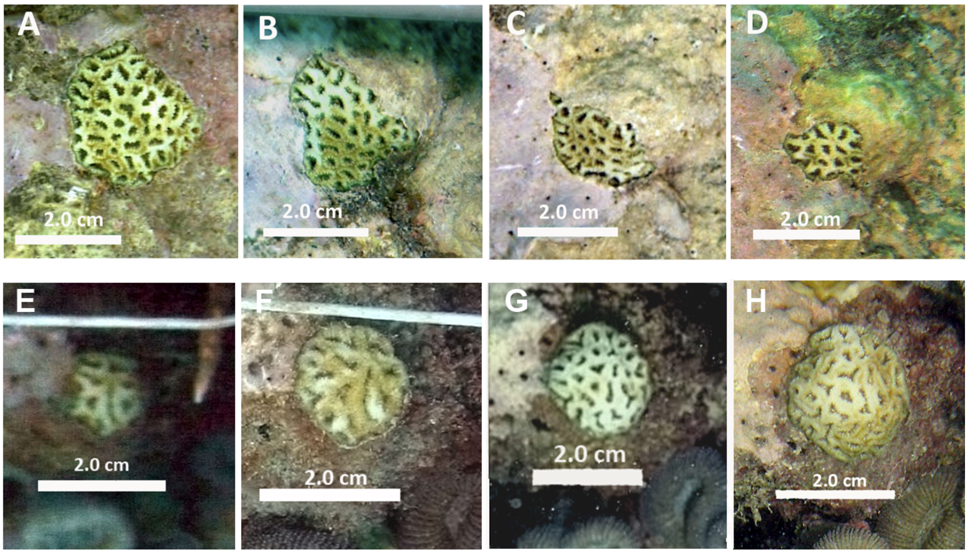

Fig. 2S Sequence of growth of *Favia gravida* between 2006 and 2009: negative (A, B, C, D) and positive (E, F, G, H) growth of two moderate bleached colonies.

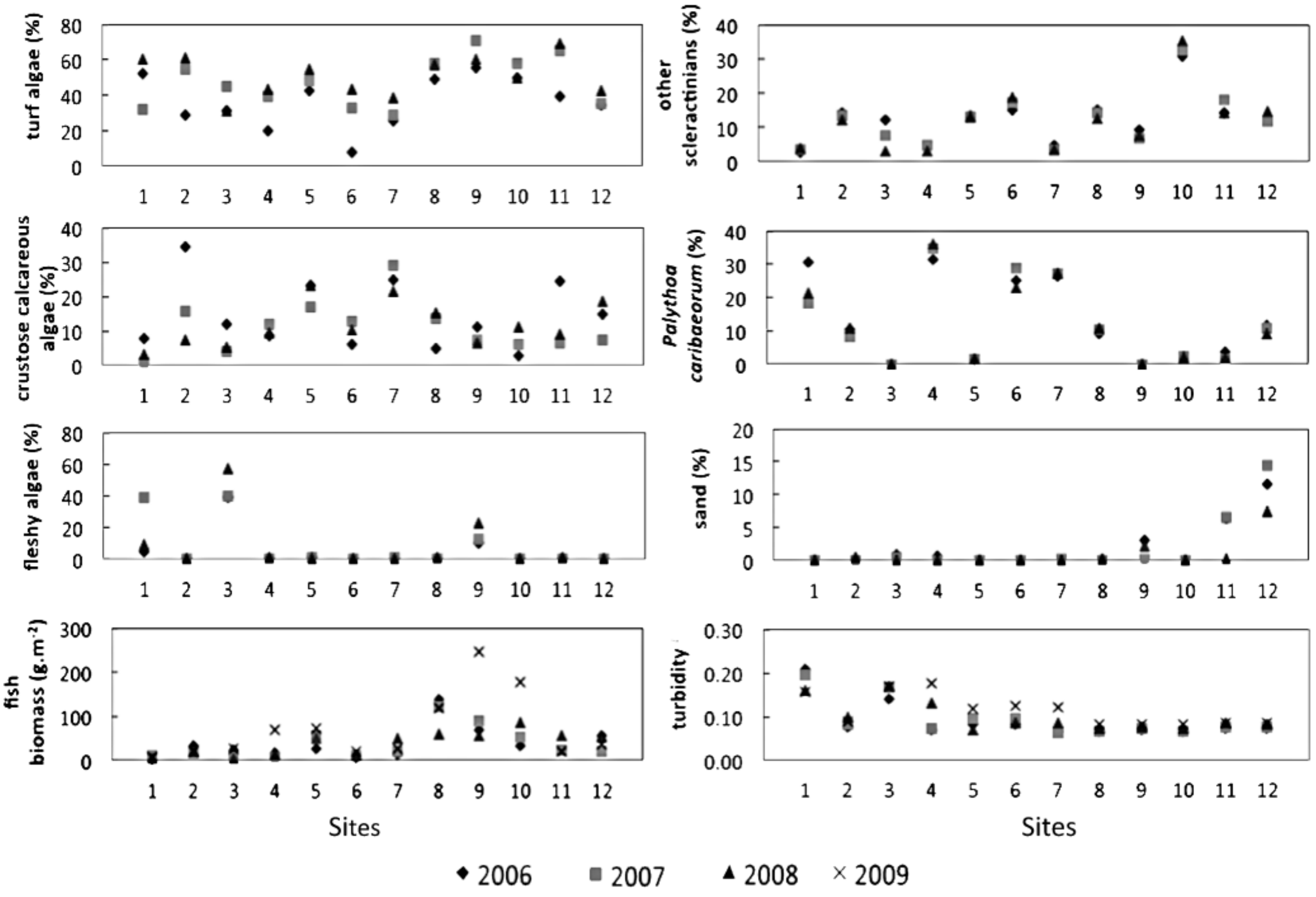

Fig. 3S Means of biotic and abiotic variables at the site level. Number 1 to 12 refer to the sites: (1) SGOM, (2) PA2, (3) PLEST, (4) ARENG, (5) TIM1, (6) TIM2, (7) TIM3, (8) GUA, (9) MV, (10) PNORT; (11) PAB2 and, (12) PAB3.

CONCLUSÕES

No primeiro trabalho (FRANCINI-FILHO et al., 2013) foi evidenciado que a maior parte da variabilidade espacial nas comunidades bentônicas se manifestou em escalas espaciais pequenas, com poucas dezenas de metros, i.e., ao nível dos hábitats (topo e parede dos pináculos recifais). Nas paredes dos pináculos, inclinadas e com pouca incidência luminosa, foi constatada expressiva cobertura coralínea, especialmente da espécie *Montastraea cavernosa*, uma espécie anteriormente registrada como dominante em áreas fundas. Essa preponderância de *M. cavernosa* nas paredes dos recifes contraria os resultados de levantamentos anteriores em Abrolhos, que davam conta de uma cobertura coralínea incipiente nesse habitat, mas sem apresentar dados quantitativos (KIKUCHI et al., 2010). A dominância por *M. cavernosa* parece ser determinada pela intensidade luminosa baixa, seja em função da profundidade, seja em função da inclinação do substrato.

Também foi constatado que os regimes de manejo e a biomassa de peixes herbívoros tiveram uma influencia menor na configuração e na dinâmica das comunidades bentônicas, sugerindo um papel preponderante de fatores como luz e profundidade. Além dessa preponderância de variáveis oceanográficas ligadas à qualidade de água, ressalta-se que a associação entre a biomassa de peixes (= regime de manejo) e a dinâmica bêntica foi relativamente fraca. Este resultado pode ser parcialmente devido ao tempo mais lento de resposta das comunidades bênticas à proteção contra a pesca (GRAHAM et al., 2011; KAISER et al., 2006), especialmente as assembleias coralíneas compostas por organismos de crescimento extremamente lento, que se expandem na ordem de milímetros por ano (KLEYPAS et al., 2001; KNOWLTON; JACKSON, 2001).

A relação negativa entre a abundância de macroalgas e de organismos construtores (escleractíneos e algas coralináceas) encontrada ao longo de toda a região recifal do Banco dos Abrolhos corrobora a ideia de que existe forte competição entre esses organismos, com implicações importantes para o delineamento de estratégias de manejo e restauração (FRANCINI-FILHO et al., 2013). Recifes com cobertura expressiva de macroalgas não são favoráveis ao desenvolvimento de corais, nem mesmo por corais "weedy", o que pode dificultar programas de relocação de colônias produzidas em áreas mais pristinas ou em cativeiro (e.g. YOUNG et al., 2012). Por fim, destaca-se o um aumento contínuo e significativo na cobertura de tufos de algas ("turf algae") ao longo do período de estudo, que vai ao encontro da tendência global desse grupo funcional crítico em recifes coralíneos (GORGULA; CONNELL 2004; SANDIN et al., 2008), aqui registrada pela primeira vez em recifes do Atlântico Sul. A dominância por tufos de algas, que são consórcios entre algas filamentosas de pequeno porte e microorganismos (especialmente cianobactérias), pode estar ligada à diminuição na pressão de herbivoria devido à sobrepesca de peixes, associada à eutrofização das regiões costeiras, a qual tem levado a um processo de "microbialização" dos recifes de Abrolhos (FRANCINI-FILHO et al., 2008; BRUCE et al., 2012).

No segundo trabalho (OLIVEIRA et al., submetido) foi avaliada a dinâmica da cobertura relativa, do crescimento e da vitalidade de um coral "weedy" endêmico do Brasil, *Favia gravida*. Também se buscou avaliar os efeitos do substrato de entorno na vitalidade (potencial fotossintético, prevalência de branqueamento e doenças) e no crescimento desse coral, uma abordagem inovadora. Algumas características desse grupo funcional incluem o crescimento relativamente rápido, fecundação interna e incubação larval, múltiplos ciclos reprodutivos no ano, baixa longevidade e tamanho pequeno em relação a outras espécies, as quais indicam que *F. gravida* poderia fornecer respostas demográficas relativamente rápidas frente à dinâmica do ambiente. Nesse sentido, foi explorada a influência do gradiente de distancia da costa, dos níveis de proteção e a influência do substrato do entorno em variáveis demográficas (cobertura, crescimento, mortalidade, tamanho e recrutamento).

As respostas demográficas de *F. gravida* apresentaram variações espaciais mais marcantes do que variações temporais, com maior influencia relativa de fatores regionais (i.e. turbidez, distância da costa, biomassa de peixes herbívoros, cobertura bêntica) do que fatores locais (i.e. substrato no entorno da colônia). Verificou-se que a contribuição de *F. gravida,* entre os corais escleractíneos, foi maior em recifes desprotegidas costeiros do que nas áreas protegidas costeiras e distantes da costa, sugerindo que certas espécies de corais não resistem às mesmas condições as quais *F. gravida* melhor se desenvolve. Apesar de *F. gravida* se beneficiar em condições de elevada turbidez, os resultados mostram que a espécie é também vulnerável aos distúrbios associados à proximidade da costa e a falta de proteção. Dentre os fatores potencialmente prejudiciais, destacaram-se a redução na abundância de peixes herbívoros e o aumento de cobertura de macroalgas. Neste sentido, a gestão da pesca e a gestão das bacias hidrográficas deveriam ser componentes centrais em estratégias de conservação de recifes costeiros (KENNEDY et al., 2013).

A vitalidade média de *F. gravida* variou espacialmente, mas permaneceu constante ao longo do tempo, apontando para um branqueamento crônico afetando cerca de metade da população. No entanto, mesmo o branqueamento de níveis moderado a intenso não mostrou relação com a mortalidade nem com o crescimento das colônias, sugerindo que a heterotrofia tenha um papel importante para essa espécie, assim com já registrado para outros corais endêmicos do Brasil (PIRES et al, 2010). As doenças afetaram uma porção relativamente pequena (5%), porém com conseqüências severas (100% de mortalidade). A proximidade da costa foi o fator de maior importância e mais associado com a menor vitalidade nas colônias de *F. gravida*.

Considerando que os efeitos negativos associados à intensificação de distúrbios antropogênicos nas regiões costeiras de Abrolhos afetam até mesmo espécies "weedy", tais como *F. gravida,* estes efeitos tendem a ser mais agudos em espécies supostamente menos resistentes e com ciclos de vida mais longos, tais como aquelas do gênero *Mussismilia*. A compreensão adequada da dinâmica de sistemas coralíneos deve incluir estudos demográficos abrangendo espécies pertencentes a diferentes grupos funcionais, os quais podem apresentar respostas dissimilares às variações na qualidade da água e outras variáveis oceanográficas e aos regimes de manejo. A utilização de métodos amostrais de alta resolução, tais como as amostras repetidas com fotografias, também deve ser mais amplamente utilizada em programas de monitoramento de ambientes coralíneos. Essa abordagem permite a exploração de processos que operam em escalas locais (e.g. influência do substrato de entorno), bem como estimativas de parâmetros biológicos/populacionais que não podem ser acessados com as abordagens mais tradicionais baseadas em transectos e outros métodos observacionais (e.g. taxas de crescimento).

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