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ECOLOGIA E CONSERVAÇÃO DA BIODIVERSIDADE**

**LUANA COSTA REIS**

**MACROALGAL AND TURF CANOPY EFFECTS ON CORAL REEF BENTHIC  
COVER ESTIMATES AND ON UNDERSTOREY ORGANISMS**

**ILHÉUS - BAHIA  
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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade da Universidade Estadual de Santa Cruz como parte dos requisitos para obtenção do grau de Mestre em Ecologia e Conservação da Biodiversidade.

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## **EFEITOS DO DOSSEL DE MACROALGAS E DE TUFOS DE ALGAS EM ESTIMATIVAS DE COBERTURA BÊNTECA RECIFAL E NOS ORGANISMOS SUBJACENTES**

### **Resumo**

Os recifes de corais estão em declínio devido a uma combinação de estressores globais (e.g. alterações climáticas e acidificação) e locais (e.g. eutrofização e sobrepesca). A cobertura bêntica dos recifes é dominada por corais e algas bentônicas, sendo que a competição entre esses organismos modula a estrutura da comunidade. A progressiva substituição de corais construtores por organismos de crescimento rápido é tida como um dos efeitos mais conspícuos da degradação dos recifes coralíneos. Portanto, estimativas de cobertura bentônicas são fundamentais para o entendimento da dinâmica desses sistemas. As métricas utilizadas para monitorar os sistemas recifais e mensurar suas respostas frente a distúrbios, são baseadas em métodos que, na maioria, fornecem dados do recobrimento percentual dos organismos bentônicos a partir de dados bidimensionais obtidos em campo como, por exemplo transectos e, principalmente foto-quadrados. No entanto, estes métodos podem ser enviesados pelo efeito do dossel de algas, tufos de algas (*turf*), e mesmo de alguns corais, uma vez que subestimam um ecossistema altamente tridimensional. A fim de avaliar a contexto-dependência do “efeito dossel” no maior sistema recifal do Atlântico Sul, foram quantificados os grupos bentônicos subjacentes ao dossel, através da remoção experimental de macroalgas e *turf* em dois recifes com coberturas bênticas contrastantes, incluindo uma área costeira e desprotegida contra a pesca e uma área mais afastada da costa e protegida. Experimentos adicionais foram realizados com o objetivo de avaliar os efeitos da remoção do dossel na cobertura e na fisiologia dos organismos encontrados embaixo do dossel (corais e algas calcárias incrustantes - CCAs) em curto (cinco dias) e longo prazo (quatro meses), com ênfase na densidade, mortalidade e crescimento de recrutas de corais. A cobertura de CCAs e corais foi fortemente subestimada em ambos os locais, mas as diferenças foram mais acentuadas na área costeira, com dossel mais denso de macroalgas. As probabilidades de detecção também foram negativamente relacionadas com a cobertura de macroalgas, com diferenças significativas entre locais para CCAs, corais massivos e ramificados. A detecção de recrutas de corais foi fortemente influenciada pelo dossel de *turf*. Além disso, verificou-se que 80% da cobertura bentônica sob o dossel de macroalgas e *turf* estavam vivos, incluindo corais,

recrutas de corais e CCAs. Após quatro meses da remoção de macroalgas e turf não se observou nenhum efeito sobre os organismos bentônicos que estavam previamente sob o dossel, à exceção dos recrutas de corais, que cresceram menos nas parcelas manipuladas. O experimento em curto prazo não revelou qualquer efeito sobre a cobertura de corais, abundância de recrutas e atividade fotossintética de corais e CCAs. Em regiões onde os corais massivos predominam, como no Atlântico Sul, a amostragem com foto-quadrados tende a subestimar a contribuição de grupos de biomineralizadores importantes, e a magnitude desse viés varia localmente, dependendo da cobertura de macroalgas e turf. Dados obtidos a partir de métodos bidimensionais (e.g. fotoquadrados) devem ser interpretados com cautela, não apenas por serem influenciados por grupos formadores de dosséis, mas também porque os processos ecológicos sob os dosséis ainda são mal compreendidos.

Palavras-chave: Amostragem, efeito dossel, coral, algas calcárias, turf, macroalgas, Abrolhos



## MACROALGAL AND TURF CANOPY EFFECTS ON CORAL REEF BENTHIC COVER ESTIMATES AND ON UNDERSTOREY ORGANISMS

### Abstract

Coral reefs are in decline due to a combination of global (e.g. climate changes and acidification) and local stressors (e.g. eutrophication, sedimentation and overfishing), with an increasing replacement of slow-growing reef-building corals by fast-growing fleshy organisms. Benthic cover estimates are essential to the understanding of the processes underlying the decline of coral reefs, where the competition between corals and algae modulates benthic community structure. The most common metrics used to monitor reef cover rely on planar views of the benthos, such as transects and photoquadrats. However, these methods may be biased due to the effect of macroalgae, turf, and even coral canopies, as they correspond to a one or two-dimensional record of a highly three-dimensional and layered assemblage. In order to assess the context-dependency of the “canopy effect”, we quantified understory assemblages by means of experimental removal of macroalgae and turf in two South Atlantic reefs with contrasting benthic cover, including a coastal unprotected site and an offshore protected site. Additional experiments were performed in order to evaluate the effects of canopy removal on the cover and physiology of understory organisms (corals and crustose coralline algae- CCA) over shorter (five days) and longer (four months) periods, with emphasis on the density, mortality and growth of coral recruits. Cover of CCA and corals was underestimated at both sites, but differences were more acute in the coastal area, where macroalgae canopy was denser. Detection probabilities of understory organisms were also negatively related to macroalgal cover, with significant differences between locations for CCA, massive and branching corals. Detection of coral recruits was also influenced by turf canopies. In addition, we found that 80% of the benthic cover under the macroalgae and turf canopies were alive, including coral, coral recruits and CCA. After four months, the canopy removal did not affect understory benthic cover, with the exception of coral recruits, which grew faster in unmanipulated plots. The short-term experiment did not reveal any effect on coral cover and abundance of recruits, as well as on photosynthetic activity of corals and CCA. In regions where massive corals predominate, such as the South Atlantic, photoquadrats tend to underestimate the contribution of several reef-building groups. Moreover, the magnitude of this bias can vary locally, depending on turf and macroalgae cover. Data from planar views of benthic communities should be interpreted with caution, not only because

they are influenced by canopy-forming groups, but also because ecological processes under canopies remain poorly understood.

Keywords: Sampling methods, canopy effect, coral, coralline algae, turf, fleshy algae, Abrolhos

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## INTRODUÇÃO GERAL

Recifes de corais são ecossistemas estruturalmente complexos e biologicamente diversos, abrigando uma variedade de organismos (CONNELL, 1978). Além de sua importância biológica, esses ambientes proveem alimento e renda para milhões de pessoas (WILKINSON, 2008). Sua estrutura tridimensional é fornecida, principalmente, pelos corais escleractínios e algas calcárias incrustantes, organismos biomineralizadores do carbonato de cálcio (BIRKELAND, 1977; AMADO-FILHO et al., 2012). A perda da cobertura de corais afeta diretamente a biodiversidade dos recifes coralíneos, pois a complexidade estrutural desse ambiente pode ser comprometida (ALVAREZ-FILIP et al., 2009), assim como os organismos associados a ela.

Os corais estão restritos a águas rasas e quentes, apresentando uma distribuição limitada, abrangendo menos de 1,2% das zonas costeiras tropicais (SPALDING et al., 2001). No Brasil, os recifes de corais se estendem desde a costa do Amapá até o Banco dos Abrolhos, no extremo sul da Bahia (MOURA et al., 2016). Cerca de 20% dos recifes de coral do mundo já foram perdidos e 35% estão ameaçados de serem extintos nos próximos 20-40 anos (WILKINSON, 2008). Esse declínio se deve principalmente à interação entre estressores globais, como mudanças climáticas e acidificação e estressores locais, como a sobrepesca, poluição, doenças, sedimentação e eutrofização (HUGHES et al., 2003; PANDOLFI et al., 2003; BELLWOOD et al., 2004; FRANCINI-FILHO et al., 2008; WEBER et al., 2012).

A competição exerce um papel fundamental na estruturação da comunidade nos recifes de corais, sendo que os corais e as algas bêmicas são os principais organismos envolvidos (MCCOOK et al., 2001; BAROTT; WILLIAMS; et al., 2012; BAROTT; ROWER, 2012). Maiores coberturas relativas de corais têm sido associadas a sistemas mais saudáveis, com alta complexidade e diversidade (SPALDING et al., 2001). No entanto, a substituição da dominância dos corais por organismos não-construtores de crescimento rápido, tais como as algas frondosas e/ou formadoras de *turfs*, fenômeno conhecido como “phase-shift” (MCCOOK, 1999; HUGHES et al., 2007), vem sendo relatada em todo o mundo, caracterizando o declínio global desses ecossistemas (HUGHES, 1994; PANDOLFI et al., 2003; HUGHES et al., 2007; BRUNO et al., 2009). A maioria dos estudos sobre a interação coral-alga reportam um declínio na cobertura de corais e um consequente aumento na

abundância de algas ou outros organismos de crescimento mais rápido (TANNER, 1995; RIVER; EDMUNDS, 2001; NUGUES; BAK, 2006; MUMBY et al., 2007). Em grandes quantidades, as algas podem ser prejudiciais para os corais e outros organismos bênticos (BAHARTAN et al., 2010). O balanço competitivo entre corais e algas é influenciado pela sobrepesca, eutrofização e mudanças climáticas, normalmente atuando como fatores que aumentam o poder competitivo das algas (MCCOOK et al., 2001; HUGHES et al., 2007; VERMEIJ et al., 2010).

Esta nova configuração da comunidade é modulada por características morfológicas e fisiológicas das espécies presentes no ambiente, pois a dominância de algas pode afetar de diferentes formas, uma variedade de organismos adjacentes (JOMPA; MCCOOK, 2003a; BENDER et al., 2012). Normalmente, assume-se que as algas são competitivamente superiores. Entretanto, diferentes tipos de algas podem ter diferentes efeitos nos corais (MCCOOK et al., 2001; JOMPA; MCCOOK, 2003a, 2003b; BAROTT; RODRIGUEZ-MUELLER et al., 2012). As algas bênticas são, usualmente, categorizadas por sua morfologia e seu papel (LITTLER et al., 1983). As categorias mais utilizadas são macroalgas, tufos de algas (conhecidos como “turf”) e algas calcárias incrustantes (CCA) (BENDER et al., 2012; CETZ-NAVARRO et al., 2013). As macroalgas são maiores que 10 mm, com formas anatômicas complexas, são as mais bem estudadas, principalmente com relação a sua interação com corais (MCCOOK, 1999; BIRREL et al., 2008; DIAZ-PULIDO et al., 2010). Elas podem causar uma série de efeitos negativos nos corais, afetando o crescimento, fecundidade e recrutamento, através de uma variedade de mecanismos (TANNER, 1995; MCCOOK et al., 2001; RIVER; EDMUNDS, 2001; TITLYANOV et al., 2007). As CCAs mineralizam carbonato de cálcio e desempenham papel importante na formação da matriz dos recifes (AMADO-FILHO et al., 2012). São associadas positivamente com a saúde dos recifes e com o recrutamento de corais (HARRINGTON et al., 2004; PRICE, 2010). Os *turfs* de algas são assembleias multiespecíficas de algas filamentosas e cianobactérias, podendo ou não apresentar sedimentos e detritos, sendo importante na reciclagem de nutrientes (ex. fixação de nitrogênio por cianobactérias) (WILLIAMS; CARPENTER, 1997; CONNELL et al., 2014). Apresentam papel importante nos recifes como produtores primários, são fonte de alimento e abrigo para diversos invertebrados (HACKER; STENECK, 1990; GONÇALVES et al., 2002), além de estarem presentes nos primeiros estágios sucessionais (FRICKE et al., 2011) e protegerem colônias de coral contra predação (VENERA-PONTON et al., 2011). Sob determinadas circunstâncias, interações entre o *turf* e os corais podem resultar em uma relação

positiva para a cobertura de corais, podendo facilitar o recrutamento (BIRREL et al., 2005; SUZUKI; HAYASHIBARA, 2011; FRANCINI-FILHO et al., 2013), enquanto que o contato com macroalgas pode ser mais deletério (HAURI et al., 2010). O *turf* também podem causar diversos efeitos negativos como diminuição na reprodução, danificação dos tecidos, branqueamento e inibição do recrutamento de corais (BIRREL et al., 2008; BAROTT et al., 2009; ARNOLD et al., 2010; HAAS et al., 2010; CETZ-NAVARRO et al., 2015). Os tufos de algas estão se tornando predominantes nos sistemas recifais (SANDIN et al., 2008; WANGRASEURT et al., 2012; BAROTT; RODRIGUEZ-MUELLER et al., 2012; BAROTT; WILLIAMS et al., 2012). Dessa forma, entender as dinâmicas das interações *turf*-coral é de fundamental importância para uma compreensão mais holística acerca do funcionamento dos sistemas recifais sob declínio.

O Banco dos Abrolhos é uma área de extrema importância biológica, apresentando a maior biodiversidade marinha do Atlântico Sul (LABOREL, 1969). Este sistema está ameaçado por diversos estressores naturais e antropogênicos (WERNER et al., 2000; DUTRA et al., 2004; FRANCINI-FILHO et al., 2008; SEGAL; CASTRO, 2011). O monitoramento desses ambientes, principalmente no que se diz respeito à mudança da cobertura bêntica no espaço e no tempo, é de fundamental importância para a identificação de potenciais estressores, fornecendo assim suporte para o desenvolvimento de estratégias de mitigação e restauração. Os diversos métodos de amostragem usados em programas de monitoramento de recifes de corais, desde os que abrangem sensoriamento remoto até aqueles que fornecem informações em escalas menores, como os transectos e os fotoquadrados (HILL; WILKINSON, 2004), fornecem visões planares de um sistema que é marcado por sua elevada tridimensionalidade. Os métodos em utilização registram apenas o dossel dos recifes, subestimando o componente vertical do ambiente e os organismos subjacentes, os quais podem desempenhar importantes papéis ecológicos (GOATLEY; BELWOOD, 2011). Assim, a abundância e a cobertura relativa de importantes componentes bênticos podem ser fortemente subestimados, resultando em um viés conhecido como “efeito dossel” (GOATLEY; BELWOOD, 2011). O efeito dossel pode ser ocasionado por corais de forma ramificada ou foliar, mas geralmente é causado por macroalgas ou turfs, influenciando diversos componentes da comunidade recifal, desde a comunidade de peixes até a cobertura de corais (HAURI et al., 2010; POGOREUTZ et al., 2012). Em regiões dominadas por espécies de corais formadores de dossel, como as encontradas no Oceano Pacífico, a cobertura coralínea é usualmente superestimada, enquanto que a cobertura de turfs e CCAs são maiores



que as quantificações através dos métodos planares (GOATLEY; BELWOOD, 2011). Entretanto, implicações do efeito dossel nos recifes do Atlântico Sul, dominados por corais massivos, são uma lacuna no conhecimento, assim como os processos ecológicos que operam sob o dossel de algas (ex. recrutamento de corais e mineralização de algas coralináceas). Recentemente, a cobertura de turf tem aumentado nos recifes ao redor do mundo, possivelmente devido ao aumento no aporte de nutrientes associado com anomalias térmicas e mudanças físico-químicas na água do mar (VERMEIJ et al., 2010). Este padrão também foi relatado para o Banco dos Abrolhos (FRANCINI-FILHO et al., 2013), reiterando a importância de se entender as interações entre o dossel de organismos de crescimento rápido (turf e macroalgas) e os organismos construtores, como os corais e CCA.

A importância do dossel de algas em comunidades de costas rochosas é mais bem conhecida, influenciando a mudança da composição e funcionalidade da comunidade. A perda do dossel pode reduzir a capacidade do ambiente a resistir a distúrbios (TAIT; SCHIEL, 2011; CROWE et al., 2013; MIGNÉ et al., 2015). Diferentes tipos de dosséis determinam associações heterogêneas com a comunidade subjacente (FOWLER-WALKER et al., 2005), indicando que a composição do dossel influencia os organismos encontrados abaixo dele. O dossel pode proteger corais da predação e luz direta, mas também podem aumentar a competição entre corais e algas (CLEMENTS; HAY, 2015). Interações entre algas e corais podem ser negativas para os corais através de diferentes mecanismos, incluindo hipóxia, abrasão, sombreamento e alelopatia (JOMPA; MCCOOK, 2003b; BAROTT et al., 2009; VERMEIJ et al., 2010; RASHER et al., 2011). Alternativamente, essas interações podem ser neutras (BIRREL et al., 2005), ou até benéficas para os corais, quando o dossel de algas funciona como proteção física (JOMPA; MCCOOK, 1998). Por exemplo, Jompa e McCook (1998) mostraram, em um estudo realizado na Austrália, que o dossel de *Sargassum* protegeu corais do branqueamento durante um período de anomalias térmicas, possivelmente porque o dossel diminuiu a exposição dos corais a altas temperaturas e intensa luminosidade. A competição entre corais e algas benthicas pode variar de acordo com a cobertura de algas ou ausência/presença de herbívoros e as espécies envolvidas (BULLERI et al., 2013), presença de sedimentos, e as fases de vida dos organismos envolvidos (MCCOOK, 1999; BIRREL et al., 2005), além de serem influenciadas pelas características ambientais (VERMEIJ et al., 2010; BAROTT; WILLIAMS et al., 2012).

Como o dossel de organismos fototrópicos pode abrigar uma variedade de organismos subjacentes, espera-se que a composição da comunidade seja influenciada pela composição do

dossel, ou seja, é contexto-dependente, assim como seus possíveis efeitos nos organismos encontrados no substrato (FOWLER-WALKER et al., 2005; IRVING; CONNELL, 2006). Desta forma, este estudo teve como objetivo quantificar a cobertura dos grupos bênticos encontrados após a remoção experimental do dossel de macroalgas e turf em dois locais com diferentes comunidades bênticas, sedimentação e regimes de manejo, explorando a possível contexto-dependência do efeito dossel. Dois experimentos adicionais foram realizados para avaliar o efeito da remoção do dossel na cobertura e fisiologia dos organismos subjacente ao dossel em curto e longo prazo com ênfase na densidade, mortalidade e crescimento de recrutas de corais.

## REFERÊNCIAS

ALVAREZ-FILIP, L.; DULVY, N. K.; GILL, J. A; CÔTÉ, I. M.; WATKINSON, A. R. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. **Proceedings. Biological sciences / The Royal Society**, v. 276, n. 1669, p. 3019–25, 2009.

AMADO-FILHO, G. M.; MOURA, R. L.; BASTOS, A. C.; et al. Rhodolith beds are major CaCO<sub>3</sub> bio-factories in the tropical South West Atlantic. **PloS one**, v. 7, n. 4, p. e35171, 2012.

ARNOLD, S. N.; STENECK, R. S.; MUMBY, P. J. Running the gauntlet: Inhibitory effects of algal turfs on the processes of coral recruitment. **Marine Ecology Progress Series**, v. 414, p. 91–105, 2010.

BAHARTAN, K.; ZIBDAH, M.; AHMED, Y.; et al. Macroalgae in the coral reefs of Eilat (Gulf of Aqaba, Red Sea) as a possible indicator of reef degradation. **Marine pollution bulletin**, v. 60, n. 5, p. 759–64, 2010. Elsevier Ltd.

BAROTT, K. L.; RODRIGUEZ-MUELLER, B.; YOULE, M.; et al. Microbial to reef scale interactions between the reef-building coral *Montastraea annularis* and benthic algae. **Proceedings. Biological sciences / The Royal Society**, v. 279, p. 1655–64, 2012.

BAROTT, K. L.; ROHWER, F. L. Unseen players shape benthic competition on coral reefs. **Trends in microbiology**, v. 20, n. 12, p. 621–8, 2012. Elsevier Ltd.

BAROTT, K. L.; SMITH, J. E.; DINSDALE, E.; et al. Hyperspectral and physiological analyses of coral-algal interactions. **PloS one**, v. 4, n. 11, p. e8043, 2009.

BAROTT, K. L.; WILLIAMS, G. J.; VERMEIJ, M.; et al. Natural history of coral–algae competition across a gradient of human activity in the Line Islands. **Marine Ecology Progress Series**, v. 460, p. 1–12, 2012.

BELLWOOD, D. R.; HUGHES, T. P.; FOLKE, C.; NYSTRÖM, M. Confronting the coral reef crisis. **Nature**, v. 429, n. 6994, p. 827–33, 2004.

BENDER, D.; DIAZ-PULIDO, G.; DOVE, S. Effects of macroalgae on corals recovering from disturbance. **Journal of Experimental Marine Biology and Ecology**, v. 429, p. 15–19, 2012. Elsevier B.V.

BIRKELAND, C. The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. **Proceedings Third International Coral Reef Symposium**, p. 15–21, 1977.

BIRRELL, C. L.; MCCOOK, L. J.; WILLIS, B. L. Effects of algal turfs and sediment on coral settlement. **Marine pollution bulletin**, v. 51, n. 1-4, p. 408–14, 2005.

BIRRELL, C. L.; MCCOOK, L. J.; WILLIS, B. L.; DIAZ-PULIDO, G. Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. **Oceanography and Marine Biology: An Annual Review**, v. 46, p. 25–63, 2008.

BRUNO, J. F.; SWEATMAN, H.; PRECHT, W. F.; SELIG, E. R.; SCHUTTE, V. G. Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. **Ecology**, v. 90, n. 6, p. 1478–1484, 2009.

BULLERI, F.; COURAUDON-REÁLE, M.; LISON DE LOMA, T.; CLAUDET, J. Variability in the effects of macroalgae on the survival and growth of corals: The consumer connection. **PLoS ONE**, v. 8, n. 11, p. e79712, 2013.

CETZ-NAVARRO, N. P.; CARPIZO-ITUARTE, E. J.; ESPINOZA-AVALOS, J.; CHEE-BARRAGÁN, G. The Effect of Filamentous Turf Algal Removal on the Development of Gametes of the Coral *Orbicella annularis*. **Plos One**, v. 10, n. 2, p. e0117936, 2015.

CETZ-NAVARRO, N. P.; ESPINOZA-AVALOS, J.; HERNÁNDEZ-ARANA, H. A.; CARRICART-GANIVET, J. P. Biological responses of the coral *Montastraea annularis* to the removal of filamentous turf algae. **PloS one**, v. 8, n. 1, p. e54810, 2013.

CLEMENTS, C. S.; HAY, M. E. Competitors as accomplices: seaweed competitors hide corals from predatory sea stars. **Proceedings of the Royal Society B**, v. 282, n. 20150714, p. 1–9, 2015.

CONNELL, J. H. Diversity in Tropical Rain Forests and Coral Reefs. **Science**, v. 199, n. 4335, p. 1302–1310, 1978.

CONNELL, S. D.; FOSTER, M.; AIROLDI, L. What are algal turfs? Towards a better description of turfs. **Marine Ecology Progress Series**, v. 495, p. 299–307, 2014.

CROWE, T. P.; CUSSON, M.; BULLERI, F.; et al. Large-scale variation in combined impacts of canopy loss and disturbance on community structure and ecosystem functioning. **PloS one**, v. 8, n. 6, p. e66238, 2013.

DIAZ-PULIDO, G.; HARI, S.; MCCOOK, L. J.; HOEGH-GULDBERG, O. The impact of benthic algae on the settlement of a reef-building coral. **Coral Reefs**, v. 29, n. 1, p. 203–208, 2010.

DUTRA, L. X. C.; KIKUCHI, R. K. P.; LEÃO, Z. M. A. N. Effects of sediment accumulation on reef corals from Abrolhos, Bahia, Brazil. **Journal of Coastal Research**, v. 39, p. 0–5, 2004.

FOWLER-WALKER, M. J.; GILLANDERS, B. M.; CONNELL, S. D.; IRVING, A. D. Patterns of association between canopy-morphology and understory assemblages across temperate Australia. **Estuarine, Coastal and Shelf Science**, v. 63, n. 1-2, p. 133–141, 2005.

FRANCINI-FILHO, R. B.; CONI, E. O. C.; MEIRELLES, P. M.; et al. Dynamics of coral reef benthic assemblages of the Abrolhos Bank, eastern Brazil: inferences on natural and anthropogenic drivers. **PloS one**, v. 8, n. 1, p. e54260, 2013.

FRANCINI-FILHO, R. B.; MOURA, R. L.; THOMPSON, F. L.; et al. Diseases leading to accelerated decline of reef corals in the largest South Atlantic reef complex (Abrolhos Bank, eastern Brazil). **Marine pollution bulletin**, v. 56, n. 5, p. 1008–14, 2008.

FRICKE, A.; TEICHBERG, M.; BEILFUSS, S.; BISCHOF, K. Succession patterns in algal turf vegetation on a Caribbean coral reef. **Botanica Marina**, v. 54, p. 111–126, 2011.

GOATLEY, C. H. R.; BELLWOOD, D. R. The roles of dimensionality, canopies and

complexity in ecosystem monitoring. **PloS one**, v. 6, n. 11, p. e27307, 2011.

GONÇALVES, E. J.; BARBOSA, M.; CABRAL, N. H.; HENRIQUES, M. Ontogenetic shifts in patterns of microhabitat utilization in the small-headed clingfish, *Apletodon dentatus* (Gobiesocidae). **Environmental Biology of Fishes**, v. 63, p. 333–339, 2002.

HAAS, A.; EL-ZIBDAH, M.; WILD, C. Seasonal monitoring of coral-algae interactions in fringing reefs of the Gulf of Aqaba, Northern Red Sea. **Coral Reefs**, v. 29, n. 1, p. 93–103, 2010.

HACKER, S. D.; STENECK, R. S. Habitat Architecture and the Abundance and Body-Size-Dependent Habitat Selection of a Phytal Amphipod. **Ecology**, v. 71, n. 6, p. 2269–2285, 1990.

HARRINGTON, L.; FABRICIUS, K.; DE'ATH, G.; NEGRI, A. Recognition and Selection of Settlement Substrata Determine Post-Settlement Survival in Corals. **Ecology**, v. 85, n. 12, p. 3428–3437, 2004.

HAURI, C.; FABRICIUS, K. E.; SCHAFFELKE, B.; HUMPHREY, C. Chemical and physical environmental conditions underneath mat- and canopy-forming macroalgae, and their effects on understory corals. **PloS one**, v. 5, n. 9, p. e12685, 2010.

HILL, J.; WILKINSON, C. **Methods for Ecological Monitoring of Coral Reefs**. Version 1 ed. Townsville, 2004.

HUGHES, T. P. Catastrophes, phase shifts, and large-scale degradation of a Caribbean Coral Reef. **Science**, v. 265, p. 1547–1551, 1994.

HUGHES, T. P.; BAIRD, A. H.; BELLWOOD, D. R.; et al. Climate change, human impacts, and the resilience of coral reefs. **Science (New York, N.Y.)**, v. 301, n. 5635, p. 929–33, 2003.

HUGHES, T. P.; RODRIGUES, M. J.; BELLWOOD, D. R.; et al. **Phase shifts, herbivory, and the resilience of coral reefs to climate change**. 2007.

IRVING, A. D.; CONNELL, S. D. Predicting understory structure from the presence and composition of canopies: an assembly rule for marine algae. **Oecologia**, v. 148, n. 3, p. 491–502, 2006.

JOMPA, J.; MCCOOK, L. J. Sargassum canopy decreases coral bleaching on inshore reefs. **Reef Res**, v. 8, n. 5, 1998.

JOMPA, J.; MCCOOK, L. J. Coral-algal competition: macroalgae with different properties have different effects on corals. **Marine Ecology Progress Series**, v. 258, p. 87–95, 2003a.

JOMPA, J.; MCCOOK, L. J. Contrasting effects of turf algae on corals: Massive *Porites* spp. are unaffected by mixed-species turfs, but killed by the red alga *Anotrichium tenue*. **Marine Ecology Progress Series**, v. 258, p. 79–86, 2003b.

LABOREL, J. L. Madreporaria and Hydrocorallia of Reefs of Brazilian Coasts - Systematics, Ecology, Vertical and Geographic Distribution. **De L Institut Oceanographique**, v. 47, 1969..

LITTLER, M.; LITTLER, D.; TAYLOR, P. Evolutionary strategies in a tropical barrier reef system: functional-form groups of marine macroalgae. **Journal of Phycology**, v. 19, p. 229–237, 1983.

MCCOOK, L. J. Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. **Coral Reefs**, v. 18, n. 4, p. 357–367, 1999.

MCCOOK, L. J.; JOMPA, J.; DIAZ-PULIDO, G. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. **Coral Reefs**, v. 19, n. 4, p. 400–417, 2001.

MIGNÉ, A.; GOLLÉTY, C.; DAVOULT, D. Effect of canopy removal on a rocky shore community metabolism and structure. **Marine Biology**, v. 162, p. 449–457, 2015.

MOURA, R. L; AMADO-FILHO, G.M; MORAES, F.C; et al. An extensive reef system at the Amazon River mouth. **Science Advances**: 2:e1501252

MUMBY, P. J.; HASTINGS, A.; EDWARDS, H. J. Thresholds and the resilience of Caribbean coral reefs. **Nature**, v. 450, n. 7166, p. 98–101, 2007.

NUGUES, M. M.; BAK, R. P. M. Differential competitive abilities between Caribbean coral species and a brown alga : a year of experiments and a long-term perspective. **Marine Ecology Progress Series**, v. 315, p. 75–86, 2006.

PANDOLFI, J. M.; BRADBURY, R. H.; SALA, E.; et al. **Global trajectories of the long-term decline of coral reef ecosystems**. 2003.

POGOREUTZ, C.; KNEER, D.; LITAAY, M.; ASMUS, H.; AHNELT, H. The influence of canopy structure and tidal level on fish assemblages in tropical Southeast Asian seagrass meadows. **Estuarine, Coastal and Shelf Science**, v. 107, p. 58–68, 2012. Elsevier Ltd.

PRICE, N. N. Habitat selection , facilitation , and biotic settlement cues affect distribution and performance of coral recruits in French Polynesia. **Oecologia**, v. 163, p. 747–758, 2010.

RASHER, D. B.; STOUT, E. P.; ENGEL, S.; KUBANEK, J.; HAY, M. E. Macroalgal terpenes function as allelopathic agents against reef corals. **Proceedings of the National Academy of Sciences of the United States of America**, v. 108, n. 43, p. 17726–17731, 2011.

RIVER, G. F.; EDMUNDS, P. J. Mechanisms of interaction between macroalgae and scleractinians on a coral reef in Jamaica. **Journal of experimental marine biology and ecology**, v. 261, n. 2, p. 159–172, 2001.

SANDIN, S. A.; SMITH, J. E.; DEMARTINI, E. E.; et al. Baselines and Degradation of Coral Reefs in the Northern Line Islands. **PLoS ONE**, v. 3, n. 2, p. e1548, 2008.

SEGAL, B.; CASTRO, C. B. Coral community structure and sedimentation at different distances from the coast of the Abrolhos Bank, Brazil. **Brazilian Journal of Oceanography**, v. 59, n. 2, p. 119–129, 2011.

SPALDING, M. D.; RAVILIOUS, C.; GREEN, E. P. **World Atlas of Coral Reefs**. University of California Press, Berkeley, USA: Prepared at The UNEP World Conservation. Monitoring Center., 2001.

SUZUKI, G.; HAYASHIBARA, T. Do epibenthic algae induce species-specific settlement of coral larvae ? **Journal of the Marine Biological Association of the United Kingdom**, v. 91, n. 3, p. 677–683, 2011.

TAIT, L. W.; SCHIEL, D. R. Legacy effects of canopy disturbance on ecosystem functioning in macroalgal assemblages. **PLoS ONE**, v. 6, n. 10, p. e26986, 2011.

TANNER, J. E. Competition between scleractinian corals and macroalgae: An experimental investigation of coral growth, survival and reproduction. **Journal of Experimental Marine Biology and Ecology**, v. 190, n. 2, p. 151–168, 1995.

TITLYANOV, E. .; YAKOVLEVA, I. M.; TITLYANOVA, T. V. Interaction between benthic algae (*Lynghya bouillonii*, *Dictyota dichotoma*) and scleractinian coral *Porites lutea*

in direct contact. **Journal of Experimental Marine Biology and Ecology**, v. 342, n. 2, p. 282–291, 2007.

VENERA-PONTON, D.; DIAZ-PULIDO, G.; MCCOOK, L. J.; RANGEL-CAMPO, A. Macroalgae reduce growth of juvenile corals but protect them from parrotfish damage. **Marine Ecology Progress Series**, v. 421, p. 109–115, 2011.

VERMEIJ, M.; MOORSELAAR, I. VAN; ENGELHARD, S.; et al. The effects of nutrient enrichment and herbivore abundance on the ability of turf algae to overgrow coral in the Caribbean. **PloS one**, v. 5, n. 12, p. e14312, 2010.

WANGPRASEURT, D.; WEBER, M.; RØY, H.; et al. In situ oxygen dynamics in coral-algal interactions. **PloS one**, v. 7, n. 2, p. e31192, 2012.

WEBER, M.; BEER, D. DE; LOTT, C.; et al. Mechanisms of damage to corals exposed to sedimentation. **Proceedings of the National Academy of Sciences**, v. 109, n. 24, 2012.

WERNER, T. B.; PINTO, L. P.; DUTRA, G. F.; PEREIRA, P. G. DO P. Abrolhos 2000 : Conserving the Southern Atlantic's Richest Coastal Biodiversity into the Next Century. **Coastal Management**, v. 28, n. 1, p. 99–108, 2000.

WILKINSON, C. **Status of coral reefs of the world: 2008**. Townsville, Australia: Global Coral Reef Monitoring Network and Reef and Rainforest Research Center, 2008.

WILLIAMS, S. L.; CARPENTER, R. C. Grazing effects on nitrogen fixation in coral reef algal turfs. **Marine Biology**, v. 130, p. 223–231, 1997.



# **Macroalgal and turf canopy effects on coral reef benthic cover estimates and on understory organisms**

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## **Introduction**

Coral reefs are declining globally due to a combination of direct anthropogenic stressors and changing climate (Spalding, Ravilious & Green, 2001). Coral cover is usually associated with the health of reefs (Bruno & Selig, 2007; Graham, 2014), and the replacement of corals by fast-growing organisms, such as macroalgae and turf algae, is the most iconic portrait of the declining coralline ecosystems (Hughes, 1994; Pandolfi et al., 2003; Hughes et al., 2007). The balance between coral and algae cover is influenced by the competitive advantage of algal turfs and macroalgae under the interaction of reduced herbivory (from overfishing and disease outbreaks), eutrophication (from anthropogenic nutrient sourcing and positive feedbacks from fast-growing primary producers) and climate changes (McCook, Jompa & Diaz-Pulido, 2001; Hughes et al., 2007; Vermeij et al., 2010). Detection of benthic cover shifts depends on accurate and precise baselines and repeated observations (Hill & Wilkinson, 2004), and is also constrained by context-specific spatial heterogeneity and temporal dynamics of coralline reefs (Sandin et al., 2008; Bruno et al., 2014).

Corals are arguably the most important organisms on reef assemblages because they provide habitat complexity, efficiently recycle nutrients, and source dissolved and particulate organic matter to the environment (Alvarez-Filip et al., 2009; Pawlik, Burkepile & Thurber, 2016). However, they rarely dominate benthic cover (Vroom et al., 2006). Major benthic players in coralline reefs include algal turfs, macroalgae and crustose coralline algae (CCA) (Littler, Littler & Taylor, 1983; Sandin et al., 2008). Algal turfs, which consist of associations between filamentous algae and microorganisms (Connell, Foster & Airoidi, 2014), can negatively impact corals by overgrowth and chemical allelopathy (Jompa & McCook, 2003a), as well as by localized hypoxia and pH changes leading to tissue mortality in contact zones (Barott et al., 2009; Barott & Rohwer, 2012). On the other hand, turf algae may play important roles in primary production and nutrient cycling, providing food to upper trophic levels and protection to coral recruits (Hacker & Steneck, 1990; Williams & Carpenter, 1997; Venera-Ponton et al., 2011). Negative effects of foliose macroalgae on corals include overgrowth, abrasion, epithelial sloughing and allelopathy (Jompa & McCook, 2002; Rasher et al., 2011), and they may also function as reservoirs of pathogenic microorganisms (Barott et al., 2012a; Barott & Rohwer, 2012). Conversely, shading by macroalgae may provide protection against predation and light stress (Jompa & McCook, 1998; Venera-Ponton et al., 2011). CCA interactions with corals are generally reported as positive (Morse et al., 1988; Heyward & Negri, 1999; Harrington et al., 2004; Price, 2010), with a few exceptions (e.g. Antonius & Afonso-Carillo, 2001). Besides being important calcium carbonate mineralizers and binders of coral fragments (Amado-Filho et al., 2012), CCA are suitable habitats for coral recruitment (Price, 2010; Tebben et al., 2015).

The most widely used methods for monitoring benthic cover on reefs include satellite and aerial imagery, point intercept transects, towed-diver surveys (with manual, video or photographic data acquisition), and photoquadrats (Hill & Wilkinson, 2004). Despite several obvious differences in spatial cover and resolution, these methods produce bi-dimensional views of the benthic canopy, underestimating the vertical component of the environment and the actual abundance of underlying organisms (Goatley & Bellwood, 2011). Therefore, the relative cover of several benthic players are often underestimated by the current sampling approaches, resulting in poorly understood biases which have been referred to as the "canopy effect" (Goatley & Bellwood, 2011).

In addition to sampling constraints, canopies influence understory organisms. The major role that canopy-forming organisms play in determining assemblage structure is widely recognized in temperate reefs (e.g. Irving, Connell & Gillanders, 2004; Fowler-Walker et al., 2005; Migné, Golléty & Davoult, 2015), but has been given much less attention in the coral-algae dominance debate that dominates tropical coral reef ecology (e.g. Dubinsky & Stambler, 2011). While the effects of turf and macroalgae on coral physiology have been widely reported by means of natural and manipulative experiments (e.g. Jompa & McCook, 2002; Cetz-Navarro et al., 2013, 2015), even the sampling biases arising from algae removal are still poorly understood. Here, in order to assess the context-dependency of the "canopy effect" on coral reefs, we quantified understory assemblages by means of experimental removal of macroalgae and turf in two reefs with contrasting benthic cover and disposed along a cross-shelf gradient of sedimentation and protection from fisheries (Bruce et al., 2012; Francini-Filho et al., 2013). Additional experiments were performed in order to evaluate the effects of canopy removal on the cover and physiology of understory organisms (corals and CCA) over shorter (five days) and longer-term (four months), with emphasis on the density, mortality and

growth of coral recruits. These experiments contribute to clarify the several ecological and biological processes that operate under algal canopies in coralline reefs.

## **Materials and Methods**

### **Study area**

The study region, Abrolhos, is the most biodiverse reef complex in the South Atlantic and encompasses unique biogenic structures that resemble giant mushroom-shaped pinnacles ("chapeirões") (Moura et al., 2013). The major coral reef builders in pinnacle's tops are massive species belonging to the Brazilian-endemic genus *Mussismilia* (Francini-Filho et al., 2013). Sampling was carried out in two contrasting reefs, Pedra de Leste (PLESTE) (17°47'01"S, 39°03'05"W) and Parcel dos Abrolhos (PAB) (17°57'32"S, 38°30'20"W). PLESTE is closer to the coast (10-15 km), unprotected from fishing, and has higher macroalgal cover, while PAB is more offshore (75 km) and located within the no-take Abrolhos Marine National Park (established in 1983), presenting very small macroalgal cover (Francini-Filho & Moura, 2008a). Bruce et al. (2012) provide a detailed description of the two study sites, including water quality (poorer nearshore), microbialization (higher nearshore) and fish biomass (higher offshore).

### **Experimental design and sampling**

The first experiment (Fig. 1A) was conducted in the summer of 2012 in PLESTE and PAB with the objective of exploring the influence of algal and turf canopies on photoquadrat-derived benthic cover estimates and its context-dependency. The follow-up experiment (Fig.

1B), carried out in 2014, was conducted in PAB and aimed to explore the short- and long-term effects of the canopy on understory organisms (14-19 Feb and 14 Feb- Jun 27, respectively). Sampling was based on digital photographs obtained within PVC quadrats, using a Canon G-12 camera inside a waterproof housing equipped with a INON strobe operated in the slave mode. Quadrats were randomly distributed in pinnacles' tops of PLESTE and PAB (n=5 in each reef) and their position was fixed with metal pins for initial and subsequent sampling. Each quadrat consists of 15 contiguous subunits with 0.033 m<sup>2</sup> (corresponding to the area of each individual photograph), totaling 0.49 m<sup>2</sup>. For the first experiment, carried out at both sites, an initial set of photographs was obtained without any manipulation, followed by a second set obtained immediately after manual macroalgae removal (only present in PLESTE) and a third set obtained immediately after the removal of algal turfs with a flexible brush. A rugosity index (surface contour to linear distance ratio) was calculated with a 10 m metal chain (n=4 samples per site), following Hill & Wilkinson (2004). For the follow-up experiment, carried out only at the offshore site (PAB), 20 quadrats were photographed without any manipulation (Fig. 1B). These quadrats were also randomly placed on pinnacle's tops and further fixed with metal pins. Turf canopy removal with a brush was performed in 10 quadrats, which were immediately sampled, while the other 10 remained intact as controls. Five of the 10 manipulated quadrats were also sampled after five days, in order to explore possible coral recruit predation/mortality and photochemical stress, comprising a short-term assessment of the turf canopy effect. Four months later, turf canopy was cleared again in the 10 initially manipulated quadrats, which were immediately sampled, as were the 10 control quadrats, comprising a longer-term assessment of the effect of turf on understory organisms. Temperature and light levels were measured across the experiment with a continuous-recorder HOBO data logger.

Relative cover of benthic organisms was estimated from the photographs, with software *Coral Point Count with Excel Extensions*, CPCe v. 4.1 (Kohler & Gill 2006), using 1500 randomly distributed sampling points per quadrat (100 per photo). Organisms below each point were identified at the lowest possible taxonomic level and later grouped into five broader categories: coral, crustose coralline algae (CCA), turf, macroalgae and others. Corals were also grouped as massive, branching (only *Millepora* spp.) and encrusting functional groups. Abundance, incidence (i.e. input of new corals during the sampling lag), growth and mortality of coral recruits (colonies with max. diameter < 15 mm) were estimated on manipulated and control quadrats. Mortality was assigned when a recruit was recorded dead or was not found at the initial location. Growth was estimated as the difference between the area and maximum diameter of individual colonies at each time-point, as measured with CPCe. This procedure, although limited for larger branching colonies, provides reliable size estimates for encrusting coral recruits, which show limited tridimensionality. As diameter and area changes were significantly correlated ( $p < 0.05$ ;  $r^2 = 0.72$ ), only area changes are shown.

The photosynthetic physiology of corals and CCAs was assessed with a Pulse Amplitude Modulation fluorometer (diving-PAM). A detailed description PAM fluorometry is provided by Hennige et al. (2008, 2010). Briefly, the equipment delivers rapid light curves (RLCs) that allow for assessing the dissipation of absorbed excitation energy, based on measurement of the electron transport rate (ETR) of photosystem II (PSII). Photosynthetic activity under conditions of limited light and saturation, and the light saturation point, can be obtained by measuring ETRs along light intensity gradients. ETR equals to  $Y \times \text{PAR} \times 0,5 \times \text{AF}$ , where Y is the photosynthetic yield of PS II, PAR is the irradiance ( $\mu\text{mol photons m}^{-2}\text{s}^{-1}$ ) at each light intensity, and AF is a preset absorption factor (0.725 for corals and 0.56 for CCAs) (Beer & Axelsson, 2004; Ralph et al., 2005). Ratios of absorption of photon energy (photochemical

quenching, qP) or conversion to heat (non-photochemical quenching, qN) were further derived (Hennige et al., 2008; Suggett et al., 2012), as were minimum ( $F_0$ ) and maximum fluorescence ( $F_1$ ) and effective quantum yield ( $F_v/F_m$ ) (Beer et al., 1998). Sampling was carried out *in situ* with a fiber optic probe, after dark-adaptation for 15 min. Measurements were initially performed in the absence of actinic light, followed by sampling under serial increases (every 20 sec., from 0 to 2700  $\mu\text{mol photons m}^{-2}\text{s}^{-1}$ ). Fluorescence of dark acclimated samples provides information about the physiological state when photoprotectors are relaxed, PS II reaction centers are open, and the electron transport chain is oxidized (Ralph & Gademann, 2005). Measurements were performed immediately and five days after manipulation. As responses to changes in light intensity can be heterogeneous (Iglesias-Prieto et al., 2004; Suggett et al., 2012), coral and CCA specimens adjacent to the manipulated quadrats were sampled as controls.

### **Data analyses**

All analyses were performed with R (R Development Team 2012), using the lme4 package (Bates et al., 2015). Response variables include percent cover of CCA, coral, coral growth forms, and other organisms, as well as abundance, incidence, growth and mortality of coral recruits. Normality and homocedasticity were verified with Shapiro-Wilk and Bartlett tests, respectively. Transformations to meet the assumptions of parametric tests were used when needed and as indicated below. Quadrats were used as replicates, except when noted.  $\text{Log}(x+1)$  transformations were applied in recruits' data. In order to evaluate differences between treatments, ANOVA for repeated measures were used at the coastal site (PLESTE), where three subsequent treatments were performed (unmanipulated, macroalgae removal, turf removal). In the offshore site (PAB), where only turf removal was performed (macroalgae

were absent), differences were assessed with paired t-tests or Wilcoxon signed-rank tests when assumptions of parametric tests were not met. Contrasts in benthic community structure were explored with multivariate analyses. Percent cover data was transformed to  $\arcsin \sqrt{x}$  and compiled into a triangular matrix (Bray-Curtis similarity) that was further submitted to non-metric multidimensional scaling (MDS) (Clarke & Warwick, 2001). One-way analyses of similarities (ANOSIM) were also employed to explore differences between locations and treatments (Clarke & Warwick, 2001). Structural complexity of both sites was compared with a two-sample test for independent samples.

Effects of canopy removal and location in the probability of detection of recruits, coral and CCA were explored with logistic regressions performed using Generalized Linear Models (GLM) with binomial distribution and logit function (Zuur, Ieno & Smith, 2007). Probability of detection was defined as the probability of detecting the real number of recruits (or benthic cover) without manipulation, based on amounts recorded after canopy removal. Response variable was the proportion of recruits before and after such manipulations. For corals and CCAs, the response variable was the proportion of points assigned to each category in the CPCe output. Explanatory variables included location and algal cover, this latter standardized to a mean of zero and one standard deviation. Differences in probability of detection were explored by fitting separate models for each category of organism.

For assessing the longer-term influence of canopy removal on understory organisms we used a two-sample test comparing the number of recruits and percent covers estimates between experimental quadrats before manipulation and controls. Variables, which were log and  $\arcsin \sqrt{x}$  transformed, included cover estimates of turf, CCA, coral, coral growth forms, and



the three most abundant corals, *Siderastrea* spp., *Agaricia* spp. and *Mussismilia hispida*. A paired t-test was used to evaluate differences in benthic cover (same variables) before and after manipulation. Wilcoxon-Mann-Whitney and Wilcoxon signed-rank tests were used when data did not meet the assumptions of parametric tests. Mortality of recruits was compared between treatments with the two-sample test. Wilcoxon-Mann-Whitney test was used to compare coral area change between manipulated quadrats and controls.

A mixed model of Factorial Analysis of Variance (ANOVA) for repeated measures was used to evaluate the effects of time (Feb–Jun) and treatment (canopy removal and control) in the response variables. Time and treatment were the fixed factors and quadrats were the random factor. Model selection was based on the Akaike information criterion (AIC), with lower values indicating better performance. A type III model with Satterwhite approximation degrees of freedom was used. Recruits' data were log-transformed and percentage cover data were arcsen  $\sqrt{x}$  transformed. Response variables that deviated from the normal distribution were not analyzed (e.g branching corals).

The short-term influence of canopy removal on understory organisms was assessed with a paired t-test comparing number of recruits, coral and CCA cover estimates after canopy removal and five days later. In addition, the potential light stress due to canopy removal ( $F_v/F_m$ ) was assessed with a factorial ANOVA with time and treatment as fixed factors.

## **Results**

Considering only unmanipulated samples, there were significant assemblage-level differences between the coastal and offshore site (ANOSIM  $R=0.39$ ;  $P=0.001$ ). The unprotected coastal site (PLESTE) had significantly higher cover of macroalgae and lower cover of corals than the protected offshore site (PAB) (Fig. 2). Structural complexity was similar in PLESTE and PAB, with rugosity values reaching  $0.87 (\pm SE 0.04)$  and  $0.72 (\pm SE 0.1)$ , respectively.

Macroalgae and turf removal evidenced that the detection of understory organisms, including several reef builders, is constrained by the canopies of fleshy organisms, and the magnitude of this effect is context-dependent. The two-dimensional MDS with all treatments (unmanipulated, macroalgae removal, turf removal) at both sites (Fig. 3), together with the ANOSIM results, evidenced greater differences between treatments ( $R=0.61$ ;  $P=0.001$ ) than between locations ( $R=0.39$ ;  $P=0.001$ ). At the coastal unprotected site (PLESTE), CCA and others organisms' cover varied significantly between unmanipulated samples and those submitted to macroalgae removal (ANOVAs  $t=-5.44$  and  $3$ , respectively,  $p<0.05$ ) (Fig. 2). In addition, coral, CCA, and other organisms' cover differed between unmanipulated samples and those submitted to turf removal (ANOVAs  $t=5.37$ ,  $26.74$  and  $15.3$ , respectively,  $p<0.05$ ). Cover estimates of massive and encrusting corals varied significantly only after macroalgae removal at PLESTE (ANOVAs  $t=2.47$  and  $3.35$ , respectively,  $p<0.05$ ) (Fig. 2), with no effects detected on branching corals or from turf removal in PAB. Abundance estimates of corals, massive corals and encrusting corals (paired t-tests  $p>0.05$ ), as well as those of branching corals and CCAs (Wilcoxon tests  $p>0.05$ ), did not differ between treatments, but estimates for other organisms did (paired t-test  $t=2.82$ ,  $p<0.05$ ) (Fig. 2).

The organisms that were more underestimated by algal and/or turf canopies were CCA and corals. At the coastal site (PLESTE), macroalgae represented 86% of the benthic cover before manipulation (Fig. 2). Accordingly, the effects of canopy removal were more acute at this site, with coral cover estimates ranging from 6.8 to 11.3% ( $\pm$ SE 1.2 and 1.8, respectively). At the offshore site (PAB) coral cover estimates ranged only from 24 to 28% ( $\pm$ SE 2.1 and 2.2, respectively). CCA cover estimates ranged from 3.9 to 57% at PLESTE ( $\pm$ SE 0.4 and 0.8, respectively), and from 7.5 to 35.6% at PAB ( $\pm$ SE 0.9 and 1.8, respectively). Remarkably, 92% of the substrate under the PLESTE macroalgae canopy was covered by living organisms (CCA 75%, corals 6.3%, other 10.8%). At PAB, where macroalgae cover was minimal (0.3%), turf covered 65% of the substrate before manipulation, and the cover of living substrate under the canopy was lower (78%) (CCA 60%, corals 8.8%, other 9.5%).

Detection of coral recruits was strongly influenced by turf canopies. In unmanipulated plots, recorded abundances were similar at both sites ( $n=28$  and  $27$  coral recruits). However, the observed number of recruits increased from  $28$  to  $98$  after turf removal in PLESTE (ANOVA  $t=5.16$ ,  $p<0.05$ ), and from  $27$  to  $65$  in PAB (paired  $t$ -test  $t=5.9$ ,  $p=0.003$ ) (Fig. 4). Detection probabilities calculated for the other benthic categories were also negatively related to algal cover (Table 1), varying significantly between locations for CCA, massive and encrusting corals. The low CCA detectability in the unmanipulated samples of the coastal site was remarkable, as was the overall high detectability of corals in the offshore site.

Turf was the most abundant benthic cover category in PAB, reaching 80% in unmanipulated samples. Manipulated and control samples had similar coral cover (18 and 16%,  $\pm$ SE 3.4 and 1.8, respectively) ( $t$ -test  $df=18$ ,  $t=0.3878$ ,  $p=0.7$ ), and no differences were detected either for coral functional groups or for the three most abundant corals (*Siderastrea* spp., *Agaricia* spp. and *M. hispida*). After turf removal, estimates of coral cover increased from 16 to 22.1% ( $\pm$

SE=1.8 and 2.2, respectively) (paired t-test  $t=-5.12$ ,  $p=0.0006$ ), but the effect was dependent on coral functional group. Encrusting corals' cover estimates increased significantly after the manipulation, from 14.6 ( $\pm$ SE 1.9) to 19.8 % ( $\pm$ SE 2.1) (paired t-test  $t=-5.54$ ,  $df=9$ ,  $p=0.0003$ ) (Fig. 5), but variation of massive coral estimates was not significant. Cover of branching corals was very low (around 1%) and data was not normally distributed. *Siderastrea* sp. was the most abundant coral, with cover estimates changing from 10 to 12.9% ( $\pm$ SE 1.58 and 1.62, respectively) (paired t-test  $t=-5.17$ ,  $d=9$ ,  $p=0.0006$ ). For the second most abundant corals, *Agaricia* spp., cover estimates increased significantly from 2.14 to 12.86% ( $\pm$ SE 0.48 and 2.03, respectively) (paired t-test  $t=-4.08$ ,  $df=9$ ,  $p=0.002$ ), but for the third, *M. hispida*, increases were smaller and non-significant, ranging from 1.06 to 1.37% ( $\pm$ SE 0.37 and 0.44, respectively). CCA cover estimates increased significantly after turf removal (Wilcoxon test  $p=0.001$ ), varying from 1.6 to 10 % ( $\pm$ SE 0.3 and 2.8, respectively) (Fig. 5). Remarkably, turf cover remained high in manipulated samples due to the difficulty of scraping these organisms from CCAs (but with highly decreased potential to influence coral detectability).

Four months after turf canopy removal at PAB, estimates of coral cover did not change, with the same pattern holding for massive and encrusting corals, *Siderastrea* spp. and *M. hispida* (Table 2; Fig. 6). Cover estimates CCA increased significantly, but with no difference between treatments (Table 2; Fig. 6). Only *Agaricia* spp decreased significantly in manipulated plots. The model that best explained the amount of coral recruit detection included treatment and time. Number of recruits was higher in manipulated plots ( $n=360$ ) than in controls ( $n=183$ ). Before manipulation, the number of recruits detected in both areas was statistically identical (paired t-test  $t=-1.18$ ,  $df=18$ ,  $p=0.25$ ), but increased significantly after turf removal (paired t-test  $t=-5.05$ ,  $df=9$ ,  $p=0.0006$ ). After the four month lag, significant

increases in the number of recruits were recorded in both unmanipulated and manipulated plots (Fig. 7), with similar magnitudes (time and treatment interaction) (Table 2). Mortality was also similar (t test  $t=0.81$ ,  $df=18$ ,  $p=0.4$ ). Although the turf canopy did not affect recruitment, recruits within unmanipulated plots grew faster during the four-month sampling interval ( $0.23 \text{ cm}^2 \pm \text{SE } 0.03$ ) than those in the manipulated ones ( $0.19 \text{ cm}^2 \pm \text{SE } 0.03$ ) (Wilcoxon-Mann-Whitney test  $p=0.03$ ).

The short-term experiment did not reveal any coral cover loss in the five days after turf canopy removal (t-test paired  $t=-1.19$ ,  $p=0.3$ ). Despite the fact that 70% more coral recruits were detected immediately after turf removal, there were no detectable abundance changes after the five exposure days (t-test paired  $t=2.59$ ,  $p=0.06$ ) (Table 3). Effective quantum yield ( $F_v/F_m$ ) of corals and CCAs did not vary according to treatment (factorial ANOVA  $F_{0,86}=4.28$ ,  $p>0.05$ ), but varied with time, being higher after five days of manipulation than immediately after turf removal (factorial ANOVA  $F_{5, 07}=4.28$ ,  $p<0.05$ ) (Fig. 8). Temperature change during the five experiment days was minimal ( $27.9$ -  $28.1 \text{ }^\circ\text{C}$ ).

## Discussion

Understanding coral reef dynamics depends on relatively long (years to decades) series of data on benthic cover, fish biomass and water quality, among other variables. In addition, representative datasets are inevitably large, due to the high spatial heterogeneity of the traits associated with the state of reef ecosystems, such as the balance between fast-growing fleshy organisms and slow-growing biomineralizers (Jenkins & Uyá, 2016). Benthic photoquadrats are allegedly accurate and relatively cost-effective, being the most widely used sampling units for reef assessment and monitoring, either randomly placed or spatially fixed for repeated

measures. However, akin to any other ecological sampling (e.g. Krebs, 1999), photoquadrats do not provide unbiased community structure data. Biases arising from the bi-dimensional views delivered by photoquadrats have been recognized in *Acropora*- and *Porites*-dominated (branching/tabulate and massive corals, respectively) reefs, which encompass dissimilar understory assemblages (Goatley & Bellwood, 2011). Here, we confirm and expand Goatley & Bellwood's (2011) findings by exploring a phase-shifting coralline reef, i.e., spanning a more typical tropical Atlantic seascape characterized by macroalgae- and turf-dominated reefs with reduced coral diversity and cover (e.g. Silveira et al., 2015; Pawlik, Burkepile & Thurber, 2016).

There is considerable interoceanic variation in coral reef diversity and community structure (Goldberg, 2013), which is also mirrored by several functional properties at the ecosystem level (Norström et al., 2009; Roff & Mumby, 2012). Despite such disparity, reefs often encompass large carbonate-accreting areas with little coral (Chadwick & Morrow, 2011; Moura et al., 2016) that, by their turn, are subject to high temporal variability in algal cover (Mumby, 2009). Our first experiment contrasted a coastal unprotected site with high macroalgae cover (82-92%, mostly *Dictyota* spp.) with an offshore site with higher turf (54-81%) and coral cover (6-30%), as revealed by a standard photoquadrat sampling scheme. From this experiment we show that the “canopy effect” is not only ubiquitous, but is stronger at the coastal site. Massive and encrusting corals, as well as CCA and coral recruits, presented lower detectability in unmanipulated plots at the coastal site, while only CCA and coral recruits presented lower detectability in the offshore site. In both cases, probability of detection increased sharply after canopy removal. When macroalgae were removed from the coastal site, turf became the dominant benthic cover category, reaching a percent cover similar to that observed on unmanipulated plots of the offshore site (Fig. 2). Upon the

subsequent turf removal, CCA dominated benthic cover estimates (Fig. 2), and coral cover also increased significantly, revealing a complex layered structure that prevents the actual dominance by macroalgae.

Besides being poorly detected by photoquadrats, the layered benthic structure of reefs may also be related to the maintenance of critical ecosystem processes, such as mineralization by CCA (Reis et al., 2016), in coral-poor or even in phase-shifting reefs. Despite the measurable effects of climatic and local anthropogenic stressors over the Abrolhos' reef fish and benthic assemblages (Bruce et al., 2012; Francini-Filho et al., 2013; Silveira et al., 2015), the system is still largely under a positive carbonate balance derived from crustose coralline algae (CCA) and bryozoan accretion (Reis et al., 2016), and such processes may be compatible with high macroalgae and turf cover. On the other hand, it is unlikely that the observed macroalgal dominance is the baseline state of the unprotected coastal reefs (Francini-Filho & Moura, 2008b; Francini-Filho et al., 2013), but evidence that corals once dominated benthic assemblages is also lacking. Most herbivorous fish selectively graze turf algae at all sites, but are unable to remove macroalgae once they become established over large reef areas (Francini-Filho et al., 2010). The Abrolhos Reef decline is definitely associated to overfishing (e.g. Freitas, Abilhoa & da Costa Silva, 2011) and water quality loss (e.g. Bruce et al. 2012), but coral diseases (Francini-Filho et al., 2008) and changes in Dissolved Organic Carbon (DOC) processing by sponges and water-column microbes (Silveira et al., 2015) seem to play a major role in its degradation loop.

There is an overall lack of branching corals in the Southwestern Atlantic, which bears only three fire-coral (Hydrozoa) species of genus *Millepora* (Coni et al., 2012). No effects of macroalgae and turf removal were detected on branching corals, and only the cover estimates

of the most abundant massive and encrusting forms were affected by the macroalgae canopy at the coastal site. Massive colonies have been previously linked to high abundance of algae and high sedimentation, in Abrolhos (Francini-Filho et al., 2013) and elsewhere (Rachello-Dolmen & Cleary, 2007). For instance, Stimson (1985) reported similar abundances and growth rates of massive corals in shaded and unshaded areas. Conversely, branching corals are more sensitive to disturbance, predation, bleaching and competition (Loya et al., 2001; Haas, el-Zibdah & Wild, 2010; Bulleri et al., 2013)

Despite the overall low coral cover in the Atlantic, especially when compared with Indo-Pacific reefs, interactions between scleractinians and benthic algae are regarded as one of the core processes driving the dynamic equilibrium of coral reefs (Bruno & Selig, 2007; Dinsdale & Rohwer, 2011). Non-algal fast-growing organisms may become alternate dominants under stressful conditions (e.g. Nortsrom et al. 2009), but coral:macroalgae ratios are the most widely used metrics to assess reef health (Hughes, 1994). Coral and algae interactions, which are often mediated by macro and microorganisms (Dinsdale et al., 2008), represent a mainstream, controversial and long-standing theme in reef ecology (McCook, Jompa & Diaz-Pulido, 2001). For instance, the paradigmatic top-down control of macroalgae by herbivorous fish has been increasingly challenged by mounting evidence that bottom-up controls are often prominent (Burkepile et al., 2013; Russ et al., 2015; Pawlik, Burkepile & Thurber, 2016). Here, we provide further evidence that high macroalgae and turf cover may be associated with a significant (~20%) cover of scleractinians, and that high fleshy canopies cover may not be always associated to unhealthy understory CCA and coral assemblages. As recently emphasized by Russ et al. (2015), multiple benthic change controls should be consistently investigated, and the layered structure reported herein adds complexity to coral reef dynamic assessments in macroalgae- and turf-dominated systems.



The protection from predators, allelopathy and abrasion (e.g. Paul et al., 2007, 2011) by turf and macroalgal canopies imply in complex interactions and yet poorly understood tradeoffs. Algal turfs, as multi-specific assemblages of filamentous algae and microorganisms, especially cyanobacteria, may provide an equally broad spectrum of outcomes in neighboring organisms, depending on nutrient levels, temperature and other conditions that affect microbial activity (McCook, Jompa & Diaz-Pulido, 2001; Jompa & McCook, 2003b; Diaz-Pulido et al., 2010). For instance, coral recruitment has been negatively correlated with turf cover (e.g. Vermeij & Sandin, 2008; Arnold, Steneck & Mumby, 2010; Suzuki & Hayashibara, 2011). On the other hand, Jompa & McCook (1998) showed that *Sargassum* protected coral from bleaching by decreasing exposure to high temperatures and ultraviolet light, and Venera-Ponton et al. (2011) found that algae protected recruits against predation, although reducing coral growth. In our study, recruits were ubiquitous under macroalgal and turf canopies, with unexpected higher abundances in the coastal site. It seems that protection from predation (e.g. Venera-Ponton et al., 2011) was not responsible for such pattern, as our long- and short-term experiments showed that canopy removal did not increase mortality nor affect corals' photobiology. Indeed, recruits presented slightly lowered growth rates after canopy removal, which can be related to physiological stress or shifts for less efficient but stress-tolerant zooxanthellae (Jones & Berkelmans, 2010), and even to a more limited DOC and nutrient sourcing.

Small corals tend to be more successful competitors with algae than larger colonies (Barott et al., 2012b), probably because they are not reproductively active, concentrating energy in growth and competition (Soong, 1993). Canopy removal did not affect coral and CCA cover along the longer-term experiment, with the exception of the weedy coral *Agaricia agaricites*,

which decreased its relative cover. As this is a relatively short-living coral, it is expected that its decreased abundance does not represent a steady state of decreased dominance (Jenkins & Uya, 2016). CCA are usually considered competitively inferior to turf (Dethier, 1994), but our results suggest a more variable array of outcomes, depending of the environmental conditions. For instance, turf definitely provide protection against light irradiance (e.g., Melville & Connell, 2001), and may also benefit calcification under high  $p\text{CO}_2$  by increasing local pH via photosynthetic  $\text{CO}_2$  removal (Short et al., 2014). In polar ecosystems, photosynthetic activity of CCA decreased after canopy removal (Irving, Connell & Elsdon, 2004), but our study did not reveal such effects, as indicated by similar values of the effective quantum yield in both control and manipulated plots. In Abrolhos, the understory of phototrophic organisms is dominated by CCAs, which is consistent with their increased abundance in low light habitats (Steneck, 1986; Connell, 2003) and elevate participation in reef framework building (Reis et al., 2016).

The limitations of planar views of benthic reef assemblages are still poorly understood and their implications for monitoring community dynamics and processes (e.g. Goatley et al., 2016) deserves further attention. While photoquadrads shall remain as the standard reef monitoring sampling units, detectability assessments and manipulative experiments assessing the interaction between canopy-forming and understory species shall be carried out to support conclusions from longer-term (and costly) sampling programs and to correct negative biases on density and abundance assesments.

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## References

- Alvarez-Filip L., Dulvy NK., Gill J a., Côté IM., Watkinson AR. 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings. Biological sciences / The Royal Society* 276:3019–25.
- Amado-Filho GM., Moura RL., Bastos AC., Salgado LT., Sumida PY., Guth AZ., Francini-Filho RB., Pereira-Filho GH., Abrantes DP., Brasileiro PS., Bahia RG., Leal RN., Kaufman L., Kleypas J a., Farina M., Thompson FL. 2012. Rhodolith beds are major CaCO<sub>3</sub> bio-factories in the tropical South West Atlantic. *PloS one* 7:e35171.
- Antonius A., Afonso-Carillo J. 2001. Pneophyllum conicum killing reef-corals in Mauritius: A new Indo-Pacific syndrome? *Bulletin of Marine Science* 69:613–618.
- Arnold SN., Steneck RS., Mumby PJ. 2010. Running the gauntlet: Inhibitory effects of algal turfs on the processes of coral recruitment. *Marine Ecology Progress Series* 414:91–105.
- Barott KL., Smith JE., Dinsdale E., Hatay M., Sandin SA., Rohwer FL. 2009. Hyperspectral and physiological analyses of coral-algal interactions. *PloS one* 4:e8043.
- Barott KL., Rodriguez-Mueller B., Youle M., Marhaver KL., Vermeij M., Smith JE., Rohwer FL. 2012a. Microbial to reef scale interactions between the reef-building coral

- Montastraea annularis and benthic algae. *Proceedings. Biological sciences / The Royal Society* 279:1655–64.
- Barott KL., Williams GJ., Vermeij M., Harris J., Smith JE., Rohwer FL., Sandin SA. 2012b. Natural history of coral–algae competition across a gradient of human activity in the Line Islands. *Marine Ecology Progress Series* 460:1–12.
- Barott KL., Rohwer FL. 2012. Unseen players shape benthic competition on coral reefs. *Trends in microbiology* 20:621–8.
- Bates D., Mächler M., Bolker BM., Walker SC. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Beer S., Ilan M., Eshel A., Weil A., Brickner I. 1998. Use of pulse amplitude modulated ( PAM ) fluorometry for in situ measurements of photosynthesis in two Red Sea faviid corals. *Marine Biology* 131:607–612.
- Beer S., Axelsson L. 2004. Limitations in the use of PAM fluorometry for measuring photosynthetic rates of macroalgae at high irradiances. *European Journal of Phycology* 39:1–7.
- Bruce T., Meirelles PM., Garcia G., Paranhos R., Rezende CE., de Moura RL., Filho R-F., Coni EOC., Vasconcelos AT., Amado-Filho GM., Hatay M., Schmieder R., Edwards R., Dinsdale E., Thompson FL. 2012. Abrolhos bank reef health evaluated by means of water quality, microbial diversity, benthic cover, and fish biomass data. *PloS one* 7:e36687.
- Bruno JF., Precht WF., Vroom PS., Aronson RB. 2014. Coral reef baselines: how much macroalgae is natural? *Marine pollution bulletin* 80:24–9.

- Bruno JF., Selig ER. 2007. Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS one* 2:e711.
- Bulleri F., Couraudon-Reále M., Lison De Loma T., Claudet J. 2013. Variability in the effects of macroalgae on the survival and growth of corals: The consumer connection. *PLoS ONE* 8:e79712.
- Burkepile DE., Allgeier JE., Shantz A a., Pritchard CE., Lemoine NP., Bhatti LH., Layman C a. 2013. Nutrient supply from fishes facilitates macroalgae and suppresses corals in a Caribbean coral reef ecosystem. *Scientific Reports* 3:1493.
- Cetz-Navarro NP., Espinoza-Avalos J., Hernández-Arana H a., Carricart-Ganivet JP. 2013. Biological responses of the coral *Montastraea annularis* to the removal of filamentous turf algae. *PLoS one* 8:e54810.
- Cetz-Navarro NP., Carpizo-Ituarte EJ., Espinoza-Avalos J., Chee-Barragán G. 2015. The Effect of Filamentous Turf Algal Removal on the Development of Gametes of the Coral *Orbicella annularis*. *Plos One* 10:e0117936.
- Chadwick N., Morrow K. 2011. Competition among sessile organisms on coral reefs. In: Dubinsky Z, Stambler N eds. *Coral reefs: an ecosystem in transition*. New York: Springer, 347–371.
- Clarke KR., Warwick RM. 2001. *Change in marine communities - An approach to statics analysis and interpretation*. Plymouth: PRIMER-E ltd.
- Coni EOC., Ferreira CM., Moura RL., Meirelles PM., Kaufman L., Francini-Filho RB. 2012. An evaluation of the use of branching fire-corals (*Millepora* spp.) as refuge by reef fish in the Abrolhos Bank, eastern Brazil. *Environmental Biology of Fishes* 96:45–55.

- Connell SD. 2003. The monopolization of understory habitat by subtidal encrusting coralline algae : a test of the combined effects of canopy-mediated light and sedimentation. *Marine Biology* 142:1065–1071.
- Connell SD., Foster M., Airoidi L. 2014. What are algal turfs? Towards a better description of turfs. *Marine Ecology Progress Series* 495:299–307.
- Dethier MN. 1994. The ecology of intertidal algal crusts: variation within a functional group. *Journal of Experimental Marine Biology and Ecology* 177:37–71.
- Diaz-Pulido G., Harii S., McCook LJ., Hoegh-Guldberg O. 2010. The impact of benthic algae on the settlement of a reef-building coral. *Coral Reefs* 29:203–208.
- Dinsdale E., Pantos O., Smriga S., Edwards R a., Angly F., Wegley L., Hatay M., Hall D., Brown E., Haynes M., Krause L., Sala E., Sandin SA., Thurber RV., Willis BL., Azam F., Knowlton N., Rohwer FL. 2008. Microbial ecology of four coral atolls in the Northern Line Islands. *PloS one* 3.
- Dinsdale E., Rohwer F. 2011. Fish or germs? Microbial dynamics associated with changing trophic structures on coral reefs. In: Dubinsky Z, Stambler N eds. *Coral Reefs: An Ecosystem in Transition*. Springer, 231–240.
- Dubinsky Z., Stambler N. 2011. *Cora reefs: An Ecosystem in Transition*. Springer Netherlands.
- Fowler-Walker MJ., Gillanders BM., Connell SD., Irving AD. 2005. Patterns of association between canopy-morphology and understory assemblages across temperate Australia. *Estuarine, Coastal and Shelf Science* 63:133–141.
- Francini-Filho RB., Moura RL., Thompson FL., Reis RM., Kaufman L., Kikuchi RKP., Leão

- ZM a N. 2008. Diseases leading to accelerated decline of reef corals in the largest South Atlantic reef complex (Abrolhos Bank, eastern Brazil). *Marine pollution bulletin* 56:1008–14.
- Francini-Filho RB., Ferreira CM., Coni EOC., De Moura RL., Kaufman L. 2010. Foraging activity of roving herbivorous reef fish (Acanthuridae and Scaridae) in eastern Brazil: influence of resource availability and interference competition. *Journal of the Marine Biological Association of the United Kingdom* 90:481–492.
- Francini-Filho RB., Coni EOC., Meirelles PM., Amado-Filho GM., Thompson FL., Pereira-Filho GH., Bastos AC., Abrantes DP., Ferreira CM., Gibran FZ., Güth AZ., Sumida PYG., Oliveira NL., Kaufman L., Minte-Vera C V., Moura RL. 2013. Dynamics of coral reef benthic assemblages of the Abrolhos Bank, eastern Brazil: inferences on natural and anthropogenic drivers. *PloS one* 8:e54260.
- Francini-Filho RB., Moura RL. 2008a. Dynamics of fish assemblages on coral reefs subjected to different management regimes in the Abrolhos Bank , eastern Brazil. *Aquatic Conservation: Marine and Freshwater Ecosystems* 18:1166–1179.
- Francini-Filho RB., Moura RL. 2008b. Evidence for spillover of reef fishes from a no-take marine reserve: An evaluation using the before-after control-impact (BACI) approach. *Fisheries Research* 93:346–356.
- Freitas MO., Abilhoa V., da Costa Silva GH. 2011. Feeding ecology of *Lutjanus analis* (Teleostei: Lutjanidae) from Abrolhos Bank, Eastern Brazil. *Neotropical Ichthyology* 9:411–418.
- Goatley CHR., Bonaldo RM., Fox RJ., Bellwood DR. 2016. Sediments and herbivory as sensitive indicators of coral reef degradation. *Ecology and Society* 21:29.

- Goatley CHR., Bellwood DR. 2011. The roles of dimensionality, canopies and complexity in ecosystem monitoring. *PloS one* 6:e27307.
- Goldberg W. 2013. *The Biology of Reefs and Reef Organisms*. University of Chicago Press.
- Graham NAJ. 2014. Habitat complexity: Coral structural loss leads to fisheries declines. *Current Biology* 24:R359–R361.
- Haas A., el-Zibdah M., Wild C. 2010. Seasonal monitoring of coral-algae interactions in fringing reefs of the Gulf of Aqaba, Northern Red Sea. *Coral Reefs* 29:93–103.
- Hacker SD., Steneck RS. 1990. Habitat Architecture and the Abundance and Body-Size-Dependent Habitat Selection of a Phytal Amphipod. *Ecology* 71:2269–2285.
- Harrington L., Fabricius K., De'ath G., Negri A. 2004. Recognition and Selection of Settlement Substrata Determine Post-Settlement Survival in Corals. *Ecology* 85:3428–3437.
- Hennige SJ., Smith DJ., Perkins R., Consalvey M., Paterson D., Suggett D. 2008. Photoacclimation, growth and distribution of massive coral species in clear and turbid waters. *Marine Ecology Progress Series* 369:77–88.
- Hennige SJ., Smith DJ., Walsh S-J., McGinley MP., Warner ME., Suggett DJ. 2010. Acclimation and adaptation of scleractinian coral communities along environmental gradients within an Indonesian reef system. *Journal of Experimental Marine Biology and Ecology* 391:143–152.
- Heyward AJ., Negri A p. 1999. Natural inducers for coral larval metamorphosis. *Coral Reefs* 18:273–279.
- Hill J., Wilkinson C. 2004. *Methods for Ecological Monitoring of Coral Reefs*. Townsville.



- Hughes TP. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean Coral Reef. *Science* 265:1547–1551.
- Hughes TP., Rodrigues MJ., Bellwood DR., Ceccarelli D., Hoegh-Guldberg O., McCook LJ., Molschaniwskyj N., Pratchett MS., Steneck RS., Willis B. 2007. *Phase shifts, herbivory, and the resilience of coral reefs to climate change*.
- Iglesias-Prieto R., Beltrán VH., LaJeunesse TC., Reyes-Bonilla H., Thomé PE. 2004. Different algal symbionts explain the vertical distribution of dominant reef corals in the eastern Pacific. *Proceedings. Biological sciences / The Royal Society* 271:1757–63.
- Irving AD., Connell SD., Elsdon TS. 2004. Effects of kelp canopies on bleaching and photosynthetic activity of encrusting coralline algae. *Journal of Experimental Marine Biology and Ecology* 310:1–12.
- Irving AD., Connell SD., Gillanders BM. 2004. Local complexity in patterns of canopy-benthos associations produces regional patterns across temperate Australasia. *Marine Biology* 144:361–368.
- Jenkins SR., Uyá M. 2016. Temporal scale of field experiments in benthic ecology. *Marine Ecology Progress Series* 547:273–286.
- Jompa J., McCook LJ. 1998. Sargassum canopy decreases coral bleaching on inshore reefs. *Reef Res* 8.
- Jompa J., McCook LJ. 2002. Effects of competition and herbivory on interactions between a hard coral and a brown alga. *Journal of Experimental Marine Biology and Ecology* 271:25–39.
- Jompa J., McCook LJ. 2003a. Contrasting effects of turf algae on corals: Massive *Porites* spp.

- are unaffected by mixed-species turfs, but killed by the red alga *Anotrichium tenue*. *Marine Ecology Progress Series* 258:79–86.
- Jompa J., McCook LJ. 2003b. Coral-algal competition: macroalgae with different properties have different effects on corals. *Marine Ecology Progress Series* 258:87–95.
- Jones A., Berkelmans R. 2010. Potential costs of acclimatization to a warmer climate: growth of a reef coral with heat tolerant vs. sensitive symbiont types. *PloS one* 5:e10437.
- Kohler KE., Gill SM. 2006. Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Computers & Geosciences* 32:1259–1269.
- Krebs CJ. 1999. *Ecological Methodology*. University of British Columbia, Vancouver: Benjamin/Cummings.
- Littler M., Littler D., Taylor P. 1983. Evolutionary strategies in a tropical barrier reef system: functional-form groups of marine macroalgae. *Journal of Phycology* 19:229–237.
- Loya Y., Sakai K., Yamazato K., Nakano Y., Sambali H., van Woesik R. 2001. Coral bleaching: the winners and the losers. *Ecology Letters* 4:122–131.
- McCook LJ., Jompa J., Diaz-Pulido G. 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19:400–417.
- Melville a. J., Connell SD. 2001. Experimental effects of kelp canopies on subtidal coralline algae. *Austral Ecology* 26:102–108.
- Migné A., Golléty C., Davoult D. 2015. Effect of canopy removal on a rocky shore community metabolism and structure. *Marine Biology* 162:449–457.
- Morse DE., Hooker N., Morse ANC., Jensen A. 1988. Control of larval metamorphosis and

recruitment in sympatric agariciid corals. *Journal of experimental marine biology ecology* 116:193–217.

Moura RL., Secchin NA., Amado-Filho GM., Francini-Filho RB., Freitas MO., Minte-Vera CV., Teixeira JB., Thompson FL., Dutra GF., Sumida PYG., Guth AZ., Lopes RM., Bastos AC. 2013. Spatial patterns of benthic megahabitats and conservation planning in the Abrolhos Bank. *Continental Shelf Research* 70:109–117.

Moura RL., Amado-Filho GM., Moraes FC., Brasileiro PS., Salomon PS., Mahiques MM., Bastos AC., Almeida MG., Silva JM., Araujo BF., Brito FP., Rangel TP., Oliveira BC V., Bahia RG., Paranhos RP., Dias RJS., Siegle E., Figueiredo AG., Pereira RC., Leal C V., Hajdu E., Asp NE., Gregoracci GB., Neumann-Leitao S., Yager PL., Francini-Filho RB., Froes A., Campeao M., Silva BS., Moreira APB., Oliveira L., Soares AC., Araujo L., Oliveira NL., Teixeira JB., Valle RAB., Thompson CC., Rezende CE., Thompson FL. 2016. An extensive reef system at the Amazon River mouth. *Science Advances* 2:e1501252.

Mumby PJ. 2009. Phase shifts and the stability of macroalgal communities on Caribbean coral reefs. *Coral Reefs* 28:761–773.

Norström A V., Nyström M., Lokrantz J., Folke C. 2009. Alternative states on coral reefs: Beyond coral-macroalgal phase shifts. *Marine Ecology Progress Series* 376:293–306.

Pandolfi JM., Bradbury RH., Sala E., Hughes TP., Bjorndal K a., Cooke RG., McArdle D., McClenachan L., Newman MJH., Paredes G., Warner RR., Jackson JBC. 2003. *Global trajectories of the long-term decline of coral reef ecosystems.*

Paul VJ., Arthur KE., Ritson-Williams R., Ross C., Sharp K. 2007. Chemical defenses: from compounds to communities. *The Biological bulletin* 213:226–51.

- Paul VJ., Kuffner IB., Walters LJ., Ritson-Williams R., Beach KS., Becerro MA. 2011. Chemically mediated interactions between macroalgae *Dictyota* spp. and multiple life-history stages of the coral *Porites astreoides*. *Marine Ecology Progress Series* 426:161–170.
- Pawlik JR., Burkepile DE., Thurber RV. 2016. A Vicious Circle? Altered Carbon and Nutrient Cycling May Explain the Low Resilience of Caribbean Coral Reefs. *BioScience* XX:1–7.
- Price NN. 2010. Habitat selection , facilitation , and biotic settlement cues affect distribution and performance of coral recruits in French Polynesia. *Oecologia* 163:747–758.
- R Core Team (2012).R: A language and environment for statistical computing
- Rachello-Dolmen PG., Cleary DFR. 2007. Relating coral species traits to environmental conditions in the Jakarta Bay/Pulau Seribu reef system, Indonesia. *Estuarine, Coastal and Shelf Science* 73:816–826.
- Ralph PJ., Schreiber U., Gademann R., Kühl M., Larkum AWD. 2005. Coral photobiology studied with a new imaging pulse amplitude modulated fluorometer. *Journal of Phycology* 41:335–342.
- Ralph PJ., Gademann R. 2005. Rapid light curves: A powerful tool to assess photosynthetic activity. *Aquatic Botany* 82:222–237.
- Rasher DB., Stout EP., Engel S., Kubanek J., Hay ME. 2011. Macroalgal terpenes function as allelopathic agents against reef corals. *Proceedings of the National Academy of Sciences of the United States of America* 108:17726–17731.
- Reis VM dos., Karez CS., Mariath R., de Moraes FC., de Carvalho RT., Brasileiro PS., Bahia

- R da G., Lotufo TM da C., Ramalho LV., de Moura RL., Francini-Filho RB., Pereira-Filho GH., Thompson FL., Bastos AC., Salgado LT., Amado-Filho GM. 2016. Carbonate Production by Benthic Communities on Shallow Coralgal Reefs of Abrolhos Bank, Brazil. *Plos One* 11:e0154417.
- Roff G., Mumby PJ. 2012. Global disparity in the resilience of coral reefs. *Trends in Ecology and Evolution* 27:404–413.
- Russ GR., Questel SLA., Rizzari JR., Alcala AC. 2015. The parrotfish–coral relationship: refuting the ubiquity of a prevailing paradigm. *Marine Biology* 162:2029–2045.
- Sandin SA., Smith JE., DeMartini EE., Dinsdale E., Donner SD., Friedlander AM., Konotchick T., Malay M., Maragos JE., Obura D., Pantos O., Paulay G., Richie M., Rohwer FL., Schroeder RE., Walsh S., Jackson JBC., Knowlton N., Sala E. 2008. Baselines and Degradation of Coral Reefs in the Northern Line Islands. *PLoS ONE* 3:e1548.
- Short J., Kendrick GA., Falter J., McCulloch MT. 2014. Interactions between filamentous turf algae and coralline algae are modified under ocean acidification. *Journal of Experimental Marine Biology and Ecology* 456:70–77.
- Silveira CB., Silva-Lima AW., Francini-Filho RB., Marques JSM., Almeida MG., Thompson CC., Rezende CE., Paranhos R., Moura RL., Salomon PS., Thompson FL. 2015. Microbial and sponge loops modify fish production in phase-shifting coral reefs. *Environmental Microbiology* 17:3832–3846.
- Soong K. 1993. Colony size as a species character in massive reef corals. *Coral Reefs* 12:7.
- Spalding MD., Ravilious C., Green EP. 2001. *World Atlas of Coral Reefs*. University of California Press, Berkeley, USA: Prepared at The UNEP World Conservation.

Monitoring Center.

Steneck RS. 1986. The ecology of coralline algal crusts: Convergent Patterns and Adaptive Strategies. *Annual Review of Ecology and Systematics* 17:273–303.

Stimson J. 1985. The effect of shading by the table coral *Acropora hyacinthus* on understory corals. *Ecology* 66:40–53.

Suggett DJ., Kikuchi RKP., Oliveira MDM., Spanó S., Carvalho R., Smith DJ. 2012. Photobiology of corals from Brazil's near-shore marginal reefs of Abrolhos. *Marine Biology* 159:1461–1473.

Suzuki G., Hayashibara T. 2011. Do epibenthic algae induce species-specific settlement of coral larvae? *Journal of the Marine Biological Association of the United Kingdom* 91:677–683.

Tebben J., Motti CA., Siboni N., Tapiolas DM., Negri AP., Schupp PJ., Kitamura M., Hatta M., Steinberg PD., Harder T. 2015. Chemical mediation of coral larval settlement by crustose coralline algae. *Scientific Reports* 5:1–11.

Venera-Ponton D., Diaz-Pulido G., McCook LJ., Rangel-Campo a. 2011. Macroalgae reduce growth of juvenile corals but protect them from parrotfish damage. *Marine Ecology Progress Series* 421:109–115.

Vermeij M., van Moorselaar I., Engelhard S., Hörnlein C., Vonk SM., Visser PM. 2010. The effects of nutrient enrichment and herbivore abundance on the ability of turf algae to overgrow coral in the Caribbean. *PloS one* 5:e14312.

Vermeij M., Sandin SA. 2008. Density-dependent settlement and mortality structure the earliest life phases of a coral population. *Ecology* 89:1994–2004.

Vroom PS., Page KN., Kenyon JC., Brainard RE. 2006. Algae-dominated reefs. *American scientist* 94:430–437.

Williams SL., Carpenter RC. 1997. Grazing effects on nitrogen fixation in coral reef algal turfs. *Marine Biology* 130:223–231.

Zuur AF., Ieno EN., Smith GM. 2007. *Analysing Ecological Data*. New York, NY, USA: Springer Science + Business Media.

Figures and tables



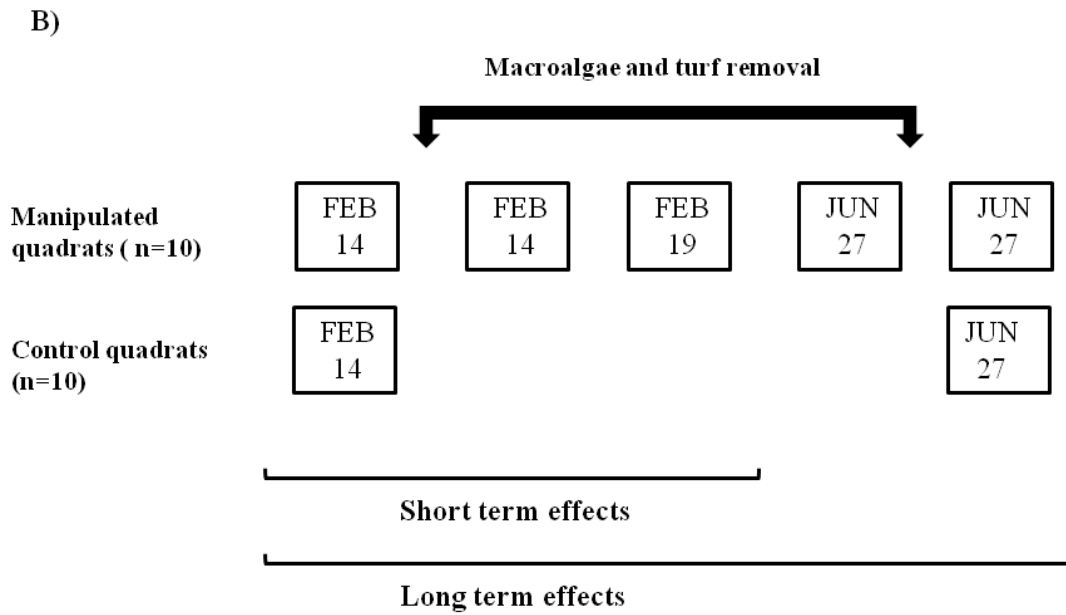


Figure 1. Schematic representation of the experiments. A) Canopy effect in benthic cover estimates from photoquadrats obtained at Pedra de Leste (PLESTE, coastal) and Parcel dos Abrolhos (PAB, offshore), showing subunits before manipulation, after macroalgae removal (PAB had inexpressive macroalgae cover) and after turf removal. B) Short- (5 day lag) and long-term (4 months) evaluation of canopy removal carried out at PAB.



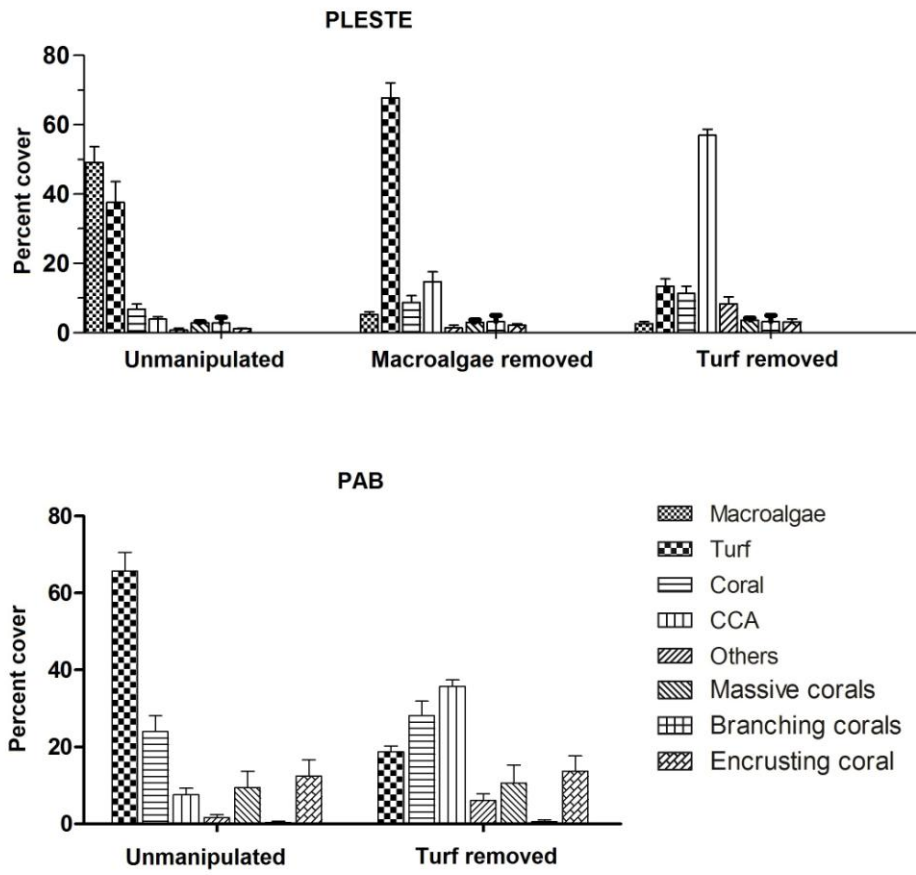


Figure 2. Participation of major benthic categories (mean  $\pm$  SE) in photoquadrat estimates from the coastal (PLESTE) and offshore (PAB) sites, in unmanipulated and manipulated plots.

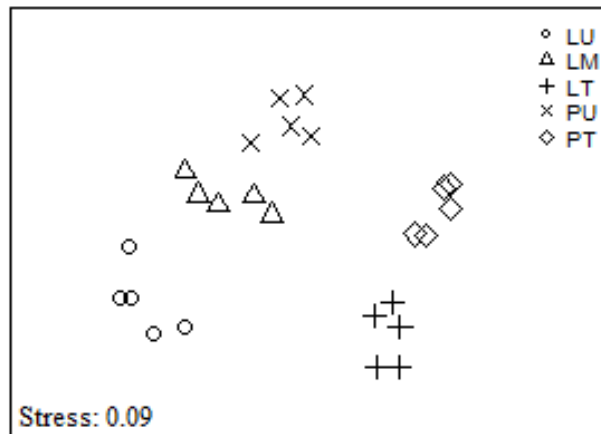


Figure 3. Multidimensional scaling (MDS) with percent cover estimates from both sites and different treatments.

LU: PLESTE (coastal) unmanipulated, LM: PLESTE after macroalgae removal, LT: PLESTE after turf removal,

PU: PAB (offshore) unmanipulated, PT: PAB after turf removal.

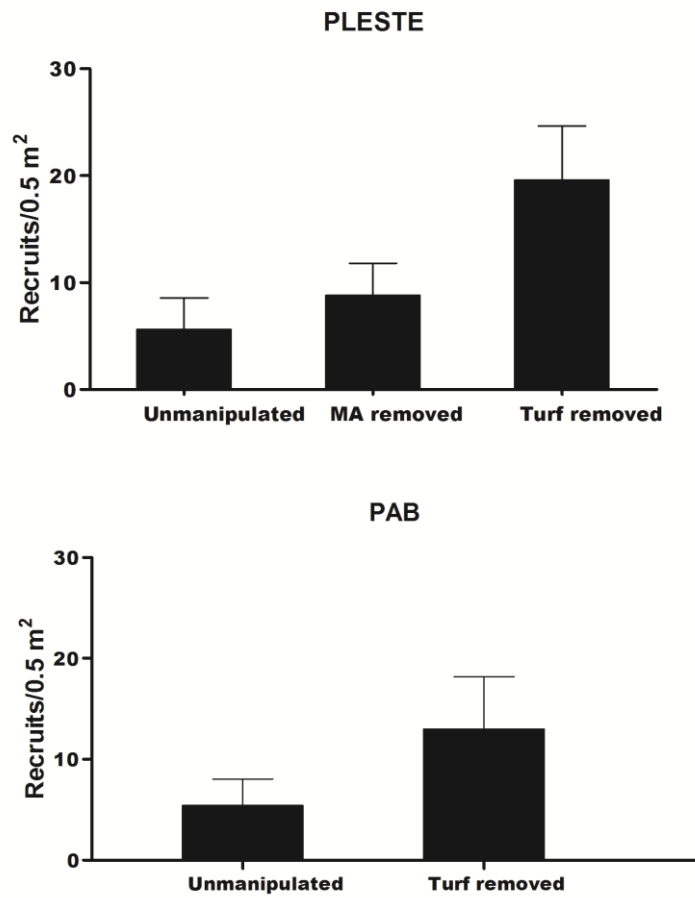


Figure 4. Coral recruit counts in unmanipulated and manipulated plots at the coastal (PLESTE) and offshore (PAB) sites (bars: SE). MA = macroalgae.

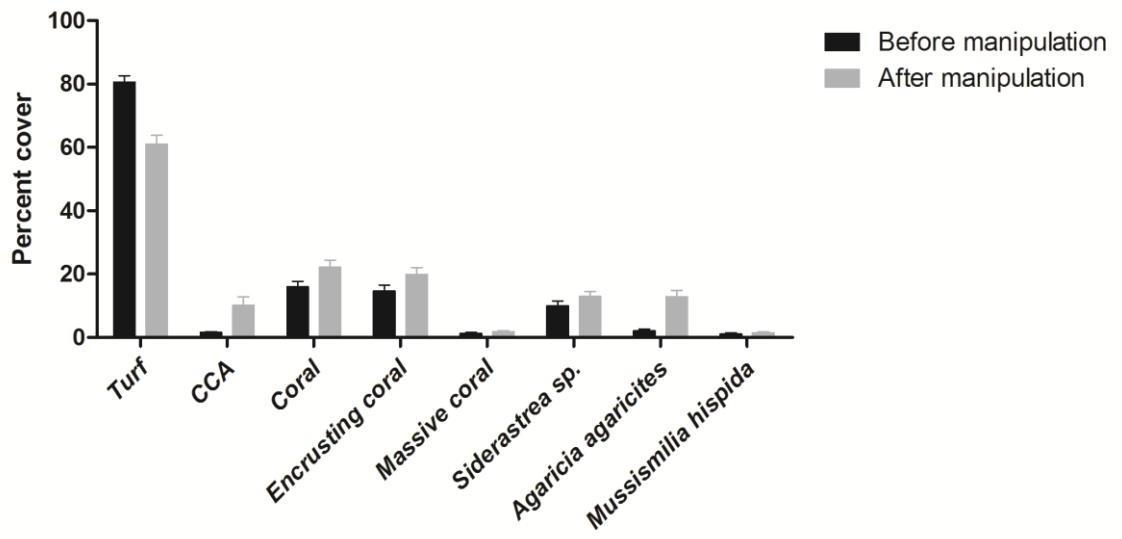


Figure 5. Benthic cover (mean  $\pm$  SE) before and after manipulation at the offshore site (PAB).

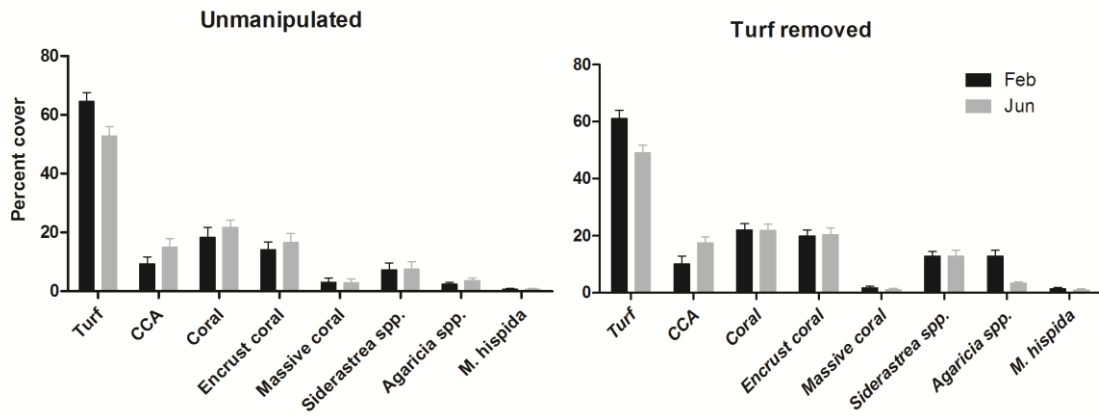


Figure 6. Benthic cover estimates (mean  $\pm$ SE) at the offshore site (PAB), spanning control and manipulated plots sampled immediately after turf removal (Feb) and after four months (Jun).

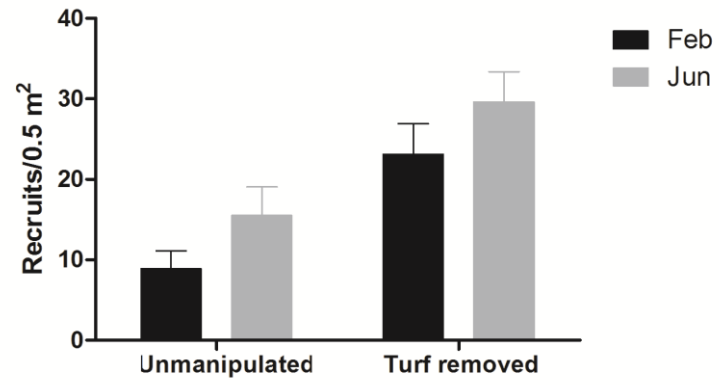


Figure 7. Abundance of coral recruits in each treatment at the offshore site (PAB) (bars= SE).

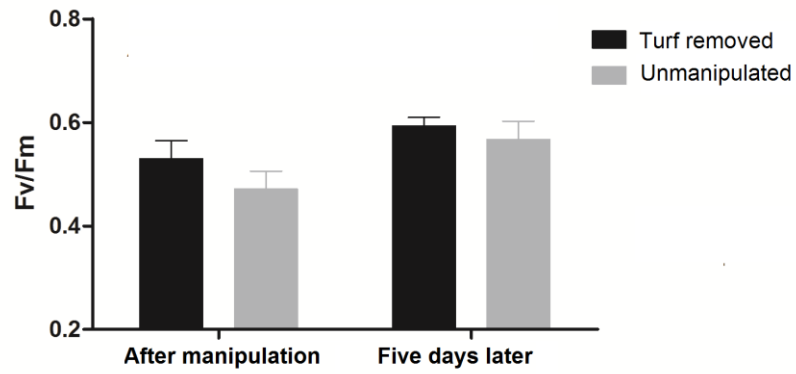


Figure 8. Effective quantum yield of corals and CCAs after manipulation and five days later in manipulated and control samples (bars=SE)

Table 1. Probability of detection for different benthic organisms according to treatment and location. Asterisks denote significant differences between the coastal and offshore sites. Benthic categories with asterisks are those with significant differences between treatments. ( $\pm$  SE) (\* $p < 0.05$  \*\* $p < 0.001$  , \*\*\* $p < 0.0001$ ).

Categories	Site		
	PLESTE		PAB
	Unmanipulated	Macroalgae removed	Unmanipulated
Branching	62% $\pm$ 0.04	69% $\pm$ 0.03*	95% $\pm$ 0.04
Massive***	78% $\pm$ 0.02	81% $\pm$ 0.24*	87% $\pm$ 0.12
Encrusting***	42% $\pm$ 0.02	52% $\pm$ 0.03	78% $\pm$ 0.01
CCA***	7% $\pm$ 0.003	21% $\pm$ 0.006***	20% $\pm$ 0.006
Recruits	28% $\pm$ 0.4	45% $\pm$ 0.05	41% $\pm$ 0.06



Table 2. Linear mixed models explaining the amount and cover of different benthic organisms. Values are ranked and correspond to the Akaike Information Criterion (AIC)

Categories	Time	Treatment	Time*Treatment	Null model
Recruits	78.5	94.6	75.68	99.58
CCA	255.96	274.9	258.49	270.76
Coral	232.7	233.47	232.51	229.42
Massive corals	203.15	206.16	204.18	202.82
Encrusting corals	229.48	231.1	228.69	228.64
<i>Siderastrea</i> spp.	218.28	213.72	216.39	213.46
<i>Agaricia</i> spp.	195.91	200.2	198.96	197.32
<i>M. hispida</i>	181.15	182.02	184.05	179.87

Table 3. Coral recruit density (recruits/0.5m<sup>2</sup>) and coral and CCA cover recorded during the short-term experiment in the offshore reef (PAB).

Organisms	Treatment		
	Unmanipulated	After turf removal	Five days after manipulation
Recruits	9.5 (± SE 6.5)	16.2 (± SE 6.5)	15 (± SE 5.9)
Coral	16.85% (± SE 2.27)	23.95% (± SE 2.02)	24.90% (± SE 2.37)
CCA	1.4 % 1 (± SE 0.37)	12.74 % (± SE 1.92)	4.02% (± SE 0.53)

## CONCLUSÃO

Demonstramos aqui que, nos recifes do Atlântico Sul, a formação de dosséis de macroalgas e turf têm o potencial de influenciar significativamente as estimativas da cobertura bêntica. Além disso, o efeito dossel mostrou ser contexto-dependente, i.e. dependente da cobertura predominante do substrato que, por sua vez, é influenciada pelos gradientes ambientais e regimes de manejo. A comunidade subjacente ao dossel é predominantemente viva e com expressiva participação de corais, CCA e recrutas de corais, organismos chave no ecossistema recifal. Nesse contexto, concluímos que uma parte importante da comunidade bêntica é sistematicamente subestimada, o que pode prejudicar as interpretações acerca do status do recife, visto que sistemas recifais com dominância de macroalgas e turf, como os de Abrolhos, podem abrigar assembleias subjacentes de corais e algas calcárias saudáveis. O dossel pode desempenhar um papel fundamental na construção dos recifes, fornecendo alimento e abrigo para outros organismos, além de facilitar a manutenção de processos ecossistêmicos críticos. Considerando a vitalidade observada sob o dossel, estes recifes seriam diferentes em termos de diversidade e estrutura de um sistema coberto por algas onde corais não estariam presentes. Além disso, os processos ecológicos essenciais como competição e facilitação entre algas e corais tendem a ser subestimados ou incompreendidos, devido a métodos de amostragem que produzem um registro planar da cobertura bêntica. Dada à falta de métodos de amostragem acurados, não destrutivos e de baixo custo, sugerimos cautela na interpretação dos padrões e processos nas áreas afetadas pelo efeito dossel, ou seja, praticamente todas as áreas de recifes do planeta.