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FELIPE DE VARGAS RIBEIRO

ESTRESSES ECOLÓGICOS MULTIPLOS SUSTENTADOS POR CORAIS DO BANCO DOS ABROLHOS, BA, BRASIL.

MULTIPLE ECOLOGICAL STRESS SUSTAINED BY CORALS OF THE ABROLHOS BANK, BA, BRAZIL.

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Tese apresentada ao Programa de Pós-Graduação em Dinâmica dos Oceanos e da Terra do Departamento de Geologia do Instituto de Geociências da Universidade Federal Fluminense, como requisito parcial à obtenção do título de Doutor em Dinâmica dos Oceanos e da Terra.

Orientadores: RENATO CRESPO PEREIRA
PAULO SÉRGIO SALOMON

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BANCA EXAMINADORA

_____
Prof. Renato Crespo Pereira, Dr. (Orientador)
Universidade Federal Fluminense

_____
Prof. Paulo Sergio Salomon, Dr. (Orientador)
Universidade Federal do Rio de Janeiro

_____
Prof. Ricardo Coutinho, Dr.
Instituto de Estudos do Mar Almirante Paulo Moreira

_____
Prof. Bernardo Antônio Perez da Gama, Dr.
Universidade Federal Fluminense

_____
Daniela Bueno Sudatti, Dra.
Instituto de Pesquisas Jardim Botânico do Rio de Janeiro

_____
Profa. Betina Kozlowsky-Suzuki, Dra.
Universidade Federal do Estado do Rio de Janeiro

_____
Prof. Gustavo Muniz Dias, Dr.
Universidade Federal do ABC

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"On the time and space scales relevant to coral reef management, it is not appropriate to make decisions based on a presumption that a specific reef or system of reefs has 'ability always to regenerate after catastrophes' (Davies, 1988). Neither is it correct to assume that a degraded reef will remain so forever, or that those reefs which do regenerate will do so in time scales which are convenient to human users of the reef." (T.J. Done, 1992)

RESUMO

O maior e mais rico sistema de recifes coralinos do Atlântico Sul, o Banco dos Abrolhos, vêm sofrendo com impactos periódicos por florações de cianobactérias e anomalias térmicas. Os recifes de coral, em sua grande maioria, tiveram a estrutura de sua comunidade alterada em épocas recentes, frequentemente envolvendo alternâncias de dominância de corais pétreos de crescimento lento para invertebrados bênticos de crescimento rápido e fotossintetizantes efêmeros. A generalidade de modelos de declínio de recifes de coral ainda precisa ser verificada em recifes de zonas túrbidas. Aqui, documentamos o resultado de interações entre uma espécie de coral endêmica à costa brasileira, e ameaçada (*Mussismilia braziliensis*), e os organismos mais abundantes em contato com a mesma. O estudo foi baseado numa série de longo prazo (2006-16) de amostragem de sítios costeiros não-protegidos, e protegidos fora da costa, por meio da amostragem de quadrados fixos. Além disso, foram descritos exemplares de cianobactérias filamentosas bentônicas oriundos dos recifes de Abrolhos através de caracteres morfológicos e sequenciamento do marcador 16S rDNA. Também, foram investigados contatos naturais entre cianobactéria e a construtora de recifes *M. braziliensis*, e os potenciais efeitos alelopáticos de cianobactérias sobre esta espécie através de bioensaios em laboratório utilizando exsudados de isolados, cultivados a partir de coletas de campo, e incubados com *Symbiodinium* sp. obtidos de *M.braziliensis*. O extrato bruto de cianobactéria foi testado em bioensaios similares. Ainda, foram resumidos os eventos pretéritos de branqueamento no Atlântico Sudoeste Tropical (do inglês: South-western Atlantic - SWA), e as tendências de branqueamento de acordo com: taxon, distância da costa e habitat, nos recifes de Abrolhos, foram exploradas. Os contatos coral-alga predominaram perto da costa, enquanto que os contatos com cianobactéria e *turf* eram dominantes fora da costa. Uma tendência geral de crescimento de corais foi detectada de 2009 em diante nos sítios costeiros, enquanto uma retração no tecido vivo de corais foi observada fora da costa. Turbidez (+) e cianobactéria (-) foram os melhores preditores do crescimento de corais. O decréscimo da turbidez e da abundância de macroalgas nos sítios mais afastados, sugere um efeito positivo direto da turbidez sobre o crescimento de corais, ou um efeito indireto relacionado com a maior cobertura de macroalgas foliosas perto da costa, restringindo a abundância de cianobactéria. De acordo com os nossos resultados, exsudados e o extrato orgânico reduziram significativamente a contagem de células do simbionte quando comparado ao controle. A inibição do aparato fotossintético de endossimbiontes *in-hospite* foi detectada no contato com filamentos no campo, mas o nosso desenho amostral não permite a separação dos efeitos alelopáticos potenciais de sombreamento. 16S rDNA identificaram os filamentos morfologicamente similares a *Lyngbya majuscula* como *Moorea producens, Moorea bouillonii* e *Okeania erythroflocculosa*, a primeira ocorrência destes táxons para o Atlântico Sul. O branqueamento persistiu ao longo de dois verões austrais (2016-17) e foi registrado em detalhe em Fevereiro, Maio, Junho e Outubro de 2016, e Março de 2017. A prevalência de branqueamento foi maior nos recifes rasos costeiros e fora da costa do que nos recifes mesofóticos mais profundos. Todas as espécies de coral branquearam, entretanto houveram tendências taxonômicas e relativas ao habitat na prevalência do branqueamento. Diversas espécies branquearam menos nos locais e habitats onde sua abundância era menor. Nossos resultados adicionam às evidências recentes de que recifes profundos fornecem refúgio parcial para algumas espécies de coral e que recifes de zonas túrbidas podem ser menos suscetíveis a estresse climático devido ao sombreamento, e aos altos níveis de heterotrofia e adaptações locais. Finalmente, desafiamos a ideia de a alta cobertura de macroalga estar sempre associada à saúde comprometida de corais, e elucidamos os mecanismos de supressão de tecido coralíneo por cianobactérias bentônicas em Abrolhos.

Palavras-chave: Recife de coral, Cianobactéria,Temperatura da Superfície do Mar, Recifes de zona túrbida, Abrolhos, Brasil, Turbidez, *Symbiodinium*, Alelopatia, Alga *Turf*

ABSTRACT

The richest coralline reef system in the South Atlantic, the Abrolhos Bank, has been suffering from periodic impacts by cyanobacteria outbreaks and thermic anomalies. Most coral reefs have recently experienced changes in benthic community structure, often involving dominance shifts from slow-growing hard corals to fast-growing benthic invertebrates and ephemerous photosynthesizers. In addition, the generality of coral reef decline models still needs to be verified on turbid-zone reefs. Here, we documented the outcome of interactions between an endangered Brazilian-endemic coral (*Mussismilia braziliensis*) and its most abundant contacting organisms. The present study was based on a long-term (2006-16) series of fixed photoquadrats sampled in a coastal unprotected reef and in an offshore protected site. In the present study we describe conspicuous benthic filamentous cyanobacteria of Abrolhos reefs through morphological traits and 16S rDNA sequencing. Also, we investigate natural contacts between cyanobacteria and the reef builder *M.braziliensis,* and the potential allelopathic effects of cyanobacteria over these species, through laboratory bioessays with exudates from cultured isolates of field collections, incubated with *Symbiodinium* sp. obtained from *M.braziliensis*. The crude extract of cyanobacteria was tested in similar bioessays. Previous bleaching events in the tropical South-western Atlantic Ocean (SWA) were summarized and the taxonomic, cross-shelf and habitat-related bleaching trends in the Abrolhos reefs explored. Coral-algae contacts predominated inshore, while cyanobacteria and turf contacts dominated offshore. An overall trend in positive coral growth was detected from 2009 onward in the inshore reef, whereas retraction in live coral tissue was observed offshore. Turbidity (+) and cyanobacteria (-) were the best predictors of coral growth. The cross-shelf trend of decreasing turbidity and macroalgae abundance suggests either a direct positive effect of turbidity on coral growth, or an indirect effect related to the higher inshore cover of foliose macroalgae, constraining cyanobacterial abundance. According to our results, both exudates and the organic extract significantly decreased the count of symbiont cells when compared to the control. Inhibition of *in*-hospite endosymbionts photosynthetic apparatus was detected at the contact of filaments in the field but our design does not allow for separation of potential allelochemical effects from shading. Sequencing of the 16S rDNA gene identified Abrolhos filamentous cyanbacteria morphologically similar to *Lyngbya majuscula Moorea producens, Moorea bouillonii* and *Okeania erythroflocculosa*, the first occurrence of these taxa in South Atlantic. Bleaching persisted across two austral summers (2016-17) and was recorded in detail in February, May, June and October 2016, and March 2017. Bleaching prevalence was higher in shallow coastal and offshore reef arcs than in deeper mesophotic reefs. All coral species bleached, but there were taxonomic and habitat-related trends in bleaching prevalence. Several species bleached less in the sites and habitats where their abundance was lower. Our results add to the recent evidence that deep reefs provide partial refugia for a few coral species, and that turbid-zone reefs may be less susceptible to climate stress due to shading, higher heterotrophy levels, and local adaptations. Finally, we challenge the idea that high macroalgal cover is always associated with compromised coral health and shed light on the mechanisms behind the suppression of coral tissue benthic cyanobacteria in Abrolhos.

Key words: Coral reefs, Cyanobacteria, Sea surface temperature, Turbid zone reefs, Abrolhos, Brazil, Turbidity, *Symbiodinium*, Allelopathy, Turf algae

SUMMARY

FIGURES

1 INTRODUCTION

In recent decades countless robust and putative evidences that marine ecosystems worldwide are changing in response to an array of disturbances from both anthropogenic and natural sources emerged (Pandolfi et al. 2003; Bellwood et al. 2004). Ocean acidification and global warming due to increased atmospheric greenhouse gases are considered the main drivers of transoceanic patterns (Veron et al. 2009). Coastal systems in immediate range of human populations use and pollution sustain increased pressure, that piles up with the natural cycles of disturbances, which are already stressful to marine communities (Hughes 1994). Depauperate watersheds deliver altered riverine inputs that enhances eutrophication and sedimentation in ecosystems associated to deltas and estuaries (Otaño-Cruz et al. 2017), and deeply impact the structure of reef assemblages (Hughes and Connell 1999). Overfishing of remaining stocks weakens top-down control of benthic species, with cascading effects over abundance, distribution of taxa, and the spread of diseases (Edwards et al. 2014; Mumby et al. 2006).

The consequences of these multiple stressors, whether they are synergistic or not, are shaping marine communities, and the responses to the ongoing impacts are visible in massive bleaching events (Eakin et al. 2016), frequent cyanobacteria outbreaks (Taylor et al. 2014), and composition and distributional shifts (Wernberg et al. 2016). These processes may act as catalysts of coral degradation since their usual outcome is loss of reef builders' live tissue, what leads to increased availability of substrate in the reef. Fast growing, ephemerous photo synthesizers colonize newly available substrata and enhance algal contact onto live tissue. The underlying mechanism of algae-coral interaction is usually explained by the DAM model, which considers the associational aspect of dissolved organic matter (DOM) availability and production, with the contact between algae and corals, their microbes and diseases, and a positive feedback that keeps the loop going (Barott and Rohwer 2012). Therefore, much of the observed pattern of changes in biological communities is context-dependent, with a strong local element to it and, in consonance with biogeochemical traits and ecological interactions (O'Brien and Scheibling 2018; Davidson et al. 2014).

In this way, the importance of scale in approaching environmental generalizations must be considered in ecological studies, since the structure of benthic communities may vary within (Veron 1995; Moura et al. 2013). Turbid zone reefs from the eastern coast of South America are exceptions to the archetypical Caribbean/Indo-Pacific healthy-reef model (high coral-low

algal cover) (Perry & Larcombe 2003). Once perceived as marginal habitats for healthy coral growth, they occupy large areas (Moura et al. 2016), grow as fast as oligotrophic reefs, and often support high coral cover (Morgan et al. 2017). In addition, corals from turbid-zone reefs may be more effective in sediment sloughing and in the concurrent use of phototropic/heterotrophic feeding, besides being more resistant and resilient to thermal anomalies (Anthony 2006; Morgan et al. 2017). The increased physiological plasticity of South Atlantic corals in terms of fecundity (Pires et al. 2011) and photoacclimation (Sugget et al. 2012) under marginal conditions are indicative of stress tolerant species and might sustain a distinct model of dominance shift and resilience in turbid zone reefs.

The Abrolhos Bank harbors a turbid reef system, the most prolific marine biodiversity hot-spot in the sub-tropical South Atlantic, which comprehends several associated habitats (Moura et al. 2013). Besides the periodic effect of natural wind, pluviosity and sedimentation regimes, eventually influenced by polar fronts (Segal et al. 2008), there are also anthropogenic sources of disturbance upon reef organisms like overfishing, dredging, mining and oil operations in the vicinity of marine reserves, and an incidental mud spill from a mining dam (Moura et al. 2013; Mazzei et al. 2017). Recently, cyanobacteria outbreaks, along with microbialization and diseases were reported across the region (Ribeiro et al. 2017; Bruce et al. 2012; Francini-Filho et al. 2008). In addition, it has been demonstrated that corals from areas of high influence of coastal discharge and high algae cover, have higher fitness and resilience in comparison with their offshore counterparts (Pires et al. 2011; Ribeiro et al. 2018). The thesis presented herein aimed at verifying the generality of coral reef stress response in turbid zone corals and their endosymbionts, towards environmental mediated spatial competition, increased frequency of contact with benthic cyanobacteria and thermal anomalies.

2 LONG-TERM EFFECTS OF COMPETITION AND ENVIRONMENTAL DRIVERS ON THE GROWTH OF THE ENDANGERED CORAL *MUSSISMILIA BRAZILIENSIS* (VERRIL, 1867)

2.1 INTRODUCTION

Coral reef ecosystems are facing a sharp loss of biodiversity and habitat structure (Bruno et al. 2009; Hoegh-Guldberg 1999). At the global scale, this decline is associated to thermal anomalies and ocean acidification, which affect coral fitness through bleaching and reduced calcification rates (e.g. Veron et al. 2009). Local and regional level drivers from anthropogenic impacts also play a major role in reef degradation (Hughes 1994). As watersheds become degraded from poor land-use practices and urbanization, rivers deliver increased sediment loads, as well as industrial, agricultural, deforestation and domestic by-products (Doney 2010). Increased nutrification and sedimentation may have a severe impact in coral reefs, which most often thrive in meso- and oligotrophic tropical shallow waters (Sanders & Baron-Szabo 2005). Locally, overfishing promotes an overall trophic downgrading of the coral reef, with severe consequences to ecosystem functioning (Edwards et al. 2014).

Increased sediment load and turbidity, either from dredging or terrigenous/riverine sources, impact reef organisms by smothering and altering light regimes, inherently changing community structure and net productivity (Roger 1990). Coral responses to sedimentation comprise a decrease in live tissue, growth rates and skeletal density, as well as increased overgrowth by macroalgae and cyanobacteria, resulting in lowered recruitment, diversity and species richness at the assemblage level (Fabricius 2005). In addition, wastewater discharges often carry organic and inorganic compounds from industry and agriculture fertilizers, as well as trace metals that affect coastal reefs (Doney 2010). Nutrient enrichment is likely followed by acute changes in benthic community composition and abundance, including mortality of less tolerant taxa, and increased cover of turf, cyanobacteria and macroalgae (Albert et al. 2005). Higher levels of dissolved organic carbon (DOC) and particulate organic matter (POM) disrupts coral microbiomes, leading to outbreak of pathogens, sloughing and death (Kline et al. 2006).

Overfishing of large herbivorous fish contributes to algal outbreaks and increases in DOC concentrations (Edwards et al. 2014). In addition, fishing pressure on top predators may increase disease prevalence through the predation release of lower level vector species (Raymundo et al. 2009). Once the overall biomass and size of higher trophic levels have sufficiently decreased, the system undergoes cascading effects that may disable the top down control of the entire benthic community, ultimately resulting in the loss of biodiversity and ecosystem services (Mumby et al. 2006). Such cumulative effects of multiple stressors have driven several reefs toward a phase-shift from a coral dominated environment to ephemeral soft-coral, turf and macroalgae dominance (Done 1992; Mumby et al. 2006). Since successive

perturbations can disrupt ecological interactions, a degradation loop takes place, releasing algae from competition and predation, allowing less palatable forms to take over, ultimately preventing coral populations from being replenished (Done 1992; Hughes 1994).

Cyanobacteria are important players in phase-shifting reefs, growing as dense mats and tufts, as well as part of the so-called turf consortia (Connell et al. 2014). Abundance of cyanobacteria in reef systems is positively correlated with eutrophication and thermal anomalies (Taylor et al. 2014). When in direct contact with corals, cyanobacteria may disrupt the microbial community within the coral mucus biofilm and trigger an exacerbated growth of pathogens (Morrow et al. 2011). Cyanobacteria are known to inhibit coral recruitment (Kuffner et al. 2006) and to produce toxins and enzymes with grazing deterrence properties (Smith et al. 2010). Despite their relatively ephemeral/opportunistic nature, cyanobacteria can render permanent impacts on corals by overgrowth and progressive deterioration of live tissue (Bender et al. 2012), shading and abrasion (McCook et al. 2001), as well as allelopathy (Rasher et al. 2011). In addition, they can affect coral larvae settlement (Box & Mumby 2007) and attract larvae to ephemeral surfaces (Vermeij et al. 2009).

Long-term (i.e. decadal) time series of data are lacking for most regions, despite being needed to assess the dynamics of coral reef cover, as scleractinians grow a few centimetres per year and climate-oceanographic forcing may operate either episodically or in cycles deviating from seasonal oscillation (Hughes 1994). In addition, percent cover data from transects, which are usually employed in reef monitoring (e.g. Shuman 2007), may not allow for disentangling the outcomes of coral competition with their surrounding faster-growing organisms. For instance, the negative effect of cyanobacteria on living coral tissue may not be detected from estimates of percent cover gathered with randomly distributed transects, as these ephemeral organisms tend to be replaced by longer-living canopy-forming macroalgae, or complex turf-like consortia structured by articulated calcareous and other algae (Titlyanov & Titlyanova 2009). Here, we circumvented this bias by sampling fixed coral colonies along 11 years.

Brazilian reefs are characterized by high endemism levels within low diversity assemblages subjected to high turbidity and heavy terrigenous sedimentation (Laborel 1969). Therefore, the Eastern South American coast comprises several notable examples of turbid-zone reefs in the tropical West Atlantic (see Moura et al. 2016), departing from the archetypical Caribbean/Indo-Pacific healthy-reef model (high coral-low algal cover) (Perry & Larcombe 2003). Turbid zone reefs, traditionally perceived as marginal habitats for healthy coral growth, occupy large areas, grow as fast as oligotrophic reefs, and often support high coral cover (Morgan et al. 2016). In addition, corals from turbid-zone reefs may be more effective in

sediment sloughing and in the concurrent use of phototropic/heterotrophic feeding, besides being more resistant and resilient to thermal anomalies (Anthony 2006; Morgan et al. 2017).

Despite such characteristics, coastal development, overfishing and climate changes deeply affected the community structure of Brazilian reefs in the last decades (Leão & Kikuchi 2005; Dutra et al. 2006). For instance, fisheries yields and fish biomass already show sharp declines in the Abrolhos Bank (Francini-Filho & Moura 2008; Freitas et al. 2011), a region that comprises the largest, richest and best-protected reefs in the South Atlantic (Laborel, 1969; Moura et al, 2013). Turf algae cover has increased across the region (Francini-Filho et al. 2013), whereas one of the main endemic reef corals, *Mussismilia braziliensis*, a stress-tolerant Neogene relic, is predicted to be nearly extinct in less than a century if the current rate of mortality due to diseases is not reversed (Francini-Filho et al. 2008; Bruce et al. 2012). The Abrolhos reefs are distributed along a cross-shelf gradient of terrigenous influence and fishing effort (Moura et al. 2013), providing a propitious context to study the relative effects of coastal influence and protection. Here, we present the results of an 11-year survey of sixteen *M. braziliensis* colonies and their neighbouring organisms. Our study addresses the coupling between environmental drivers and competitive processes in the contact zone between corals and other organisms.

2.2 MATERIAL AND METHODS

2.2.1 STUDY SITE

The Abrolhos Bank (16°40'-19°40'S, 39°10'-37°20'W) comprises a 40,000 km^2 benthic mosaic of reefs, rhodolith beds and unconsolidated sediments, encompassing the largest and richest reefs within the South Atlantic (Moura et al. 2013). The reefs are remarkable for their mushroom-shaped pinnacles with flat tops, which result in strong habitat variation at relatively small spatial scales (pinnacles' walls and tops) (Bastos et al. 2018). Pinnacles are dominated by massive and encrusting corals, reaching up to 30% of the benthic cover (Francini-Filho et al. 2013). Most corals are Brazilian-endemic, and there is an overall lack of branching forms, with the exception of milleporans (Laborel 1960; Moura et al. 2016;). The studied species, *M. braziliensis*, is restricted to the shallow (5-10 m depth) pinnacles' tops, where it is regarded as one of the most important reef builders (Leão & Kikuchi 2005, but see Bastos et al. 2018) and covers up to 10% of the reef (Francini-Filho et al., 2013). Sampling was carried out in one inshore and unprotected reef (Pedra de Leste - PLES) and in one offshore no-take reef (Parcel dos Abrolhos - PAB), this latter within the Abrolhos National Marine Park (Figure 1). When compared to the offshore reef, the inshore reef has lower fish biomass (Francini-Filho & Moura et al., 2008) and higher turbidity, sedimentation, nutrient, DOC levels and microbial loads

(Segal et al., 2008; Bruce et al., 2012), as well as a higher cover of fleshy macroalgae (mostly *Dictyota* spp.) reaching up to 20% of the reef tops (less than 5% offshore) (Francini-Filho et al., 2013).

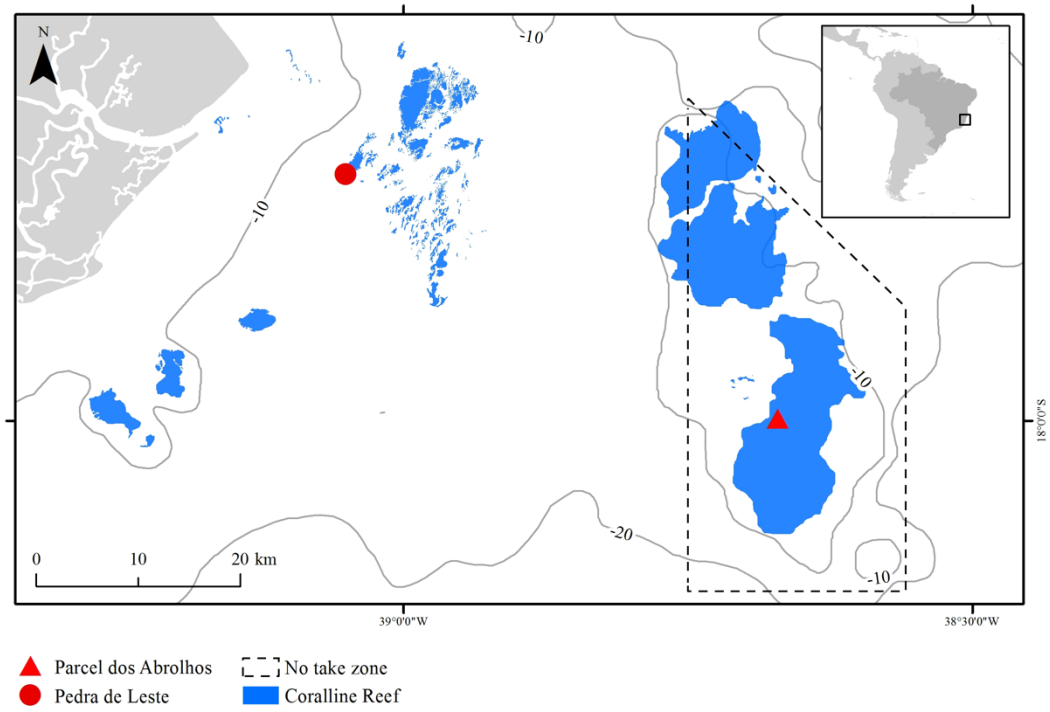


Figure 1 The Abrolhos reefs off Southern Bahia, Brazil. Solid lines represent depth contours, dashed line delimits the no-take zone and sampling sites are shown in red. Coralline reefs are represented in blue.

2.2.2 Sampling and Sample Processing

Coral colonies (n=16, 8 from PLES and 8 from PAB) were selected from the database of a long-term monitoring with fixed photo-quadrats, based on the completeness and quality of the time series. Sampling was carried out yearly during the austral summer (January-March), from 2006-2016. No data is available for 2007, 2010 and 2011 (both sites), and from 2008 (PLES). The living area of each coral colony and the perimeter in contact with each organism were measured with ImageJ software (Schneider et al. 2012). Categories of surrounding organisms included the most abundant functional groups: turf algae, cyanobacteria, corals, crustose coralline algae (CCA) and foliose macroalgae. Turf algae comprise a matrix of fine-branched filamentous macroalgae of distinct taxa interwoven within 2-5 cm thick mats (Connell et al. 2014), while cyanobacteria appeared as homogeneous brown-red mats and tufts (Figure 2). Coral growth (planar area change, which is not equivalent to liner extension) and changes in the relative perimeter of surrounding organisms were estimated from the difference between measurements from each sampling period.

2.2.3 Environmental Data

Summer sea surface temperatures (SSTs) (4 μ nighttime, January-March) and turbidity data (Diffuse Attenuation Coefficient at 490 nm - KD 490) for both reefs were extracted and processed with SeaDas software (ver. 7.4) using level-3 imagery from the MODIS sensor (https://oceancolor.gsfc.nasa.gov) onboard the Terra satellite, using a monthly compositing period and 9 km spatial resolution.

2.2.4 Statistical Analyses

A distance-based linear model (DISTLM; Legendre & Anderson, 1999; McArdle & Anderson, 2001) was used to investigate the relationships between coral growth and its predictors (turf algae, cyanobacteria, foliose macroalgae, CCA, coral, temperature and turbidity), using different time lags for temperature and turbidity (0, 1 and 2 years). We retained only the 1-year lag in subsequent models (i.e. used temperature and turbidity from the previous year), as it presented the higher explanatory power. Distance offshore was not incorporated in the models due to its colinearity with turbidity. The most significant predictors were selected using the best selection procedure, and the Akaike's information criterion (AIC) was used to select the most parsimonious models. A distance-based redundancy analysis (dbRDA, Legendre & Anderson, 1999; McArdle & Anderson, 2001) was used to quantify the associations between predictors and colony area change. Multiple partial correlations of the selected predictors according to DistLM analysis with the dbRDA axis were also examined in order to interpret the relationship and identify the dominant forces driving the coral growth response to the environmental variables. PERMANOVA pairwise tests were performed in order to discriminate differences in coral growth among years, as well as the frequency of contact with neighbouring organisms between sites. Analyses were performed with software Primer 6 (Anderson et al., 2008).

2.3 RESULTS

Mean summer SSTs ranged from 26.4 to 27.5^{o} C during the 11-year survey period and presented only slight spatial variation, with less than 0.2^{o} C differences between the two sites, whereas turbidity (KD 490) in PLES (inshore) was consistently higher (1.5 times higher on average) than that recorded in PAB (offshore). Turbidity spikes in PLES occurred in 2010, 2011 and 2016. Positive temperature anomalies with mean summer SSTs up to 0.5^{o} C above the study period average were recorded in 2010 (Figure 3).

Turbidity and the coral perimeter in contact with cyanobacteria were significant predictors of coral growth, accounting for 27.5% of coral growth variation (Table 1). Turbidity

was positively correlated with the first dbRDA axis, indicating a positive association with coral growth, while cyanobacteria was negatively correlated (Figure 4).

Coral growth responded negatively to direct contact with cyanobacteria (Figures 4 and 5) and contact length with surrounding organisms was significantly different between reefs (Table 2). Along the entire study, coral-algae contacts predominated inshore, while cyanobacteria and turf dominated the contacts with corals in the offshore reef. An overall trend of positive coral growth was detected from 2009 onwards in the inshore reef, whereas retraction in live coral tissue was observed offshore during this same period. The PERMANOVA pairwise comparisons confirmed statistical differences in coral growth between years and sites ($p<0.05$) (Table 5 SM), as well as in the frequency of cyanobacteria, foliose macroalgae and CCA contacting coral colonies (Table 2).

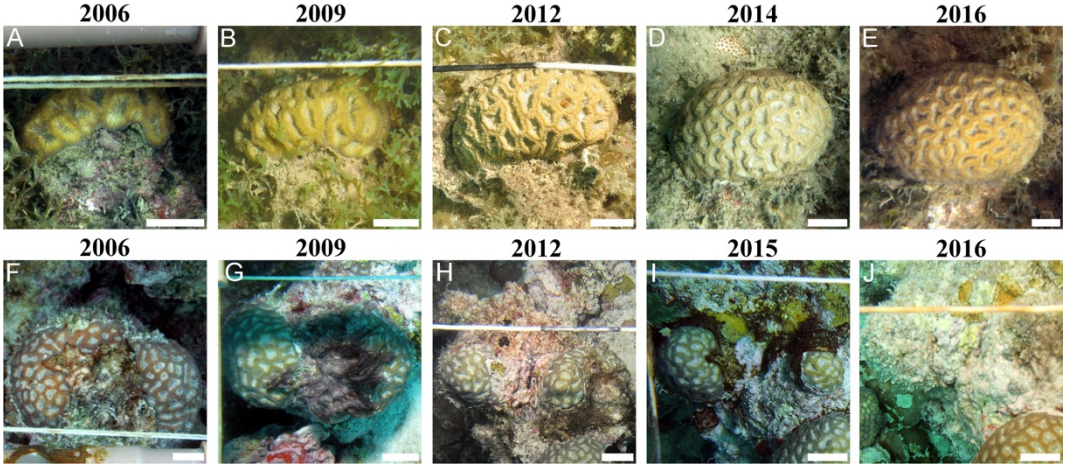


Figure 2 Sequential images from individual colonies in the inshore (PLES, upper row) and offshore (PAB, lower row) reefs showing contrasting growth trajectories and turf / cyanobacteria dominance. Scale bars=2 cm.

Tabela 1 DistLM marginal test results and model selection.

DistLM Marginal Test					
Variable	Variable	SS(trace)	Pseudo-F	P	Prop.
1	Turf	24.055	0.16538	0.678	0.0016
2	Cyano	1929.7	15.29	0.001	0.134
3	Dicty	61.884	0.42658	0.495	0.0042
4	CCA	240.7	1.6801	0.205	0.0167
5	Coral	123.31	0.85364	0.382	0.0085
6	Turbidity	2068.7	16.576	0.001	0.143
7	Temperature	49.772	0.3428	0.568	0.0034
Overall best solution					
AIC	R^2	RSS	No. Of Variables	Selections	
474.62	0.27512	10456	2	2;6	

Figure 3 Summer sea surface temperatures (triangles) and turbidity (squares) for the inshore (PLES) and offshore (PAB) reefs during the study period (2006-2016). Dashed horizontal lines represent average values.

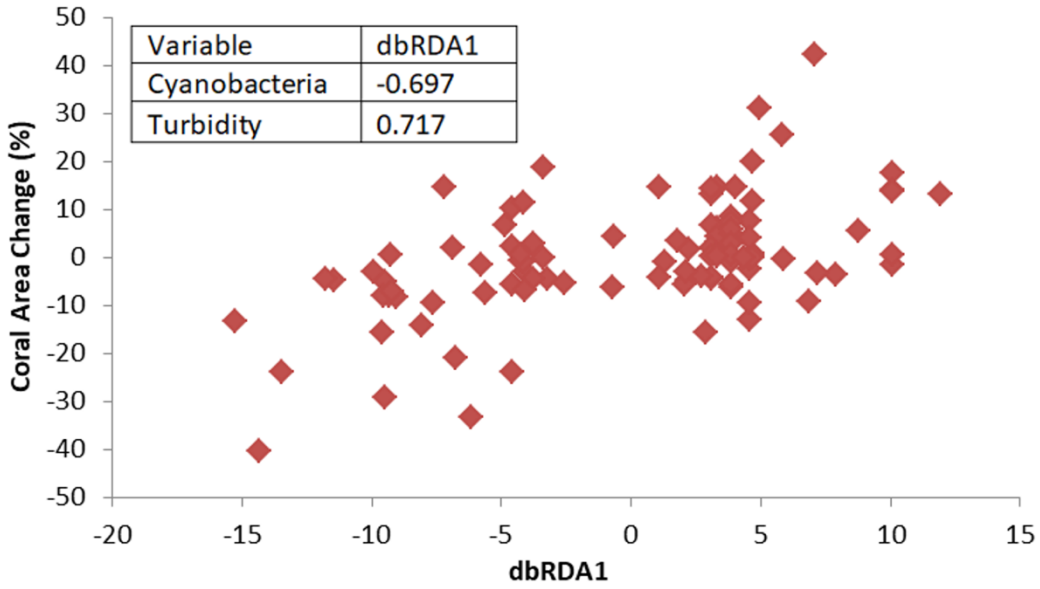


Figure 4 Coral growth response relationship with the first Distance-based Redundancy Analysis (dbRDA) axis, related to turbidity and cyanobacteria perimeter.

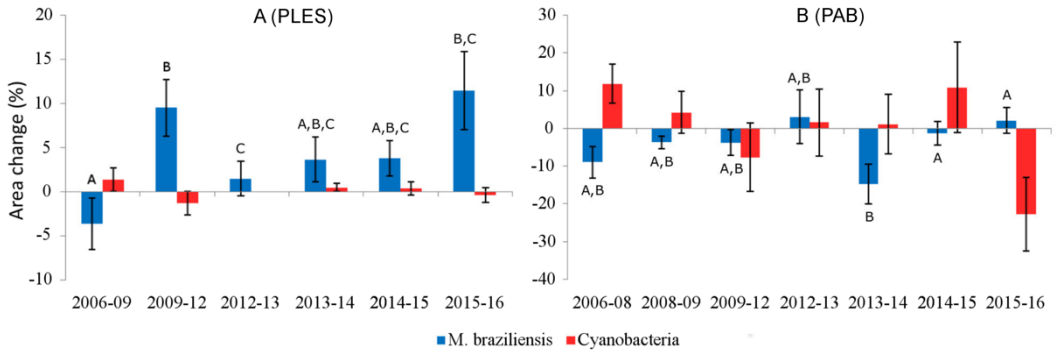


Figure 5 Mean values of coral and cyanobacteria area change. Letters show pairwise results from PERMANOVA for each sampling time and bars represent SE. Letters show significant PERMANOVA results for pairwise comparisons of *M. braziliensis* area change between each sampling time.

Tabela 2 Mean extension of contacts with *M. braziliensis* colonies (2006-2016) and PERMANOVA pairwise tests results contrasting inshore and offshore samples.

Variable	PLES **(%, ±SD)**	PAB **(%, ±SD)**	**t**	**P**	**Permutations**
Turf	12.62 (±9.92)	14.55 (±8.40)	0.7887	0.4349	9582
Cyanobacteria	0.10 (±0.42)	3.90 (±5.37)	4.8866	0.0001	9364
Foliose macroalgae	6.89 (±6.35)	0.02 (±0.14)	8.4528	0.0001	9481
CCA	0.83 (±2.10)	4.68 (±5.50)	4.3167	0.0002	9372
Coral	2.16 (±3.51)	1.23 (±1.77)	1.8772	0.0661	9021

2.4 DISCUSSION

Turbid zone reefs, often considered marginal sites for coral communities, may harbour a significant cover of fast-growing and/or stress-tolerant coral species within low diversity assemblages (Anthony 2006; Cacciapaglia & van Woesik 2016; Morgan et al. 2017). Rather than being local or "marginal" features, these reefs cover vast and yet unmapped areas of invaluable coralline habitat in several ocean basins (Kleypas 1996; Moura et al. 2016). Understanding the dynamics of turbid-zone reefs is essential to evaluate the generality of the models explaining the decline of coral reefs, which often involve a positive feedback loop of DOC, disease, algae, and microorganisms (DDAM model, Haas et al. 2016), among other climate and anthropogenic stressors (Hughes, 1994). The Abrolhos Bank is a foremost example of turbid zone reef (Leão & Ginsburg 1997), with a strong cross-shelf gradient of turbidity and sedimentation, related to coastal/riverine inputs and seasonal resuspension of autochthonous fine sediments during winter intrusions of polar fronts (Leão & Kikuchi 2005; Segal et al. 2008).

Long-term (i.e. decadal) time series of data are lacking for most regions, despite being needed to assess the dynamics of coral cover, as scleractinians grow a few centimetres per year

and climate-oceanographic forcing may operate either episodically or in cycles deviating from seasonal oscillation (Hughes 1994). In addition, percent cover and relative abundance data from transects, which are usually employed in coral reef monitoring (e.g. Shuman 2007), may not allow for disentangling the outcomes of coral competition with their surrounding faster-growing organisms. We circumvented this bias by sampling fixed colonies along 11 years. For instance, the negative effect of cyanobacteria on living coral tissue may not be detected from estimates of percent cover gathered with randomly distributed transects distributed at larger spatial scales, as these ephemeral organisms tend to be replaced by longer-living canopy-forming macroalgae, or complex turf-like consortia structured by articulated calcareous and other algae (Titlyanov & Titlyanova 2009).

Our DistLim model evidenced that cyanobacteria and turbidity were the best predictors of coral growth in Abrolhos (see Table 1), the former presenting a negative effect. Conversely, turbidity (Kd490) was associated with positive changes in living coral surface. For instance, the larger positive change in net coral growth in the inshore reef (2009-12) followed the 2010-11 turbidity peak (Figure 5), suggesting improved conditions to the corals. Despite the higher nearshore turbidity and sedimentation, there were no significant cross-shelf differences in SST (Figure 3). Indeed, we failed to detect an effect of SST on *M. braziliensis* growth, evidencing a stronger influence of the turbid regime and competition with cyanobacteria. Turbidity inherently alters light penetration and reduces the incidence of coral-damaging UV radiation. Akin to shading (Jompa & McCook 2003), this widespread "sunblock effect" in turbid zone reefs may interact antagonistically with other disturbances to alleviate the impact of coral bleaching during severe thermal stress (Guest et al. 2016; Morgan et al. 2017). In addition, higher nutrient availability may contribute to enhanced growth of *M. braziliensis*, possibly related to heterotrophic feeding, and previous studies have demonstrated increased reproductive output on inshore reefs of the Abrolhos Bank (Pires et al. 2011). However, increased sedimentation and nutrification from land-based sources may have a detrimental effect on coral growth. Indeed, corals may increase growth under physiological stress and display a "maximum-accretion-to-turnoff" response (Wooldridge 2014). Under such circumstances, skeletal density may decrease, and extension rates may increase until abrupt cessation of growth.

Benthic cyanobacteria produce a broad array of secondary metabolites, with several bioactive compounds that interfere with bacterial *quorum sensing* and coral diseases (Engene et al. 2011; Puglisi et al. 2014). Such compounds could also be cytotoxic and exert allelopathic effects in corals (Morrow et al. 2011). Contact with chemically defended algal species may

trigger immune responses in *Symbiodinium*, depending on exposure, length and specific activities of secondary metabolites (Shearer et al. 2014). Contact with chemically defended algal species may trigger immune responses in *Symbiodinium*, depending on exposure length and specific activities of secondary metabolites (Shearer et al. 2014). Cyanobacteria affect dinoflagelates' development and reduce their *in hospite* density and photochemical efficiency, ultimately impairing coral growth (Titlyanov et al. 2007). Although cyanobacteria density is positively correlated with nutrient availability from coastal sources (Ahern et al. 2007), both inshore and offshore Abrolhos' sites have similar DOC and total nitrogen concentration (Bruce et al. 2012). Therefore, the recent cyanobacteria outbreaks, along with microbialization and diseases reported across the region (Ribeiro et al. 2017; Bruce et al. 2012; Francini-Filho et al. 2008), may have not been driven solely by nutrification. An allelopathic effect is consistent with the negative effect of cyanobacteria on coral growth shown by the DistLim model (see Table 1). While water temperature had a limited effect over the long-term *M. braziliensis* growth trends, it may trigger cyanobacteria outbreaks and indirectly affect coral health (Ribeiro et al. 2017)

The cross-shelf trend of decreasing turbidity and macroalgae abundance suggests either a direct positive effect of turbidity on coral growth, or from the higher inshore cover of foliose macroalgae that constrain cyanobacterial abundance, such as recorded in the offshore reef site. Altered light regimes may lead to shifts in cyanobacteria abundance (Castenholz & Garcia-Pichel 2013). When compared to primary succession organisms (e.g. turf and cyanobacteria), foliose macroalgae establish relatively stable assemblages with dense canopies (Steneck & Dethier 1994), which may be considerably resistant to herbivory (Francini-Filho et al. 2010). Although macroalgae are able to compete and damage coral tissue (Tanner 1995, McCook et al. 2001), their negative effects over corals may be less important than those from chemically-driven cyanobacteria outbreaks. In addition, macroalgae may provide shelter for coral recruits (McCook et al. 2001) and epiphytism control of cyanobacteria, ultimately rendering reduced contact of toxic filaments with coral colonies (Fong et al. 2006). Although some CCA species may be deleterious to corals, these organisms generally facilitate coral growth in heterogenous landscapes (Price 2010). In our study, the strong effect of cyanobacteria may have obliterated the statistical effect of CCA on coral growth trends. Similarly, temperature was not a significant predictor of coral growth, even though coral growth declined after the 2010 temperature spike (Figures 2 and 5).

In Abrolhos, roving herbivorous fish are more abundant in offshore protected reefs (Francini-Filho & Moura 2008). From 2003 to 2008, Francini-Filho et al. (2013) monitored the

region's benthic assemblages and failed to detect significant temporal changes in foliose macroalgae cover in both inshore and offshore reefs, despite recording consistent cross-shelf differences in macroalgal abundance. Although it is unclear whether the higher inshore macroalgal abundance (10-20% of reef cover) is a stable phase related to a long-standing high turbidity background, or a contemporary response to overfishing (Freitas et al. 2011), increased macroalgal abundance implies in a higher contact frequency with corals (Grillo et al. 2018). Poor land use and coastal development enhances sedimentation and reduce the overall vitality of reef systems, which is generally inversely related to distance offshore (Dutra et al. 2006). However, our results challenge the idea that high macroalgal cover is always associated with compromised coral health, as baselines for turbid zone reefs may derive sharply from those of coral-dominated reefs that dwell under more oligotrophic conditions (Rogers 1990; Kleypas 1996). Indeed, our results add to the growing evidence of increased physiological plasticity of South Atlantic corals in terms of fecundity (Pires et al. 2011) and photoacclimation (Sugget et al. 2012) under marginal conditions. In Abrolhos, instead of being additive or synergistic (e.g. Diaz-Pulido et al. 2011), the effects of turbidity and cyanobacteria were antagonistic.

Conservation concerns are higher in inshore unprotected reefs, due to their proximity to anthropogenic stressors and overfishing (e.g. Francini-Filho & Moura 2008). However, coral decline was faster in offshore reefs, which may be more vulnerable to stressors that operate at larger spatial scales, such as light and temperature anomalies. The anomalous growth of cyanobacteria, leading to toxic amounts of cyanotoxins (Rastogi et al. 2015), are often attributed to temperature anomalies and anthropogenic impacts such as nutrient input. However, as we demonstrated herein, distance offshore and no-take zoning are not always sufficient to keep reefs from harmful cyanobacterial blooms. For instance, despite the significantly higher fish abundances inside the offshore no-take zone (Francini-Filho & Moura 2008), roving herbivorous were never recorded eating cyanobacteria mats and tufts (authors' obs.). Avoiding coral decline goes well beyond no-take zoning and shall include water quality control and climate change mitigation, as well as appropriate local baselines for long term monitoring, as health indicators are geographically variable and context dependent.

2.5 CONCLUSION

Our results, which are derived from a long-term high-resolution time series, add to the growing evidence that turbid zone reefs present unique functional properties that challenge the current models explaining the global decline of coral reefs, which are largely based on DOC, disease, algae, and microorganisms. Here, we show that the growth of one of the main reef

builders of the Abrolhos reefs, *M. braziliensis*, was positively influenced by turbidity, which is greater nearshore. On the other hand, filamentous cyanobacteria were the most aggressive coral competitors. The negative effect of filamentous cyanobacteria was detected both in unprotected nearshore reefs and in no-take offshore reefs with less turbidity. We emphasize the importance of building local baselines for long term monitoring, as health indicators are geographically variable and context dependent. We also note that avoiding coral decline goes well beyond no-take zoning and shall include a longer road that includes water quality control and climate change mitigation.

3 ALLELOPATHIC EFFECTS OF BENTHIC FILAMENTOUS CYANOBACTERIA OF ABROLHOS BANK, BRAZIL.

3.1 INTRODUCTION

Cyanobacteria are photosynthetic prokaryotes broadly spread through most ecosystems. Their biological diversity encompasses unicellular and multicellular taxa, divided in three functional groups: single celled, non-heterocystous and hetercystous filamentous, capable of synthesizing chlorophyll (Whitton & Potts 2012). In marine environments, these primitive life forms thrive in practically every compartment, from free-living unicellular planktonic species to benthic filaments, mats and symbiotic strains (Paerl 2012). In mutualistic associations they provide energy, nutrients, and protection from UV radiation and predation, deeply impacting hosts ecology and evolution pathways (Usher et al. 2007). Moreover, cyanobacteria are key builders of calcified structures known as microbialites, formed by sediment trapping, binding or precipitation of calcium carbonate (Stal 2012). Because cyanophytes assimilate significant amounts of atmospheric carbon and nitrogen, they globally impact biogeochemical cycles in the ocean. The distribution and abundance of these organisms is greatly limited by organic and inorganic nutrients and, the eutrophication of water bodies might trigger blooms of several taxa (Reed et al. 2016; Rollwagen-Bollens et al. 2018).

Coastal eutrophication coupled with climate change and warming ocean waters provide nurturing conditions for cyanobacteria to keep blossoming in upcoming years (Gao et al. 2012; O'Neil et al. 2012; Chaffin & Bridgeman 2014). Among the several potential harmful algae bloom species (HAB), one group that will potentially benefit from this projection is the benthic filamentous *Lyngbya*-like taxa (Schopf 2012), which are conspicuous components in coastal systems (Taylor et al. 2014). Most often observed on hard substrate as tuft colonies of trichomes, cyanobacteria species may resemble filamentous macroalgae (Engene et al. 2013), and/or may occur as epiphytes on algal canopies (Fong et al. 2006), or as massive mats on sediment (Stal 2012). Outbreaks of this kind of cyanobacteria are usually reported during warmer periods, associated with longer periods of low wave energy and high nutrient input (Albert et al. 2005; Sneed et al. 2017), but such correlations seem to be both site and species-specific, therefore caution is needed when approaching these phenomena in larger scales (O'Neil et al. 2012; Davidson et al. 2014).

The most common outcomes of such exacerbated cyanobacteria growth in coastal biomes are depletion of bioavailable nutrients and hypoxia along with toxic compounds accumulation (Taylor et al. 2014), since the taxa that build up the gross biomass of these blooms are in fact a consortia of prolific secondary metabolites producers (Engene et al. 2011). Molecular investigations revealed a significant diversity in what was thought to be a

monophyletic group under the single genera *Lyngbya*, as well as a high specialized apparatus for biosynthetizing complex secondary metabolites which has been isolated from filaments of distinct taxa (Engene et al. 2012, 2013).

For long time cyanobacteria have been refered to produce different forms of cyclic and linear peptide, alkaloides, macrolactones and heterocyclic compounds (*e.g.* Carmichael 1986; Welker M & Von Dohren 2006). Several metabolites from cyanobacteria exhibit toxic properties (Dittmann et al. 2013), with unfolding ecological roles (Sneed et al. 2017), that may impact marine communities' dynamics and pose a threat to both human and ecosystem health (Taylor et al. 2014). For example, these compounds have been investigated towards the potential biological and ecological roles, such as protection from UVR (Singh et al. 2010), photoprotection by mycosporines and mycosporine-like amino acids (Signh et al. 2008), feeding deterrence against herbivory by fishes, urchins, mollusks and crabs (see review Leão et al. 2012).

Besides natural or anthropogenic induced outbreaks, filamentous cyanobacteria are frequently found in association with ephemeral, fast growing turf algae that colonizes virtually any hard substrate in reef systems, including reef builders exposed calcareous skeleton and even living organisms in the benthos (Carella et al. 2014; Kiryu et al. 2015). A few taxa are associated with diseases in corals such as in Black Band Disease (BBD), with Pseudoscillatoria coralii as the dominant species in the pathogen microbial community (Kramarsky-Winter et al. 2014). Such antagonistc interaction with corals is also seen during settlement, as cyanobacteria metabolites inhibits coral recruitment (Kuffner et al. 2006)The direct contact of cyanobacteria trichomes on coral holobionts may also trigger dominance shifts in the biofilm, potentially increasing the vulnerability of corals to pathogens (Morrow et al. 2011).

Benthic filamentous cyanobacteria are becoming increasingly frequent in South-western Atlantic (SWA) reefs (Ribeiro et al. 2018). In the Abrolhos Bank, the richest coralline reef system in South Atlantic Ocean and biodiversity hot-spot of coral species (i.e. anthozoans and hydrozoans) for the Brazilian coast (Laborel 1969; Moura et al. 2013), filamentous cyanobacteria are frequent on the typical mushroom-like pinnacle reefs, as algae-like upright colonies or entangled within the turf matrix (Francini-Filho et al. 2013). Outbreaks were reported for the region during summer with exacerbated cyanobacteria epiphytism over *Halimeda* beds and turf (Ribeiro et al. 2017). These reefs are home to a stress-tolerant Neogene relic, *Mussismilia braziliensis* which is predicted to be nearly extinct in less than a century if the current rate of mortality due to diseases is not reversed (Francini-Filho et al. 2008; Bruce et al. 2012). Recent evidence of a long-term antagonistic effect of filamentous cyanobacteria on

the growth of *M. braziliensis*, reveals an ongoing deleterious process through periodic pulses of increased cyanobacteria biomass (i.e. outbreaks), partially mediated by turbidity and indirectly by temperature anomalies (Ribeiro et al. 2018). In the present study we describe the most conspicuous benthic filamentous cyanobacteria of Abrolhos pinnacle-reefs and reveal their taxonomic identity through morphological traits and 16S rDNA sequencing. Also, we investigate the micro scale effect of direct contact of the trichomes with coral tissue, and the effect of their organic extracts and culture filtrates, by using different experimental approaches. We addressed the question of to what extent the proximity of filaments is toxic to corals, their endosymbionts and the holobiont microcosms.

3.2 Materials & Methods

3.2.1 Study Area

The Abrolhos Bank (16°40'-19°40'S, 39°10'-37°20'W) comprises a 40,000 km2 benthic mosaic of reefs, rhodolith beds and unconsolidated sediments, encompassing the largest and richest reefs within the South Atlantic (Moura et al. 2013). The reefs are remarkable for their mushroom-shaped pinnacles with flat tops, which result in strong habitat variation at relatively small spatial scales - pinnacles' walls and tops (Bastos et al. 2018). Pinnacles are dominated by massive and encrusting corals, reaching up to 30% of the benthic cover (Francini-Filho et al. 2013). The model coral species for experiments performed herein, *M. braziliensis*, is restricted to the shallow (5-10 m depth) pinnacles' tops, where it is regarded as one of the most important builders of the “recent” reef layers (Leão & Kikuchi 2005; Bastos et al. 2018) and covers up to 10% of the reef (Francini-Filho et al. 2013). Sampling was carried out in one inshore and unprotected reef (Pedra de Leste - PLES) and in one offshore no-take reef (Parcel dos Abrolhos - PAB); this latter within the Abrolhos National Marine Park (see Figure 1). When compared to the offshore reef, the inshore one has lower fish biomass (Francini-Filho & Moura 2008) and higher turbidity, sedimentation, nutrient, dissolved organic carbon (DOC) levels and microbial loads (Segal et al. 2008; Bruce et al. 2012), as well as a higher cover of fleshy macroalgae (mostly *Dictyota* spp.) reaching up to 20% of the reef tops (less than 5% offshore); cyanobacteria alone make up to about 1% in inshore reefs and less than 5% cover in the offshore reefs, apart from exacerbated growth during blooms (Francini-Filho et al. 2013).

3.2.2 Establishment of cyanobacterial cultures

The cyanobacteria strains reported herein were isolated from benthic samples collected in the Abrolhos reef system. Samples were collected by scuba diving, kept at ambient temperature and protected from direct sunlight until being processed in the laboratory. Single

cyanobacterial filaments were isolated either manually (large filaments morphologically similar to *Lyngbya majuscula*) under an inverted microscope (Andersen and Kawachi, 2005) or by single-particle sorting (thin filaments morphologically similar to *Leptolyngbya* sp.) in a MoFlo model flow cytometer (Beckman Coulter) (Fistarol et al., 2018). Isolated filaments were incubated in f/2 medium (Guillard, 1975) prepared with 0.22 µm filtered Abrolhos seawater and incubated at 26 °C with a 14h photoperiod and an irradiance of ca. 20 µmol photons m^{-2} s^{-1}. Cultures were incorporated in a culture collection (CCMR, Culture Collection of Microorganisms at UFRJ) and maintained by consecutive transfers to fresh medium on a monthly to bi-monthly basis.

3.2.3 MORPHOLOGICAL AND MOLECULAR CHARACTERIZATION OF FILAMENTOUS CYANOBACTERIA

Cyanobacteria taxa were identified in field samples obtained from inshore and offshore sites, where long upright cyanobacterial tufts are conspicuous at the border of pinnacle reef tops. A total of 10 individual tufts were sampled, rinsed in sterile f/2 medium, snap frozen and/or fixed in 1% glutaraldehyde. Macroscopic traits (e.g. size and color) of each tuft were recorded still in the field. In the laboratory, single filaments morphologically similar to *Lyngbya majuscula* were picked from the tufts under an inverted microscope with the help of a pointy-end forceps and thoroughly rinsed with sterile f/2 medium. The selected filaments were photographed with digital camera (Pentax Kk) for further morphometric analysis and transferred with ca. 1 uL of medium to 0.5 mL PCR tubes. Each filament was digested with 0.5 uL of proteinase K (23 $mgmL^{-1}$) at 37ºC for 1h, followed by 80ºC for 5 min. to denaturate the enzyme. These digested mixtures were further used directly in PCR to amplify the 16S rDNA gene. For cyanobacteria cultures, DNA was extracted from a cell pellet with 2% CTAB buffer (hexadecyl-trimethyl-ammonium bromide, pH 8.0) in a water bath at 60 °C for 30 minutes and homogenized by manual inversion. After centrifugation, the supernatant was transferred to a new tube and 1 volume of chloroform: isoamyl alcohol (24:1, v/v) was added. centrifuged at 10000 x g for 15 minutes. The upper phase was transferred to a new tube to which 800µL of 95% ethanol and 0.3M NaOAc was added and kept at -20°C overnight. The mixture was then centrifuged for 30 min. at 10000 x g. The pellet was rinsed twice with cold 70% ethanol, dried in the speed-vac for 15 min, resuspended in 25 µL of TE buffer (10 mM Tris-HCl, 1 mM EDTA, pH 8.0) and stored at -20 °C. After DNA extraction, the integrity of the genetic material was checked on a 1% agarose gel. DNA quantification was done in a Nanodrop 1000 spectrophotometer (ThermoScientific).

Amplification of the 16S rDNA was performed through PCR amplification according to Lane (1991), using universal bacteria primers for 16S rDNA, with forward primer 27F (5'-AGAGTTTGATCMTGGCTCAG-3') and reverse primer 1492R (l) (5'-GGTTACCTTGTTACGACTT-3'); and cyanobacteria-specific forward primers CYA359F (5'-GGGGAATYTTCCGCAATGGG-3'), and CYA106F (5'-CGGACGGGTGAGTAACGCGTGA-3'), plus an equimolar mixture of reverse primers CYA781R (5'-GACTACTGGGGTATCTAATCCCWTT-3'), following procedures described by Nübel et al. (1997). DNA integrity was verified with eletroforesis in ultra-pure ágar (Invitrogen) with GelRed™ (1:1000, Biotium). PCR products were purified with ExoSAP-IT (USB Corporation). Reaction volume was 10 µL: 6,3 µL of PCR products 1,5 µL do BigDye® 5X Sequencing Buffer (ThermoFisher), 1,2 µL of primer (2,7 nM, GenOne) and 1 µL BigDye® Terminator v3.1 Ready Reaction Mix (ThermoFisher). After precipitation, the SANGER method was applied through a capillarity system (ABI3500). Sequences were analysed with SeqMan Pro v.11.1. 0 and compared to published sequences using the BLASTn tool in GenBank. Based on the BLASTn result, a set of 21 sequences that showed the highest similarity to the ones produced in the present study were retrieved to be used in a phylogenetic reconstruction. Sequences were aligned in ClustalW with further manual refinement. A phylogenetic reconstruction was done by the Neighbour Joining method using Jukes and Cantor distance with 500 bootstrap replications in MEGA 7 software.

3.2.4 EFFECTS OF CYANOBACTERIAL EXUDATES ON *Symbiodinium* sp.

To investigate allelopathic effects of cyanobacteria over corals, we ran incubation experiments exposing cultured *Symbiodinium* sp. isolated from the coral *M. braziliensis* (strain CCMR0100, clade A4, *viz.* Silva-Lima et al. 2015) to cell-free filtrates of cyanobacteria cultures and exudates (water sample from within cyanobacteria tufts) from naturally occurring cyanobacteria filaments collected in Abrolhos.

A total of 13 cyanobacterial strains isolated as explained above and morphologically similar to cf. *Lyngbya majuscula* (strains CCMR0174, 0175, 0176, 0219, 0229, 0236) and cf. *Leptolyngbya* spp. (0281, 0282, 0287, 0280, 0285, 0286, 0283) were used in the tests. Both, the symbiont and the cyanobacteria were grown in f/2 medium at 26ºC, ca. 20 µE m^{-2}. s^{-1}, and a 14h photoperiod. Cyanobacterial cultures were grown for ca. one month, depending on the strain, until enough biomass had accumulated. Then the cells were removed by filtration through glass microfiber filters (Whatman GF/F, 25 mm). The filtrate from each cyanobacterial culture was distributed into quadruplicate 20 mL glass vials containing 9 mL of *Symbiodinium* sp. CCMR0100 culture in f/2 medium and harvested in the late exponential phase. Each vial of

treatments and control incubations received 9 ml of culture filtrate (n = 4 - 5). Controls were made by adding f/2 medium to the symbiont cultures. Two millilitres of fresh f/2 medium were added to each vial to avoid nutrient limitation. After addition of filtrates and f/2 medium, each experimental unit had initial symbiont concentrations of 6 x 10^4 cells mL^{-1}. The experiment was run for 72h at temperature and irradiance as described above. Cell counts were performed daily either by flow cytometry (BD Accuri™ C6) or by microscopy in a Palmer-Malloney counting chambers. Allelopathic effect was accessed by measuring, for each day, the difference in the cell numbers of the symbiont and its respective control. Negative effects resulted in less cells in the treatment exposed to the filtrate than in the control, and positive effects resulted in more cells in the treatment flasks (i.e, increase in cells in relation to the control).

Water from inside five cyanobacteria tufts growing at the border of *M.braziliensis* live tissue from pinnacles tops (6 - 8m depth) at Parcel dos Abrolhos (summer, 2017) was carefully collected using a 60 mL syringe. The exudates were then filtered with Whatman® glass microfiber filters (GF/F, 25 mm) and snap frozen in liquid nitrogen still in the field. In the laboratory, the exudates were thawed and added to *Symbiodinoum* sp. CCMR0100 cultures following the same protocol used for the cyanobacterial strains cell-free filtrates as explained above.

3.2.5 Effects of cyanobacterial crude-extracts on *Symbiodinium ex*-hospite.

Cyanobacteria tufts of similar morphology (red, long filaments), here assigned to the morphotype PLECA, were harvested by scuba-diving at Pedra de Leste. A pooled biomass of ca 300g (wet weight) of tufts was frozen in the field, transported to the lab and freeze-dried. Exhaustive and successive organic extractions were done using ethyl acetate:methanol (1:1), yielding a homogeneous crude extract. Bioassays were performed through acute exposure of *ex*-hospite *M. braziliensis* symbionts to cyanobacteria crude extract. After evaporation of the solvents, the extract was solubilized in DMSO. Aliquots of this crude extract were added to 5 replicates of *Symbiodinium* sp. CCMR0100 cultures to a final concentration similar to natural levels plus three dilutions by a factor of 10 i.e. 10, 100 and 1000 times less than the natural levels. *Symbiodinium* cells were counted using an automated imaging system (FlowCam, Fluid Imaging Technologies, Inc.) prior to the experiment and after 48h of incubation with the extracts.

3.2.6 CHARACTERIZATION OF THE CORAL-CYANOBACTERIA CONTACT IN THE FIELD

Pulse amplitude modulated (PAM) fluorometry was applied as a non-invasive technique using Diving-PAM (Walz, Germany). We used effective quantum yield of photosystem II (ΔF/Fm'; ϕ PSII) as a proxy for symbiont density and photosynthetic health, to assess physiological response of endosymbionts at the point of contact between filaments and coral tissue (called cyano-coral contact), in light-adapted colonies along 15m transects on pinnacles tops (6 - 8m depth). To assess it was necessary direct contact of cyanobacteria with the coral tissue to have inhibition, we also did measurements at the top of coral, which was not in direct contact with the tufts (called distance effect point). Both these measurements (at the side border of the coral, and at the top-center of the coral) had paired samples taken from corals that had no algal canopy bordering the live tissue. These were control samples for the effect of the distance and the allelopathic contact effect of cyanobacteria and were called distance control and cyano-coral control, respectively. Measurements were made by placing the probe at right angle, 3mm from coral tissue, while avoiding self-shading, and beneath the edge of filaments swirling over the border of live coenosarc, to minimize for shading effects on coral tissue (n = 10). The controls with no algal canopy bordering the live tissue were also an attempt to control for differential irradiance along the coral surface, we took another set of samples from coral colonies with no algal canopy bordering the live tissue (n = 10). However, this design cannot differentiate between shading and allelopathic effects of cyanobacteria tufts over coral tissue. In order to ensure uniform light irradiance over the colonies, measurements took place between 1000 and 1300 h, and all target specimens were sampled within the same dive to avoid differential responses due to temporal changes in environmental conditions.

The microbial communities within the mucopolysaccharide layer of coral holobionts were obtained by collecting mucus paired samples with a sterile syringe from the point of contact (as described above), and from the top center (n = 4). The samples were fixed with 1% glutaraldehyde and snap frozen in liquid nitrogen. The microbial community was quantified by flow cytometry in BD Accuri™ C6 instrument equipped with a blue laser (488nm). Autotrophs were detected by their chlorophyll fluorescence in unstained samples (Marie et al. 2005). Heterotrophs were detected after staining the samples with the nucleic acid fluorochrome SYBRGreen I (Marie et al. 1997).

3.2.7 EFFECTS OF CYANOBACTERIAL CRUDE EXTRACTS AND EXUDATES ON *Symbiodinium* IN AQUARIA.

In order to test for cyanobacteria-whole coral interaction an open deck aquarium system was setup on board a vessel in the Abrolhos Bank. Running seawater trays provided constant

temperature for specimens of *M. braziliensis* maintained in individual tanks (2L plastic beaker, Nalgon®). Constant aeration was provided in each beaker. Colonies of *M. braziliensis* (≅ 40 cm^2), were collected from pinnacles tops (6 - 8m depth) and placed inside experimental units straight away over a platform with an upright metallic arm bended towards the platform, holding the plastic cup at the edge. The 30ml cups (food grade plastic) had a 47mm circle whole in the lid with a 0.02µm circle filter secured against the remaining cap edges by a rubber o-ring and screwed to fit the cup. The design adapted from Smith et al. (2006), ensured that only dissolved compounds would diffuse from inside the cup. Natural volumetric concentrations of crude extract (viz. Allelopathy experiments section) were incorporated into a Phytagel™ (Sigma Chemical Co.), prepared by mixing 0.5625 g of this gel powder with 30 ml of distilled water to obtain the treatment, and simulate natural diffusion of compounds in the water (Da Gama et al. 2002). Live filaments of cyanobacteria were added to cups in a distinct treatment to verify the allelopathic effect on *M. braziliensis*. Control gels were similarly prepared, but without the addition of extract, adding DMSO only (herein referred as DMSO). Additional controls consisted of beakers with no cups (herein referred as control), and cups with no contents or filters to account for possible manipulative artifacts (n = 3). Response variables were maximum quantum yield of photosystem II (Fv/Fm) as a proxy for photosynthetic health, to assess physiological response of endosymbionts at the point of contact between filaments and coral tissue, in dark-adapted colonies (15min - 24 and 48h); zooxanthellae concentration in the water of the experimental unit (24 and 48h) and in-hospite (after 48h). Additionally, rapid light curves (RLC's) were performed (0 and 48h), in order to access the photosyhtesis apparatus viability through coefficients: photosynthetic rate (α), maximum relative electron transport rate (rETRm), and minimum saturating irradiance (Ek).

3.2.8 Statistical Analysis

All statistical analysis was performed in R environment. When assumptions of parametric tests were not met, data were either square root or Tukey's Ladder of Powers transformed, in case normality or homoscedasticity still wasn't achieved, data were analyzed with Kruskal-Wallis multiple comparison (Dunn, 1964), with p-values adjusted with the Benjamini-Hochberg method, and pairwise comparisons using Wilcoxon rank sum test. When treatments had temporal or spatial dependency among samples within the response variable, data were analyzed with Repeated Measures ANOVA with autocorrelation factor (ACF), and effects verified with Tukey Post-Hoc test. Biofilm paired samples and Aquaria (PAM) paired samples were analized with Paired-t-tests. Crude extract incubations were analyzed with One-way ANOVA and Tukey Post-hoc tests.

3.3 RESULTS

3.3.1 MORPHOLOGICAL AND MOLECULAR CHARACTERIZATION OF FILAMENTOUS CYANOBACTERIA

A total of 12 16S rDNA sequences of benthic filamentous cyanobacteria from Abrolhos were obtained: (i) four sequences from single filaments picked from naturally occurring tufts (PLECA1, PLECA4, PABFA3, PABFC6) and one establish in culture (CCMR0174), all of the wide filaments of the *Lyngbya majuscula* morphotype; (ii) seven sequences (CCMR0280, CCMR0281, CCMR0282, CCMR0283, CCMR0285, CCMR0286, and CCMR0287) from cultures of the narrow filaments of the *Leptolyngbya* sp. morphotype. A phylogenetic reconstruction (Figure 6) grouped the large filaments of the *L. majuscula* type in two clades: PLECA1 and PLECA4 in the *Okeania/Lyngbya polychroa* clade with 99% bootstrap; and PABFA3, PABFC6 and the cultured strain CCMR0174 in the *Moorea/Lyngbya majuscula* clade also with 99% bootstrap. Six of the thin *Leptolyngbya*-like filaments (CCMR0280, CCMR0281, CCMR0282, CCMR0283, CCMR0286, and CCMR0287) grouped together in a clade with the genera *Leptolyngbya/Phormidium* with 99% bootstrap support, whereas the strain CCMR0285 grouped together with two representative of the genus *Halomicronema* with 99% bootstrap support.

Analysis of morphological traits of cyanobacterial filaments of the *Lyngbya majuscula* morphotype (Figure 22 SM), frequently observed on pinnacles as macroscopic colonies in the shape of upright tufts, revealed 3 categories in consonance with genomic analysis (Figure 6, Table 3). One morphotype, PABFA3 (with 16S rDNA sequence 99% similar to *Moorea producens* GU724206.1) was picked from a tuft that had a macroscopic flame-like appearance with dark-red contours and an inner pale region. The cyanobacterial filament was non-ramified and enclosed in exopolysaccharide sheaths with discoid cells arranged in trichomes, which have a width of 61µm, cell width 45 µm. The filament PABFC6 (with 16S rDNA sequence 99% similar to *Moorea producens* KC790370.1) was picked from a long pink-brown tuft. The filament was non-ramified, enclosed in an exopolysaccharide sheath with discoid cells arranged in trichomes with a width of 120 µm and discoid cells measuring 89 µm (width) by 15 µm (height). PLECA1 and PLECA4 (with 16S rDNA sequence 100% similar to *Okeania erythroflocculosa* KC986930.1) came from a long pink-brown tuft. Filaments was non-ramified, enclosed in exopolysaccharide sheaths with discoid cells arranged in trichomes with a width of 59-67 µm, cell width 49-54 µm, cell height 6 -7 µm.

Worth noting is the fact that one filament genetilcally similar to *Moorea producens* (GU724206.1), PABFA3, is within dimensions and pigmentation tones described for the taxon.

Whereas PABFC6 has cell dimensions around 100% greater than maximum values described for *Moorea producens* (KC790370.1). Also, PLECA4 has cell dimensions around 80% greater than maximum values described for *Okeania erythroflocculosa* (KC986930.1), being up to 55% wider and 130% longer. Similarly, PLECA1 has cell dimensions around 60% greater than maximum values described for *Okeania erythroflocculosa* (KC986930.1), being up to 40% wider and 96% longer (Table 3).

Table 3 Morphological traits of *Okeania erythroflocculosa, Moorea producens, Moorea bouilonii*, field collections and clonal non-axenic culture isolate CCMR0174. Traits of *M.producens* and *M.bouillonii* extracted from *Engene et al. (2012)*. Traits of *O.erythroflocculosa* from *Engene et al. (2013)*.

Traits\Tx.	*O. erythroflocculosa*	PLECA1	PLECA4	*M.producens*	PABFA3	PABFC6	*M.bouillonii*	CCMR0174
Habitat	Seagrass; reefs; beach	Pinnacles (Top-Wall)	Pinnacles (Top-Wall)	reefs; rocks; mangroves	Pinnacles (Top-Wall)	Pinnacles (Top-Wall)	reefs; rocks; mangroves	Pinnacles (Top-Wall)
Macroscopic morphology	Long dark pink tufts	Long dark pink tufts	Long dark pink tufts	Long dark pink tufts	Long dark pink tufts	Long dark pink tufts	Long dark pink mat firmly attached to corals	Long dark pink tufts
Depth (m)	2 - 20	3 - 6	3 - 6	3 - 6	6 - 8	6 - 8	2 - 25	5 - 8
Color	dark pink	dark pink	pink	dark pink to brown green	pink	salmon pink	red brown to pink	red brown
Filament width (μm)	32 - 42	59	67	30 - 82	61	120	N/A	95
Cell width (μm)	32 - 35	49	54	25 - 70	45	89	N/A	94
Cell height (μm)	2 - 3	6	7	3 - 7	N/A	15	N/A	24

One isolated cyanobacterial strain (CCMR0174) with morphological traits similar to the pink-brown, thick trichomes of the *Lyngbya majuscula* morphotype, was also processed for gene sequencing, as well as for morphometry. The 16S rDNA sequence of strain CCMR0174 was 99% similar with sequences of *Moorea producens* (KC790370.1) and *Moorea bouillonii* (GU111927.1). Morphology consisted of non-ramified, dark brown-red filament enclosed in exopolysaccharide sheaths with discoid cells arranged in trichomes with a width of 95 μm, cell width 94 μm, cell height 24 μm. It seems that the exopolysaccharide sheaths go thinner when the trichomes are placed in culture conditions, contrasting with the thicker sheaths observed in field collections samples (Figure 2, Table 1). Cells of the strains CCMR0281, 0282, 0287, 0280, 0285, 0286, 0283, morphologically similar to *Leptolyngbya* sp. were 2.5 ± 0.3 μm long and 1.3

± 0.1 μm wide, arranged in unbranched filaments linked by the narrower end of the cells. 16S rDNA sequences of strains CCMR0280, CCMR00281, CCMR0282, CCMR0282 and CCMR0286 were 100% similar to *Leptolyngbya* sp. (JX481735.1), whereas the sequence of strain CCMR0285 was 100% similar to *Halominonema* sp. (KY787126.1) and the sequence of strain CCMR0286 was 98.6% similar to *Phormidium* sp. (HM446281.1).

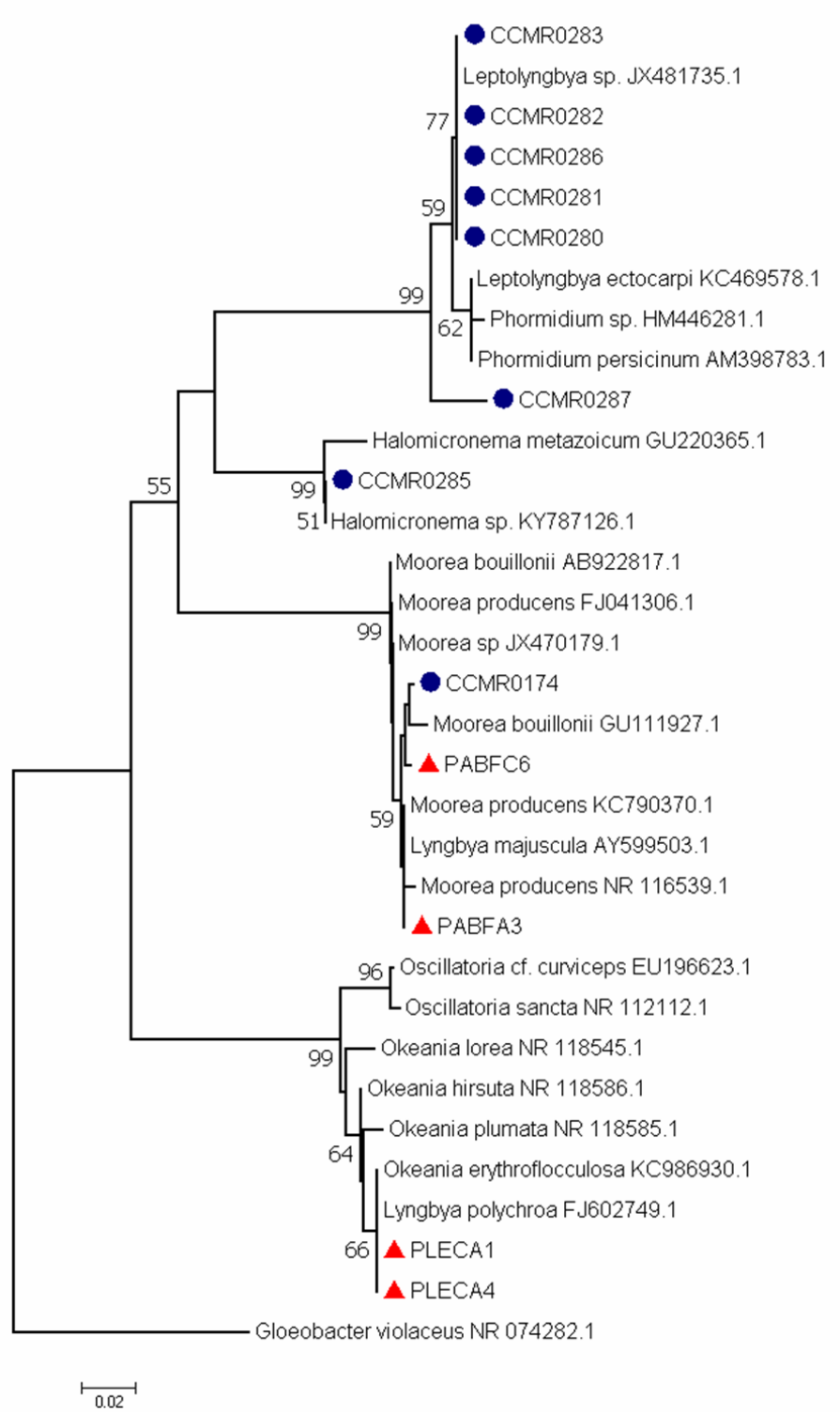


Figure 6 Evolutionary relationships of Abrolhos reefs filamentous cyanobacteria based on partial 16SrDNA sequences. Sequences obtained from single cyanobacterial filaments (red triangles) and from cultured strains (blue circles, CCMR codes) are shown. The evolutionary history was inferred using the Neighbor-Joining method (Saitou and Nei, 1987). The optimal tree with the sum of branch length = 0.56885699 is shown. The percentage of replicate trees (only values >50%) in which the associated taxa clustered together in the bootstrap test (500

replicates) are shown next to the branches (Felsenstein, 1985). The tree is drawn to scale, with branch lengths in the same units as those of the evolutionary distances used to infer the phylogenetic tree. The evolutionary distances were computed using the Jukes-Cantor method (Jukes and Cantor, 1969) and are in the units of the number of base substitutions per site. The rate variation among sites was modeled with a gamma distribution (shape parameter = 1). The analysis involved 33 nucleotide sequences. All positions containing gaps and missing data were eliminated. There was a total of 251 positions in the final dataset. Evolutionary analyses were conducted in MEGA7 (Kumar et al., 2016).

3.3.2 EFFECTS OF CYANOBACTERIAL EXUDATES AND CRUDE EXTRACT ON *Symbiodinium* sp *EX*-HOSPITE.

Cell concentration of *M. braziliensis* symbionts (CCMR0100), was affected by exudates from isolates (CCMR0174, 0175, 0176: Chisq=32.7, Df=3, $p<0.0001$), (CCMR0282: Chisq=11.9, Df=3, $p=0.007$), (CCMR0229, 0283: Chisq=37.5, Df=3, $p<0.0001$). Counts in treatments were significantly lower when compared to control vials, in all 6 incubations (Repeated Measures ANOVA with Tukey HSD, Figure 7). The effects, assumed to be the difference (calculated as percentage) between control and treatment for each day (the effect could be either positive or negative), varied throughout the multiple tests. The highest frequency of negative effects was observed after 48h (14 strains had a negative effect over *Symbiodinium* spp. in 48h). The strongest effects (higher than 40% and up to 59% decrease in cell count relative to control), on the other hand, were observed after 72h of incubation (Figure 7). A total of four strains: CCMR0174, 175, 176 and 0283, significantly reduced target cell counts in more than 40%, with CCMR0174, 175, 176 delivering such effect after 48h (Figure 8) and CCMR0283 gradually increasing the difference between exposed cells and the control towards 72h (Figure 7, Table 4). Cell concentration of *M.braziliensis* symbionts in assay vials was negatively affected by the crude extract at natural concentration and in doses diluted 10-fold. However, only the dose at natural concentration (1) decreased cell counts significantly different relative to both controls (SS=16401719, Df=5, F=9.43, $p<0.0001$, Figure 9), after 48h. The exudate from the field, negatively affected *Symbiodinium* sp. cell counts within 24h, although a significant effect was not detected. It is reasonable to expect that differences cell counts between control and treated vials would increase even more with continued exposure to exudates ($p>0.05$ Figure 10).

Table 4 Decrease percentage in *Symbiodinium* cell counts exposed to exudates CCMR0174, 0175, 0176, 0283, after 24, 48 and 72h, relative to control cell counts.

Tx.	T24(%)	T48(%)	T72(%)
CCMR0174	33	51	50
CCMR0175	38	53	50
CCMR0176	34	59	44
CCMR0283	33	16	51

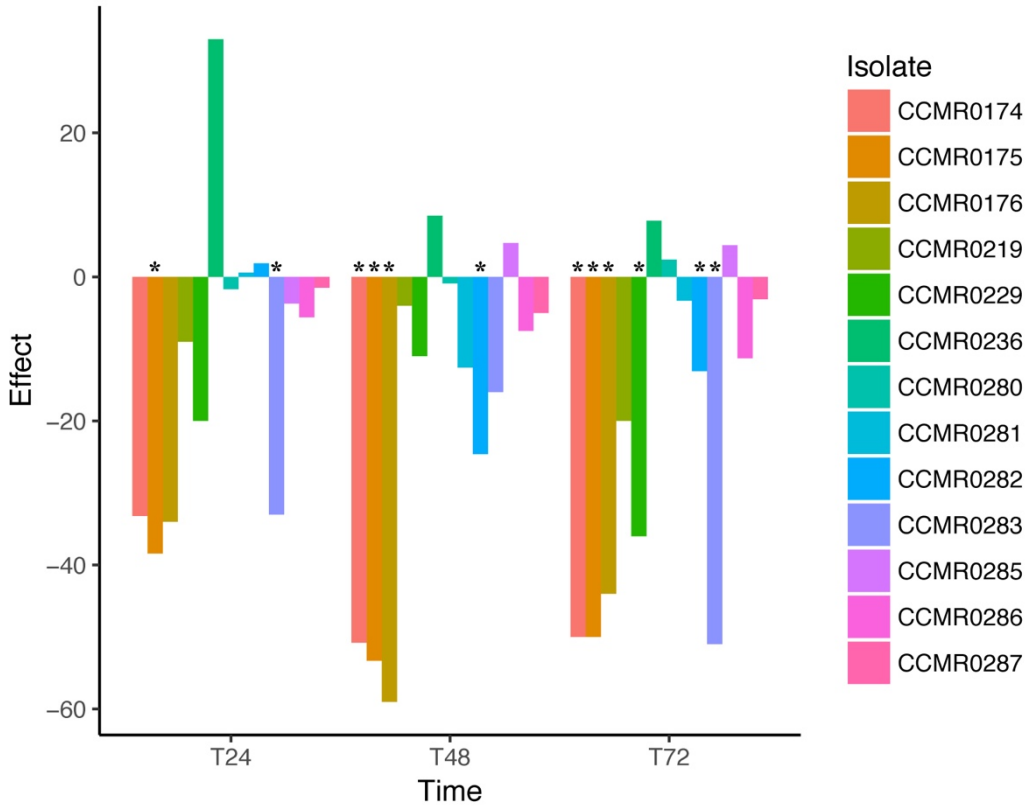


Figure 7 Allelopathic effect of cyanobacteria isolates on *Symbiodinium* cells. The effect was accessed by analysing, for each day, the difference in the cell numbers of the symbiont and its respective control. The negative bars indicate that cells exposed to cyanobacteria exudates decreased in numbers compared to the control; positive bars indicate that exposed cells grew more that in the control (although only negative effects were significant). The decrease or increase is given as percentage, i.e., how much the cells decreased/increased in relation to the control. direction (positive or negative) of *Symbiodinium* cell counts in vials treated with exudates from all strains. * = statistical significance compared to controls, p-value < 0.05 (Repeated measures ANOVA, Tukey HSD).

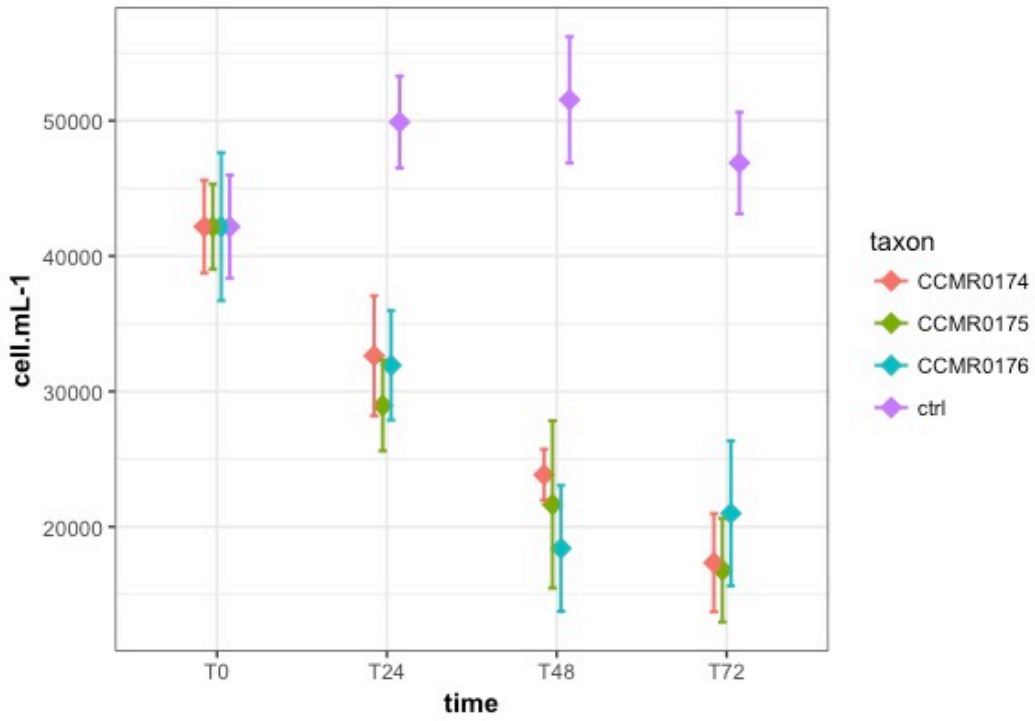


Figure 8 Cell concentration for incubations with strains CCMR0174, CCMR0175 and CCMR0176. Error bars are standard errors.

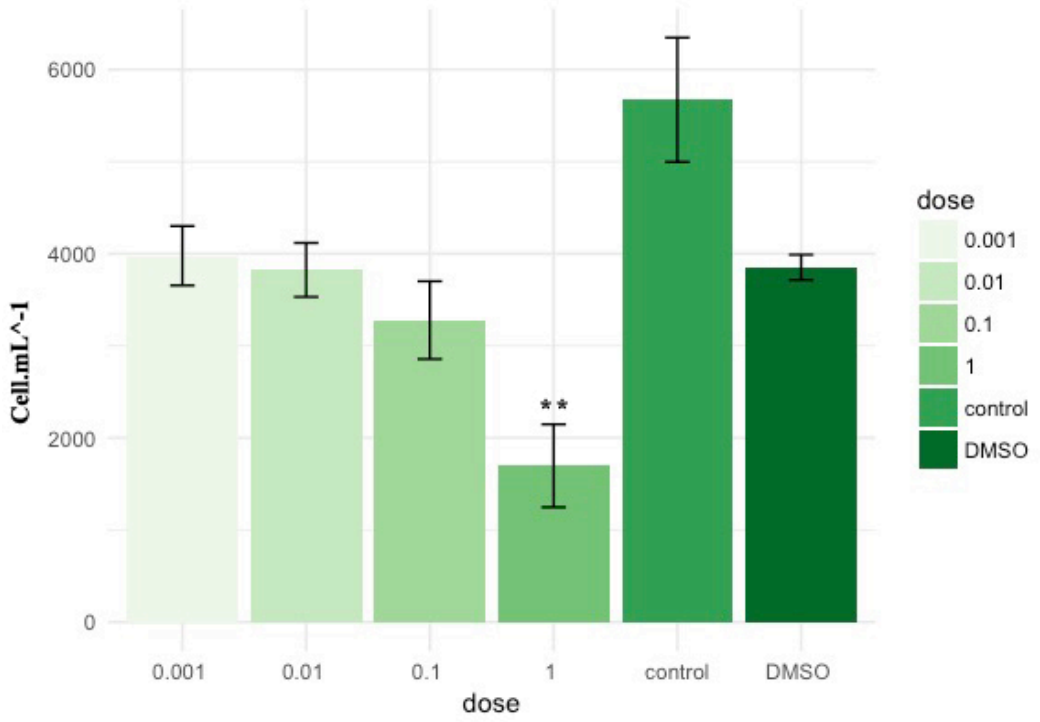


Figure 9 Cell concentration for incubations with crude extract in natural concentration (1), diluted 10x (0.1), diluted 100x (0.01) diluted 1000x (0.001). Error bars are standard errors. * = statistical significance compared to controls, p-value < 0.05. Cyanobacteria crude extract at

natural concentration (1) significantly ($p < 0.001$) reduced *Symbiodinium* cell counts in relation to controls.

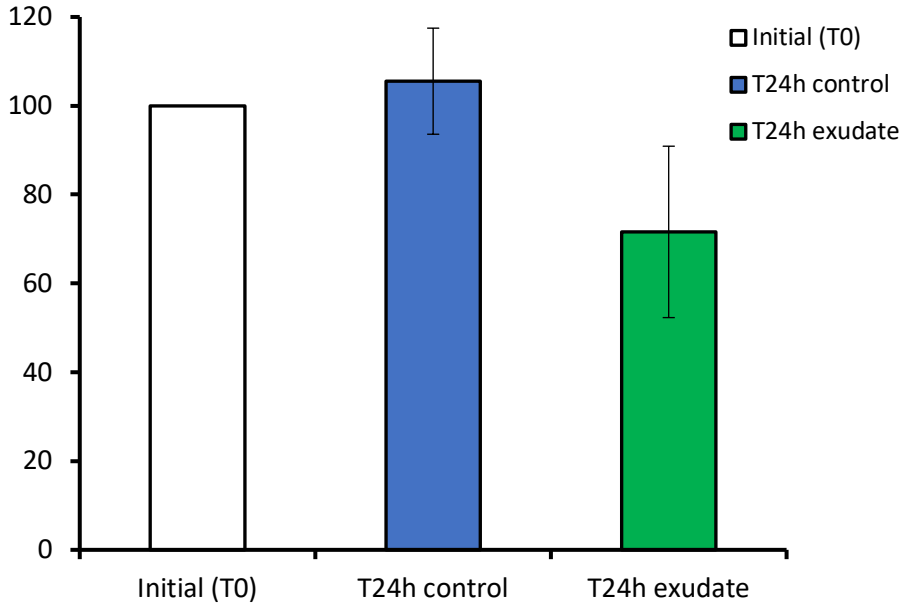


Figure 10 Cell concentration for incubations with exudates collected directly from within cyanobacteria tufts in the field. Error bars are standard errors.

3.3.3 Characterization of the coral-cyanobacteria contact in the field

In-situ readings of effective quantum yield (ϕ PSII) with Diving PAM, revealed distinct (Chisq= 41.7, Df= 3, $p<0.0001$) lower photosynthetic health of symbionts in live coral tissue in contact with cyanobacteria, in comparison to both distance - coral tissues not in contact with cyanobacteria (colony top-center); and allelopathy/shading (coral colony with no cyanobacteria) controls (Figure 11).

Also, cytometry of coral biofilm from natural encounters revealed that heterotrophic prokaryote taxa abundance was higher at the cyano-coral contact (425 cell.μl^{-1})from the top-center (223 cell.μl^{-1}) of coral colony ($t = 6.6861$, $df = 3$, p-value = 0.006824), as well as for picocyanobacteria which were more abundant at the contact (44 cell.μl^{-1}) than at the colony top-center (33 cell.μl^{-1}), according to statistical tests ($t = 3.5672$, $df = 3$, p-value = 0.03763). Also, contact with cyanobacteria affected the heterotroph/autotroph ratios within the biofilm when comparing both loci, at top center h/a = 6.4, at the contact h/a = 9.5.

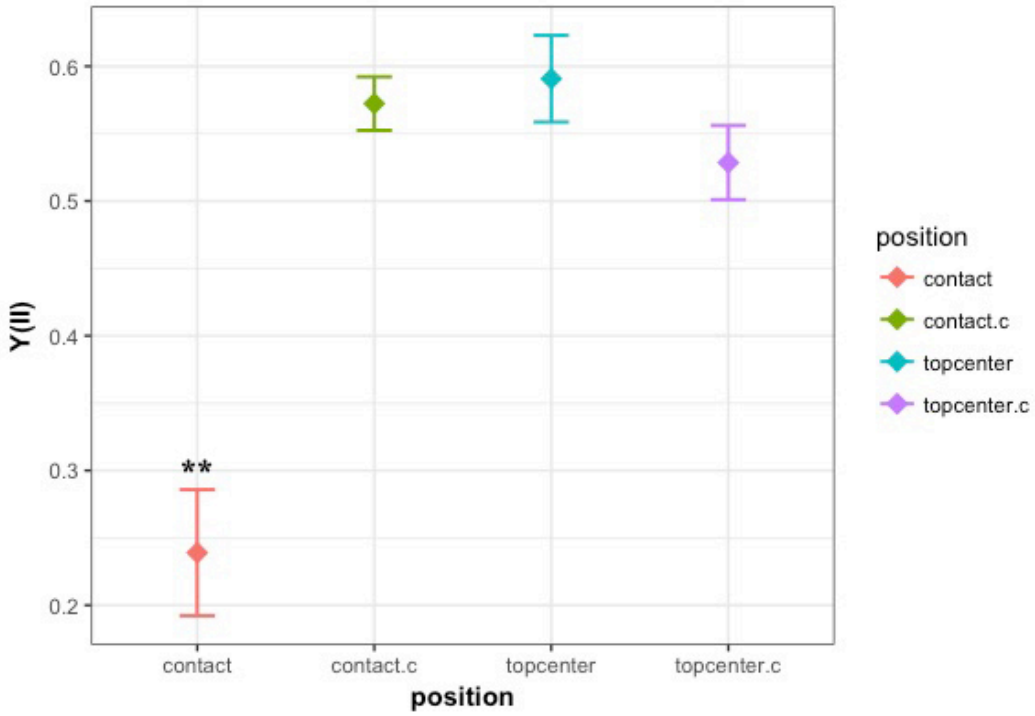


Figure 11. Effective quantum yield of photosystem II (ΔF/Fm') with Diving PAM from live tissue at the point of contact with cyanobacteria and controls: contact (point of contact between cyanobacteria and coral live tissue); contact.c (colonies with no tufts bordering live tissue); top-center (top-center of colonies with tufts bordering live tissue); topcenter.c (top-center of colonies with no tufts bordering live tissue). Photoinhibition of endosymbionts at point of contact with cyanobacteria (contact) is marked with ** = statistical significance compared to controls, p-value < 0.01. Error bars are standard errors.

3.3.4 Effects of cyanobacterial crude extracts and exudates on *Symbiodinium* in aquaria.

In hospite zooxanthellae cell counts were on average 37% and 12% lower in treatments with cyanobacterial extracts and whole filaments, respectively (Figure 12), although no statistically significant differences could be detected due to the high variability in the response (SS=11844787, df= 4, F= 1.3786, p= 0.309). Counts of symbiont cells *ex*-hospite were on average 5 times and 10 times greater in treatments with cyanobacterial extracts and whole filaments, respectively, after 24h, and counts of both treatments were 6 times greater after 48h, but such changes were not statistically significant neither in 24h (SS=3048257, df=4, F=0.7914, p = 0.5568), or 48h (SS=59173, df=4, F=0.7769, p=0.5648) (Figure 13). Also, we could not detect significant difference in Fv/Fm or RLC coefficients (α:SS=0.012928, df= 4, F= 1.3759, p= 0.3098; ETRm: SS= 86789, df= 4, F= 0.2258, p= 0.9178; and Ek SS=231486, df= 4, F= 0.2067, p= 0.9289, respectively) among treatments, however a distinct variation in relation to T0 could be observed for Fv/Fm values (Figure 14). An alteration in water color was very

pronounced in treatment beakers (live trichomes or crude extract) in which a sudden turbidity could be noticed, possibly caused by expelled *Symbiodinium* sp. from test corals.

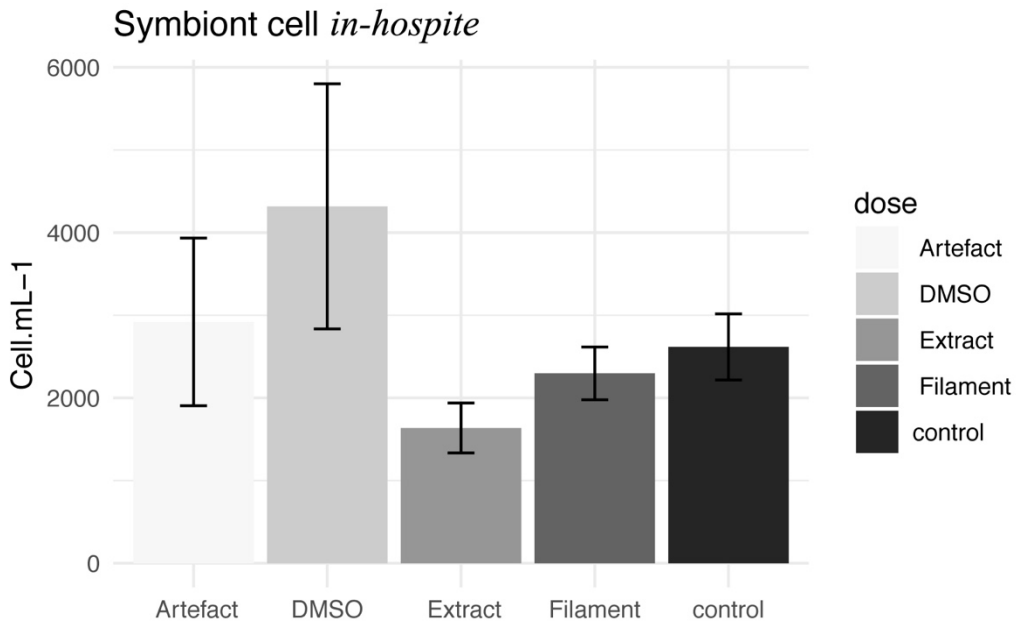


Figure 12. Cell concentration *in-hospite* in the coral tissue of experimental units for incubations with crude extract, live tufts, DMSO, artefact and control. Error bars are standard errors. Symbiodinium cell counts in treatments were lower in comparison to controls, but no significant difference was detected.

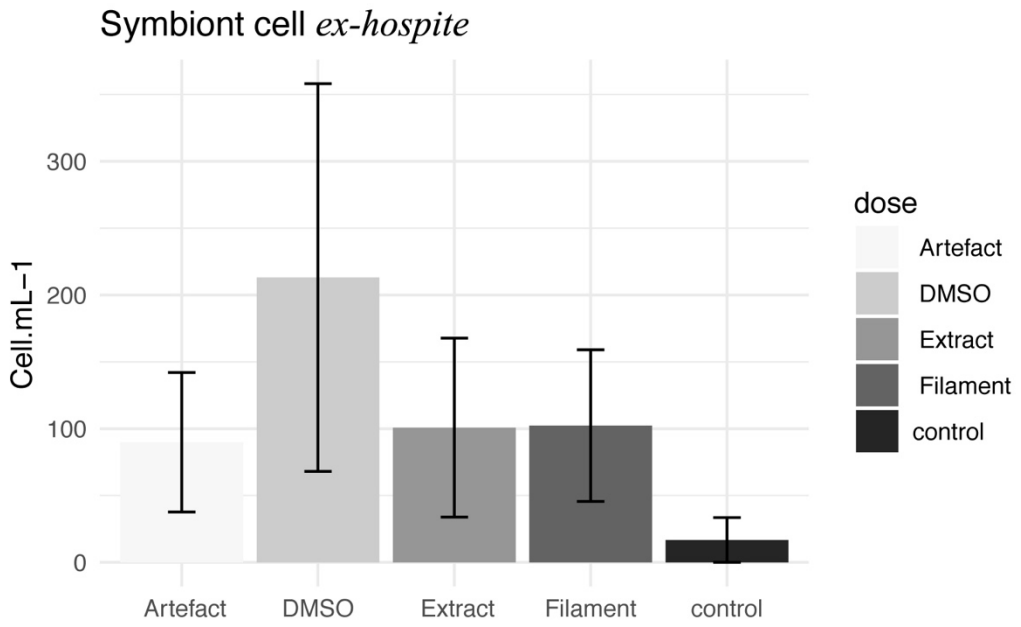


Figure 13. Cell concentration ex-hospite in the water of experimental units for incubations with crude extract, live tufts, DMSO, artefact and control. Error bars are standard errors.

Symbiodinium cell counts in treatments were higher in comparison to controls, but no significant difference was detected.

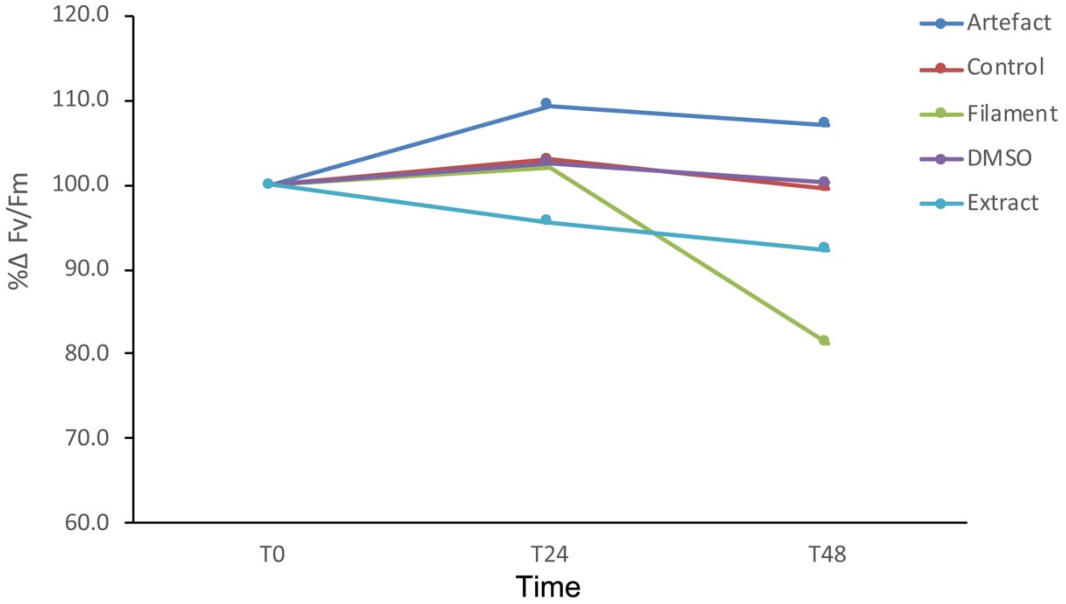


Figure 14 Effect size (% Δ in relation to T0) in maximum quantum yield of photosystem II (Fv/Fm) with Diving PAM from live tissue at the point of contact with cyanobacteria and controls along time. No significant difference.

3.4 DISCUSSION

Massive outbreaks of benthic marine cyanobacteria are of great concern worldwide and it has been related to warming temperatures and eutrophication scenarios, being also associated with direct anthropogenic disturbances (Taylor et al. 2014; Brown et al. 2017). As recent reports point out to an ever-increasing atmospheric greenhouse gases concentration (Blunden et al. 2018), it is expected that marine ecosystems will continue to undergo significant changes in order to keep up with the ongoing climate change. Massive bleaching events (Eakin et al. 2016), frequent cyanobacteria outbreaks (Taylor et al. 2014), composition and distributional shifts (Wernberg et al. 2016) are examples of a response to altered climate conditions in marine communities. Although there is a strong connection among geographically spread and yet analogous events, the scale resolution of such responses is rather regional or local (Bates 2018) with a strong element of species and site specificity to it (Davidson et al. 2014).

Benthic filamentous cyanobacteria are becoming increasingly frequent in Abrolhos reefs (Ribeiro et al. 2018). Morphology and genetic analysis of naturally occurring

cyanobacterial filaments unveiled the first occurrence of two pantropical genera, *Moorea* and *Okeania*, in SWA. These genera are previously known for its occurrence in Florida, Caribbean and the Pacific. Among the three attributed taxa *Moorea producens* is considered a cosmopolitan species, *Moorea bouillonii* have been reported to date for tropical Pacific Ocean (Engene et al. 2012). Taxonomy resolution of benthic cyanobacteria is imperative to understand consumer controls (Capper and Paul 2008), biosynthesis of secondary metabolites (Thacker and Paul 2004), and their physiological demands (Reed et al. 2016).

Allelochemicals from benthic cyanobacteria can inhibit coral tissue growth (Titlyanov and Titlyanova 2009), disrupt coral holobionts microbiome and contribute to an increased vulnerability to pathogens (Morrow et al. 2011), negatively affect coral recruitment (Kuffner et al. 2006), and act as feeding deterrents (Thacker et al. 1997). This somewhat constitutive toxicity could be inherited due to the observed fragile structure of trichomes, suggesting a relative dependency of secondary metabolite mediation in order to hold their ground in the benthos, and compete for resources while being unpalatable to consumers (Thacker et al. 1997). Together with *Lyngbya, Moorea* and *Okeania* produce more than 40% of the cyanobacteria metabolites described to date (Engene et al. 2011; Dittmann et al. 2015). Whereas *Leptolyngbya* is associated with black band disease consortia and produces cyanotoxins (Gantar et al. 2009).

For this discussion we will consider the allelopathy definition by Rizvi and Rizvi (1992) which considers any direct or indirect harmful or beneficial effect by one plant (including microrganisms) on another plant or organism through production of chemical compounds, including defense through allelochemicals, as well as resource competition. According to our results, several of the filtrates and the crude extract tested in this study are to some extent allelopathic, potentially cytotoxic, and may facilitate disruption of coral microbiome. However the production of secondary metabolites are inherently variable and species-specific (Puglisi et al. 2014), and the effects reported herein might be either not detected or exacerbated during blooms, according to the respective dominant taxa within the mat/tufts biomass.

When investigating the effect of the proximity of trichomes on the photosynthethic apparatus (PSII) of endosymbyonts, we found a photo inhibition effect along natural encounters in which tufts were growing at the border of the colony. This allelopathic mechanism is analogous to cyanobacterin, a metabolite from freshwater taxon *Scytonema hofmanni*, and fischerelin A, from *Fischerella muscicula* both compounds affect growth of photoautotrophs by inhibition of photosystem II (Gleason et al. 1986; Gleason et al. 1984; Gleason 1990). Although our design does not allow for distinguishing the effects of allelochemicals from shading (Jompa and McCook 2003), it would still be considered as allelopathy since one

organism is reaping light resources out of the competing organism. However, further investigation is needed to differentiate allelochemicals from shading effect.

Bioassays using crude organic extracts provide guidance for an initial characterization of bioactive compounds within a specific sample, and assists further refinement following progressive fractionation. Also, metabolites that are not naturally diffused into the environment are carried by organic solvents and allow inference of general toxicity. For instance, considering the wide spectrum of the organic solvents used, it is possible that the final homogenate carries cell fragments and pigments that may bias the real effect of secondary metabolites. Therefore, we tested several dilutions in order to estimate the minimum concentration and the magnitude of such effect.

Average cell counts of in-hospite *Symbiodinium* increased in parallel to a decrease in the *ex*-hospite population of the zooxanthellae within the first 24h of contact with either cyanobacterial extracts or exudates from intact cyanobacterial filaments, indicating a potential cytotoxicity by compounds produced and exudated by the cyanobacteria. Such potential was further corroborated by the negative effect on *Symbiodinium* sp. cells exposed to cell-free filtrates from six cultured cyanobacterial strains (three of them identified as *Moorea producens* and/or *Moorea bouillonii*) and exudates from inside tufts collected in the field. Leão et al. (2009) performed similar growth assays with freshwater cyanobacterial strains and reported reduction in cell numbers of *Chlorella vulgaris* after exposure to exudates. The effect was attributed to a cytostatic rather than a cytolytic effect of allelochemicals present in the filtrates. Growth inhibition potential was reported for other cyanobacteria metabolites such as hapalindole compound also from *Fischerella* sp., and calothrixin A from *Calothrix* sp., which affected growth of prokaryotic and eukaryotic cells in bioassays, and also inhibited genetic replication (Doan et al. 2000). Bioassays with Baltic Sea cyanobacteria *Nodularia spumigena* and *Anabaena* sp. reported antagonistic effects of exudates towards cryptophytes (Suikkanen et al. 2004). The cyanobacterial strains established in culture and natural cyanobacteria populations from Abrolhos investigated in the present study produce allelochemicals that could potentiallyimpair light harvesting apparatus of coral zooxhanthellae, and also affect endosymbionts cell division mechanisms, disrupting the symbiosis.

Cyanobacteria can grow as dense mats and tufts (Stal, 2012), and also as part of the so-called turf consortia (Connell et al. 2014). In the Caribbean *Moorea producens* and *Okeania erythroflocculosa* are also abundant in turf algae matrix (Engene et al. 2012, 2013). Similarly, in Abrolhos Bank, Walter *et al*. (2016) found high abundance of Oscillatoriales in metagenomic screening of turf material, where these taxa are often seen entangled within algal canopies.

Additionally, the composition of the turf influences the final effect upon competitors, with filamentous taxa being more antagonistic towards reef builders (O'Brien and Scheibling 2018). The effect of filamentous cyanobacteria on the coral biofilm seen herein yielded altered heterotrophs-autotrophs ratios, with a higher density of heterotrophs at the point of contact that could render increased vulnerability of the holobiont to pathogens or commensal microbes (Morrow et al. 2011). Wangpraseurt et al. (2012) demonstrated that such antagonistic effects are facilitated by the enhancement of diffusive boundary layers (DBL) between turf and *Porites* spp., which accumulates and transfers metabolites from algae to corals. Periodic pulses of cyanobacteria exacerbated growth pressures coral live tissue in Abrolhos reefs (Ribeiro et al. 2018), and allelopathic properties elucidated in the present study are likely to be involved in the microenvironment interaction within turf/cyanobacteria-coral boundaries, as increased biomass may render thicker DBLs and enhance dissolved organic matter (DOM) transfer mechanisms (Jorissen et al. 2016).

Furthermore, allelochemicals from microalgae might have community wide effects on the photosynthesis and carbon uptake of reef associated plankton and could also be a strategy in resource competition (Fistarol et al. 2003). The synthesis of alkaline phosphatases and siderophores that enhance affinity and consequently the uptake rates of ferric and phosphorous compounds, respectively, may deplete nutrients and exclude other taxa from ecological niches, consequently impacting local food webs (Leão et al. 2012). Accordingly, since cyanobacteria outbreaks are associated with low wave energy periods (Albert et al. 2005), the diffusion of resource harvesting compounds during such weather conditions can be more efficient since water-mediated transfers are flow speed dependent (Jorissen et al. 2016).

During a cyanobacteria outbreak in Abrolhos, a considerable large biomas of morbid individuals of the specialist consumer *Stilocheylus striatus* was observed in accumulation pits at the sea bottom or washed up on shore (Ribeiro et al., 2017). This could mean either no predation upon *S. striatus* or that satiation was reached during exponential growth phase of cyanobacteria biomass and sea hare hords kept being attracted to mats afterwards. In either way, if all the accumulated biomass of *S. striatus* is not directly transferred upward to other trophic levels through direct consumption, the ecological role of such outbreaks in Abrolhos Bank, still remains elusive as this rich nutrient pool (Ahern et al. 2007), is either being exported elsewhere, sinking and binding into the sediment or regenerated into the food web through microbial loops (Silveira et al. 2015), that might feed new bloom events (Brocke et al. 2015).

Benthic cyanobacteria blooms pose a health and economic risk to human populations, through exposure to toxins in recreational activities, seafood and health impairment of species

explored by the tourism industry (Taylor et al. 2014; Osborne 2007; Capper et al. 2013). The mitigation of this periodic disturbance will have to deal with standardization of nutrient levels from continental inputs as most cyanobacteria are a nutrient limited, and ubiquitous component of marine systems (Whitton & Potts 2012). Coordinated action must take place also outside of MPA's to ensure water quality, alleviate pressures and enhance the connectivity within MPA networks (Murray et al. 1999). Further investigation must focus in the refinement of mats/tufts composition during outbreaks and the correlation of biomass and seasonality with water chemistry and abiotic factors. The allelopathic potencial of Abrolhos benthic filamentous cyanobacteria towards corals should be considered in our attempts to predict the evolution of the reef system facing regional (e.g. nutriphication) and global (e.g. climate-induced seawater warming) drivers of ecosystem changes.

3.5 CONCLUSION

In this study we elucidate the inhibitory effects of benthic cyanobacteria, their exudates and organic extracts over *M. braziliensis ex*-hospite and *in*-hospite *Symbiodinium* sp., and the microbiome within the holobiont. This antagonistic interaction partially explains the suppression of live coral tissue in Abrolhos Bank. The dominant taxa in upright tufts were *Moorea, Okeania* and *Leptolyngbya,* HAB species known for producing toxins during blooms. Although blooms are associated with environmental drivers such as wind, pluviosity, residence time and flushing rates of water masses, they are also indicative of depauperate environmental quality and compromised ecosystem health. A cyanobacteria density dynamics index is imperative to prevent human intoxication and further habitat degradation in Abrolhos reefs.

4 SUSTAINED MASS CORAL BLEACHING (2016-17) IN BRAZILIAN TURBID-ZONE REEFS: TAXONOMIC, CROSS-SHELF AND HABITAT-RELATED TRENDS

4.1 INTRODUCTION

Mass coral bleaching episodes have been reported in scattered localities since the early 20th Century (Verrill 1902; Vaughan 1914), and after the 1980's these events reached regional to global scales (e.g. 1982-83, 1987-88, 1994-95, 1997-98, 2002-03, 2015-16). Global bleaching episodes occur during positive phases of the El Niño-Southern Oscillation (ENSO) (Glynn 1991) and can be forecasted based on the duration and intensity of sea surface

temperature (SST) anomalies (Eakin et al. 2016). For the South-western Atlantic (SWA), bleaching episodes are reported since 1993 (Migotto 1997), but systematic monitoring at the regional scale is lacking (see Ferreira and Maida 2006). The SWA encompasses turbid-zone reefs dominated by stress-tolerant species (e.g. Moura et al. 2016; Bastos et al., 2018). Akin to "marginal" reefs in the Indo-Pacific (van Woesik et al. 2012; Morgan et al. 2017) and the Caribbean (Wagner et al. 2010; García-Sais et al. 2017), SWA reefs may be more resistant and resilient to thermal anomalies. Such putative "nearshore climate-change refugia" are subjected to reduced irradiance due to dissolved and suspended matter, and their corals may be more adapted to higher temperatures typical of shallower coastal waters (van Woesik et al. 2012).

Bleaching episodes may have variable outcomes, from full recovery to mass mortality, depending on the intensity and duration of the environmental stress (Glynn 1996; Baker et al. 2008), as well as on the overall health state of the ecosystem (Hoegh-Guldberg 1999). It is recognized that coral colony morphology is related to bleaching susceptibility (Brown and Suharsono 1990; Gleason 1993), but the full array of drivers that lead to increased resistance and resilience is not fully understood. Resistance to bleaching may be associated to local conditions such as upwelling and shading (Chollet et al 2010; Morgan et al. 2017), adaptation to extreme conditions (van Woesik et al. 2012), and depth – the "deep reef refugia hypothesis" (Bongaerts et al. 2010; Smith et al. 2014). In "marginal" reefs, associations with thermo-tolerant symbionts (Marshall and Baird 2000; Loya et al. 2001) and heterotrophic feeding (Anthony 2006) may also drive increased resistance and resilience to bleaching.

Understanding the interaction among causal factors and the consequences of mass bleaching episodes is critical to evaluate the health and forecast the trajectories of reef ecosystems. Here, we present a compilation of previous bleaching events in the SWA and describe the effects of the Third Global Bleaching Event (TGBE) (Eakin et al. 2016) in the region's largest coralline system, the Abrolhos reefs. We contrasted the susceptibility and short-term resilience of the most common corals, octocorals and zoanthids, and explored the drivers of habitat-level and cross-shelf bleaching patterns across 2016 (February, May, June and October) and 2017 (March).

4.2 MATERIALS AND METHODS

4.2.1 STUDY AREA

The Abrolhos Bank is a 46,000 km² enlargement of the Eastern Brazilian shelf (16°40'-19°40'S, 39°10'-37°20'W) off Bahia and Espírito Santo states. The region encompasses the largest (>8,000 km^2) and richest reef complex in the South Atlantic (Laborel 1969; Moura et

al. 2013). The Abrolhos reefs outstand globally for occurring as mushroom-shaped pinnacles (‘chapeirões’) built by bryozoans, coralline algae and corals under a low storm disturbance regime (Bastos et al. 2018). The unique shape of these pinnacles condition two contrasting habitats that occur in close proximity but encompass highly distinct benthic assemblages (Francini-Filho et al. 2008): tops (flat and well lit, 1-10 m depths) and walls (steep and poorly illuminated, 5-25 m depths) (Figure 1). These emerging and quasi-emerging structures occur in two arcs (seabed at 20–25 m depth), one ~10 km offshore (coastal arc) and another ~55 km offshore (offshore arc) (Figure 1). Coastal reefs are subjected to higher fishing and turbidity levels from terrigenous sources, while reefs in the offshore arc are less exposed to such land-based stressors (Bruce et al. 2012) and are within a no-take zone established in 1986. Deeper mesophotic reefs occur to the east of the offshore arc, either as columnar pinnacles that lack the mushroom shape (tops between 10-20 m depths) or as eroded carbonate platforms with 1-5 m heights (seabed at 30-90 m depths) (Moura et al. 2013; Bastos et al. 2018).

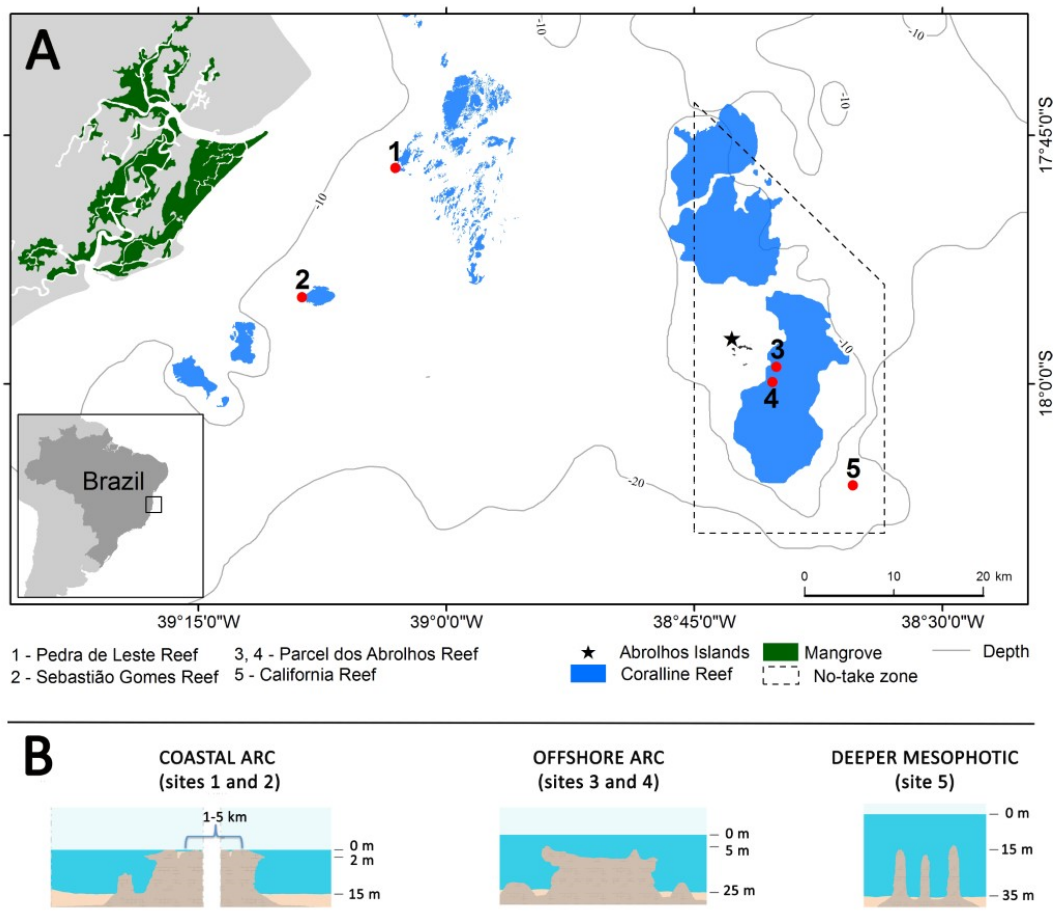


Figure 15 Study area. Sampling localities (A) and the general morphology of the pinnacles at each cross-shelf stratum (B). Isobaths in meters.

4.2.2 SAMPLING

Sampling sites were distributed in the coastal and offshore arcs (two sites in each arc) and also included one deeper mesophotic site (California Reef) between 12-30 m depths (Table 1). The high structural heterogeneity of the Abrolhos reefs has a substantial effect on benthic cover estimates obtained from different sampling approaches (Francini-Filho et al. 2013). Therefore, we used transects and photo-quadrats to estimate bleaching prevalence and to develop spatial and temporal contrasts. For spatial contrasts (habitat *vs.* arc) we sampled 2-3 line transects (100–150 m) at each habitat and locality (n=18) during the peak of the bleaching event (May 2016). All colonies intercepted by the line were assigned to one of the following categories (Guest et al. 2012): 1) Healthy (H), when colonies displayed normal coloration; 2) Partially Bleached (PB), when coloration was up to 50% lighter than H; 3) Heavily Bleached (HB), when bleaching was well evident and ranged from 50% lighter than H to completely white; 4) Bleaching and Mortality (BM), when tissue loss and/or biofilm/secondary colonization were recorded in all or part of the colony. Temporal variation was assessed from 10 randomly-placed fixed photo-quadrats repeatedly sampled at each habitat (top and wall) and site (n=5) in February, May, June and October 2016, and March 2017. Offshore arc sites (n=2) were sampled with photo-quadrats in all periods, although coastal arc sites were not sampled in October 2016, and the deeper mesophotic site (California Reef) was sampled in May and June 2016, and March 2017.

4.2.3 ENVIRONMENTAL VARIABLES

Monthly Multivariate ENSO Index (MEI) values were obtained in December 21 (2017), from NOAA's Earth System Research Laboratory (esrl.noaa.gov/psd/enso/mei). *In situ* daily mean temperatures were calculated from hourly records using Onset's HOBO$^{(r)}$ sensors installed at pinnacles' tops (5-8 m depths) in coastal and offshore arc reefs (2016 and 2017), and at the deeper mesophotic site at 20 m depth (July 2016-March 2017). Nighttime SST (4μ□, 5 km resolution) and the Degree Heating Week (DHW) index (Liu et al. 2014) were obtained in October 31st, 2017 from NOAA's Coral Reef Watch (CRW) (coralreefwatch.noaa.gov), using the Abrolhos' virtual station (18°S, 38.5°W). The CRW system uses satellite-derived nighttime SSTs to identify values of 1°C above maximum monthly means ("Hot Spot") and quantifies accumulated thermal stress over 12 weeks, delivering an associated bleaching alert scheme (Liu et al. 2006). Diffuse attenuation coefficient for downwelling irradiance at 490 nm (KD490) from the MODIS/Terra sensor were obtained at monthly frequency and 9 km spatial resolution from NASA's OceanColor Web (oceancolor.gsfc.nasa.gov) and used as a proxy for

turbidity. All remote sensing data were processed using SeaDAS software ver. 7.4 (seadas.gsfc.nasa.gov).

4.2.4 DATA ANALYSIS

Analyses included the 10 most common taxa, out of the ~19 scleractinian and 4 fire corals (*Millepora* spp.) recorded in Abrolhos (Castro et al. 2005): *Agaricia* spp., *Favia gravida*, *Madracis decactis*, *Montastraea cavernosa*, *Mussismilia braziliensis*, *M. harttii*, *M. hispida*, *Porites* spp., *Siderastrea* spp. and *Millepora* spp.. Relative cover (%) of each species was estimated from photo-quadrats and is presented as percentages of total cover of hard and fire corals. Each photo-quadrat consisted in 15 high-resolution contiguous images totaling 0.5 m^2 processed with the software Coral Point Count with Excel Extensions (Kohler and Gill 2006). Organisms' relative cover and bleaching categories were recorded using 600 randomly placed points per quadrat. The prevalence of the three first bleaching categories (H, PB and HB) for each species was estimated from transect data, while temporal trends were assessed with photo-quadrat data converted into a bleaching index (BI) following McClanahan (2004):

$$\mathrm{BI} = \frac{0 * \mathrm{H} + 1 * \mathrm{PB} + 2 * \mathrm{HB}}{2}$$

where H, PB and HB correspond to the bleaching level categories.

Spatial contrasts were explored with permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) based on a Euclidian Distance matrix, using arc and habitat as fixed factors, and the BI as the response variable (no transformations applied). Analyses were carried out with PRIMER 6 + PERMANOVA software (Anderson et al. 2008).

4.3 RESULTS

Five bleaching episodes were reported in the SWA since 1990, all associated to the previous global events (1998, 2010) and positive phases of ENSO (Fig. 2). Since 2000, the Abrolhos reefs were monitored during all austral summers, with lower than moderate bleaching (>30% of colonies bleached) recorded up to 2016. Severe bleaching (>50%) was recorded in 1993 and 1998 (see reference list in Fig. 2), with 9 and 5 affected species, respectively.

From 2014 to 2017, SSTs ranged from 24.2-29.6ºC, with highest DHW values between April and June 2016 (Fig. 3A). Satellite-derived temperatures above the regional bleaching threshold (27.9°C) were frequent and resulted in 8.4 DHW (7 days >8 DHW) and 6.7 DHW (11 days >6.5 DHW) in May 2014 and 2015, respectively. In April 2016, the Abrolhos reefs

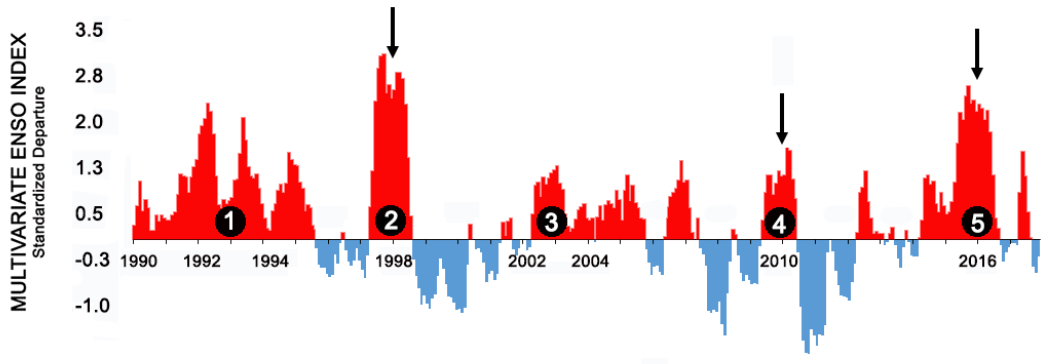
reached 9.7 DHW (57 days >8 DHW), and maximum values (47 days >9 DHW) were sustained for 37 days. Despite the subsequent colder phase, from July 2016 on (maximum DHW=4.0, April 2017), bleaching levels remained high at least until March 2017. *In situ* temperatures recorded in the coastal and offshore arcs varied similarly and did not differ from SSTs obtained from remote sensing (Fig. 3B). From July to September 2016, *in situ* temperatures from the deeper mesophotic reef were also similar to SSTs. However, from October 2016 to February 2017, *in situ* temperatures in the deeper mesophotic reef remained consistently lower than SSTs (Fig. 3B). Turbidity was significantly higher and more variable in the coastal arc (Fig. 3C).

Benthic cover in the coastal and offshore arcs was dominated by turf, macroalgae and CCA (crustose coralline algae, see Electronic Supplementary Material). Coral cover ranged from 9.4 to 39.8% in the coastal arc (values from pinnacles' tops and walls, respectively), and from 5.7 to 18.4% in the offshore arc (walls and tops, respectively; see Electronic Supplementary Material). The high coral cover in the coastal arc walls is related to the dominance (>90%) of *Montastraea cavernosa*. The 2016-17 bleaching episode was remarkable for its severity and for affecting all coral species (Table 2, Fig. 4), and also for being sustained across two summers, with bleached colonies recorded in February, May, June and October 2016, and in March 2017 (Fig. 4). Bleaching prevalence varied among species, sites, and along the study period. The most affected species on pinnacle´s tops were *F. gravida, Millepora* spp., *M. cavernosa, M. harttii, M. hispida*, *Porites* spp. and *Siderastrea* spp., with >40% of colonies bleached in at least one site during May 2016 (Tables 2 and 3, Fig. 5). On pinnacles' walls the most affected species (>40%) were *Agaricia* spp., *M. cavernosa, M. hispida, Porites* spp. and *Siderastrea* spp., the first two being more abundant in this habitat than in pinnacles' tops (Tables 2 and 3, Fig. 5). Conversely, *M. braziliensis* was less affected on tops (<40%), and *M. harttii* and *M. decactis* were less affected on walls, where the latter is more abundant (Tables 2 and 3, Fig. 5). Six species (*Agaricia* spp., *F. gravida, Millepora* spp*., M. braziliensis, M. harttii* and *M. hispida*) presented significant between-habitat differences in bleaching prevalence (Table 3). Interactions between arc and habitat effects were detected only for *Agaricia* spp. and *M. harttii* (Table 3).

In the coastal and offshore arcs, the relationship between the BI and the relative abundance of each coral species was variable (Fig. 5). For instance, the BI for *Agaricia* spp. and *M. hispida* was lower in sites and habitats where they were more abundant, while *F. gravida*, *M. decactis*, *M. cavernosa* and *M. harttii* presented an opposite trend (Fig. 5). Although we did not quantify bleaching in corals that represented <1% of total coral cover, we recorded affected colonies of *Mussismilia lepthophylla* (PB), *Meandrina braziliensis* (HB) and

Scolymia wellsi (PB and HB). In addition, the zoanthids *Palythoa caribaeorum* and *Zoanthus* spp. (PB, HB and BM), as well as the octocorals *Plexaurella grandiflora* and *P. regia* (HB, BM) were also affected.

In the deeper mesophotic site (California Reef), corals covered 14.8% of the substrate (13% scleractinian, 1.8% milleporans). The coral assemblage included nine species and was dominated by *M. cavernosa* (8.5% of total benthic cover). Six species bleached, but prevalence was lower than in the emerging reefs, not reaching the moderate bleaching status (>30% prevalence). The most affected species in June 2016 were *Agaricia* spp. (3% PB), *M. cavernosa* (4.5% PB), *M. hispida* (6% PB, 5% BM), and *Siderastrea* spp. (15% PB, 5% HB). In March 2017 prevalence increased for *Agaricia* spp. (10% PB), *M. cavernosa* (17% PB) and *Siderastrea* spp. (12% PB, 14% HB), and decreased for *M. hispida* (4% PB, 1.5% HB).



Oceanic Islands	N.D.	N.D	X	X	N.D.
Eastern Brazil	N.D.	N.D.	X	5	N.D.
Northern Bahia	N.D.	7	2	9	N.D.
Abrolhos	9	5	0	0	10
Southeastern Brazil	2	N.D.	N.D.	N.D.	N.D.

Figure 16 Multivariate ENSO Index (MEI) from 1990-2017 and the occurrence of coral bleaching. Numbers (1-5) within black circles indicate the number of bleaching events reported in Brazil during each MEI positive anomaly and arrows indicate the three global bleaching events. Numbers in the table indicate how many species were affected in each bleaching event and their respective location within the Western South Atlantic. ND= no data; X= bleaching reported, but the number of affected species is unknown. Data compiled from Migotto (1997), Castro & Pires (1999), Dutra et al. (2000), Leão et al. (2003), Ferreira and Maida (2006), Kelmo and Attrill (2013), Ferreira et al. (2013), Miranda et al. (2013), Dias and Gondim (2016).

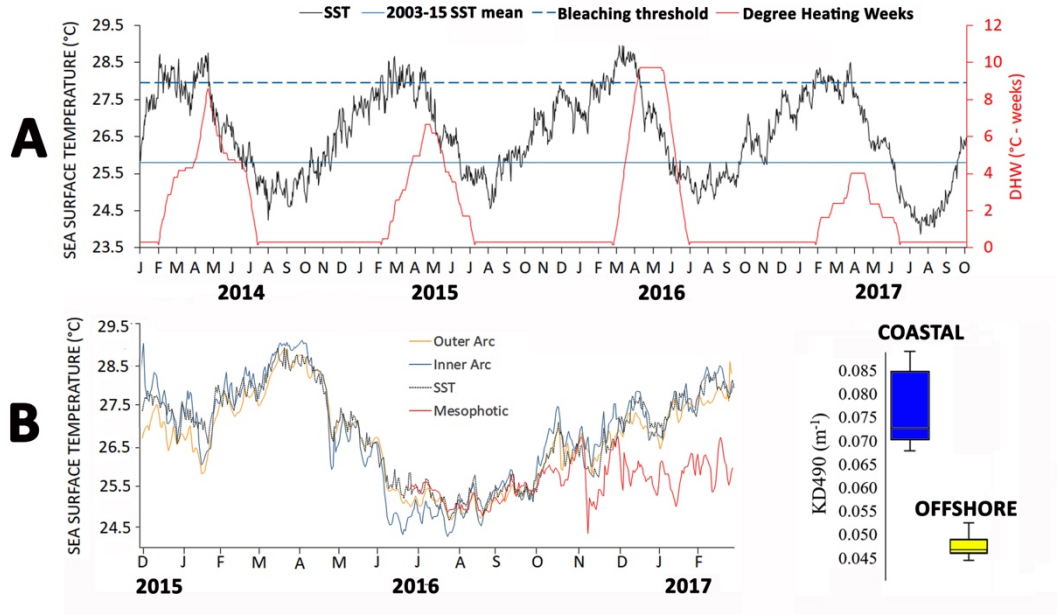


Figure 17 Recent trends in seawater temperature and turbidity in the Abrolhos reefs, Brazil. A= Satellite-derived sea surface temperature (SSTs) superimposed in the Degree Heating Weeks (DHW) Index, which indicates accumulated heat stress (2014-2017). Red horizontal line indicates the period when bleached colonies were recorded, solid horizontal blue line indicates decadal average SST, dashed line indicates the bleaching threshold. B= In situ temperature measurements in the three cross-shelf strata and SSTs (2016-2017) showing lower in situ winter temperatures in the deeper mesophotic reef. C= Turbidity in coastal and offshore reefs (2014-2017) indexed by the diffuse attenuation coefficient for downwelling irradiance at 490 nm (KD 490) derived from MODIS sensor.

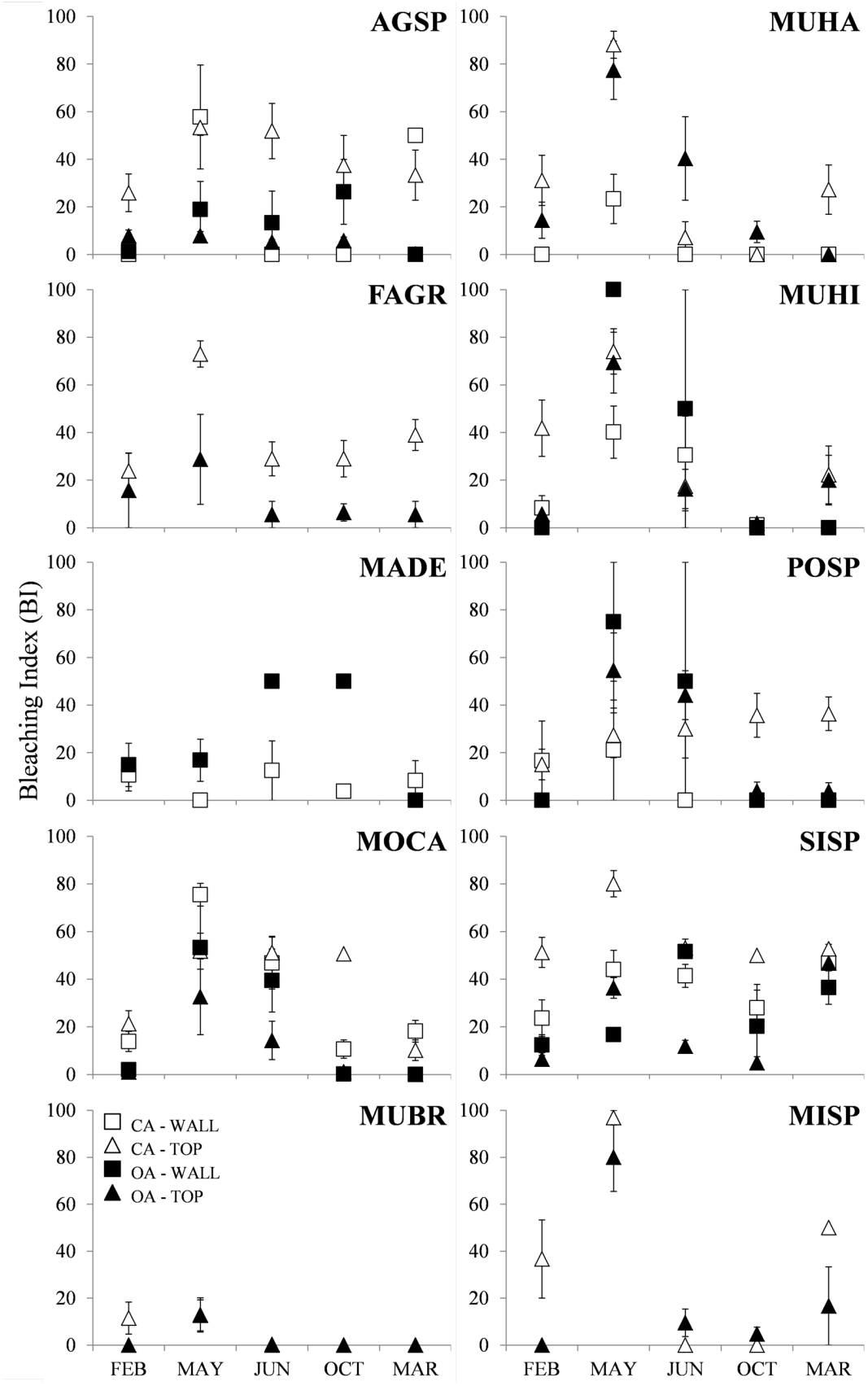


Figure 18 Temporal variation (February 2016 - March 2017) in the Bleaching Index (BI) for the 10 most abundant coral species in the different habitats and cross-shelf strata of the

Abrolhos Reefs. AGSP= *Agaricia spp*, FAGR= *Favia gravida*, MADE= *Madracis decactis*, MOCA= *Montastraea cavernosa*, MUBR= *Mussismilia braziliensis*, MUHA= *M. harttii*, MUHI= *M. hispida*, POSP= *Porites* spp., SISP= *Siderastrea* spp., MISP= *Millepora* spp. Bars represent Standard Errors.

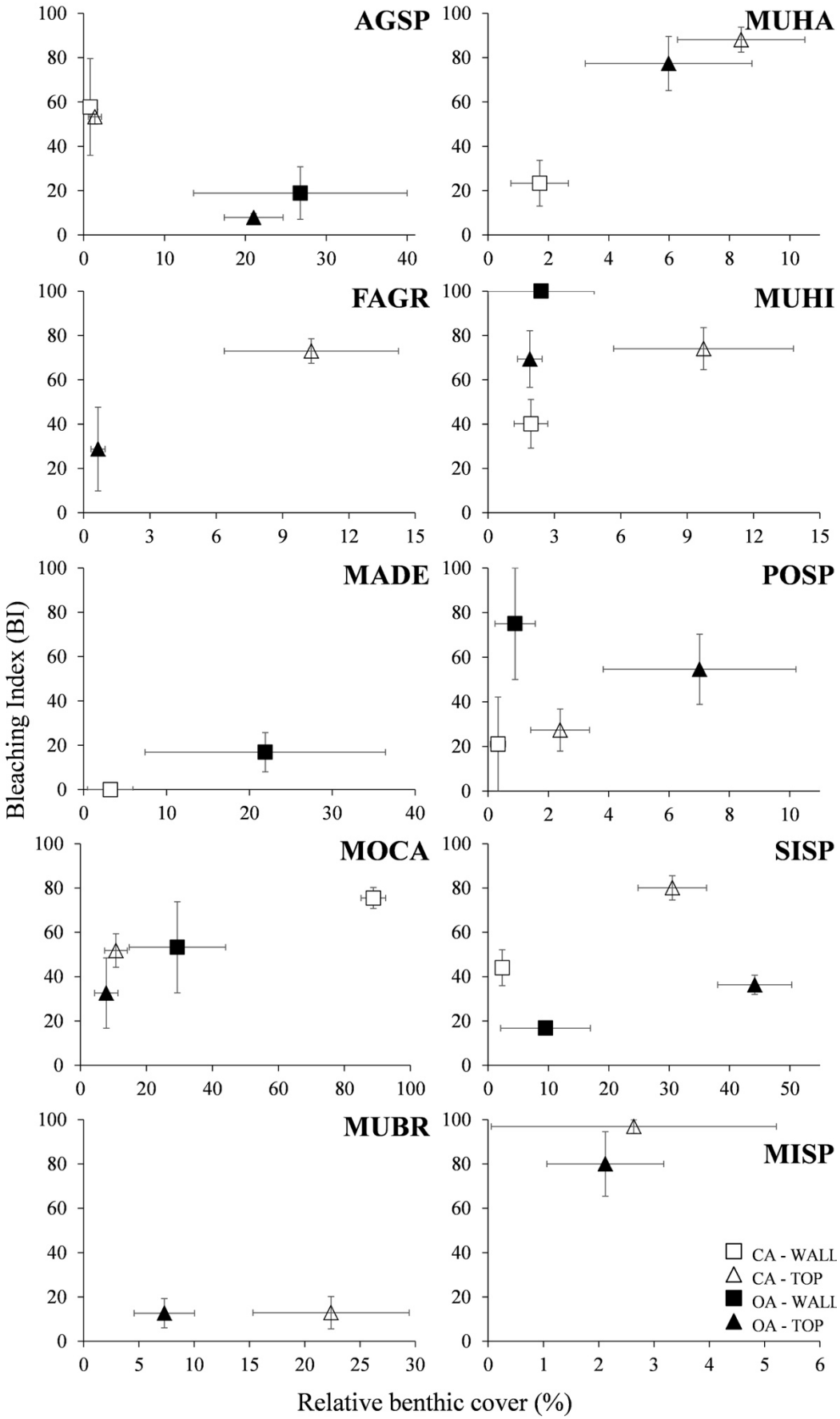

AGSP
MUHA
FAGR
MUHI
MADE
POSP
MOCA
SISP
MUBR
MISP
Bleaching Index (BI)
Relative benthic cover (%)
CA - WALL
CA - TOP
OA - WALL
OA - TOP

Figure 19 Bleaching Index (BI) and relative cover of the most abundant coral species in both habitats (pinnacles tops and walls) of the coastal and offshore arcs during the event's peak in May 2016. AGSP= *Agaricia* spp., FAGR= *Favia gravida*, MADE= *Madracis decactis*, MOCA= *Montastraea cavernosa*, MUBR= *Mussismilia braziliensis*, MUHA= *M. harttii*, MUHI= *M. hispida*, POSP= *Porites* spp., SISP= *Siderastrea* spp., MISP= *Millepora* spp. Bars represent Standard Errors.

4.4 DISCUSSION

The largest SWA reefs suffered a mass and sustained coral bleaching episode that spanned across two summers (2016-17) during the TGBE. Although the positive phase of the 2015-16 El Niño (Hu and Fedorov 2016, 2017; Rodgers et al. 2017) was followed by a colder phase, high levels of coral bleaching persisted across the Abrolhos reefs into 2017. Our results, besides providing a detailed account of the TGBE effects in the largest SWA reef system, add to the recent evidence that low-diversity turbid-zone reefs may be less susceptible to climate stress than the high-diversity reefs that dwell in clear oligotrophic waters. Peripheral provinces departing from the Caribbean and Indo-Pacific diversity centers, as well as the so-called "marginal" reefs in turbid zones (e.g. Morgan et al. 2017), are still unevenly represented in the global bleaching databases (e.g. Donner et al. 2017; Hughes et al. 2018a). With a few exceptions (e.g. Kelmo and Attrill 2013), the fragmented information from the SWA has low taxonomic and spatial resolution (e.g. Castro and Pires 1999). Five bleaching episodes were documented in scattered SWA localities since 1993-94 (see Fig. 2 for reference list), one of them with associated mass coral mortality (Kelmo and Attrill 2013). However, it is likely that there are false negatives (unrecorded events), as coral reef monitoring in Brazil is incipient (Ferreira and Maida 2006), except for the Abrolhos reefs, which are being continuously monitored since 2000 (Amado-Filho et al. 2018).

The 2016-17 episode in Abrolhos is one of the longest continuous mass bleaching episodes on record. Moderate to severe bleaching occurred from March 2016 to March 2017, and sparse bleached colonies were observed by the resident National Park staff (pers. comm.) in February 2016, and from April to May 2017. Although the 2017 summer thermal anomaly remained below bleaching alert levels, the entire 2014-17 period was also characterized by low wind speeds, clear skies and calm seas, which may have contributed to the duration of the bleaching episode (see Glynn 1996; Mumby et al. 2001). Survival along such an extended mass bleaching may be related to heterotrophic compensation (Anthony 2006; Hughes and Grottoli 2013). Indeed, heterotrophy within the coral assemblage of the turbid-zone Abrolhos reefs,

especially among *Mussismilia* spp., seems to be high (Pires et al. 2011; Ribeiro et al. 2018). The time interval between thermal anomalies is a critical aspect of bleaching, and their frequency tends to increase in the next decades (Hughes et al. 2018a, b). Sustained bleaching events may imply in widespread resilience loss and longer recovery times (Hughes et al. 2018b). Currently, every summer has the potential to cause coral bleaching and mortality at regional levels, as SSTs under colder La Niña phases may be higher than those under El Niños recorded three decades ago (Hughes et al. 2018a).

Corals with branching morphologies, which often present faster growth and thin soft tissue layers, tend to present high mortalities and are generally the first to bleach (Brown and Suharsono 1990; Glynn 1996; Smith et al. 2014). Their higher surface-to-volume ratios imply in increased exposure to warm water and solar radiation, while the thick tissue of most massive forms modulates solar radiation more effectively (Hoegh-Guldberg 1999; Loya et al. 2001). Branching hydrocorals *Millepora* spp. were among the most affected species in Abrolhos, and also in northern Bahia during the 1997-98 event (Kelmo and Attril 2013). Indeed, milleporans may even reach regional extirpation after temperature extremes (e.g. Glynn and de Weerdt 1991; Smith et al. 2014). In the SWA, decrease of milleporans (4 species) can have severe ecosystem-level consequences, as they are the region's only branching corals and play irreplaceable ecological roles (Coni et al. 2013). Besides milleporans, other severely affected species on pinnacles tops (>40% of colonies bleached) include *Porites* spp., *F. gravida*, and *Siderastrea* spp., all of which present very thin tissues (authors' observations). Plate-like forms (e.g. *Agaricia* spp.), typical of low-light environments such as pinnacle's walls, also tend to be fast-growing, have relatively thin tissues, and to be more susceptible to bleaching (Kühlmann 1983; Loya et al. 2001). Coral morphologies can be highly plastic (Forsman et al. 2009), and there are clear zonation patterns of species and/or growth forms related to collinear variations of depth, turbulence and light gradients (Graus and Macintyre 1989). These trends, associated to taxonomic/phylogenetic affinities of coral hosts and symbionts, may be important drivers of the spatial variation in coral bleaching (Berkelmans and Willis 1999).

The Brazilian-endemic and endangered coral *M. braziliensis* comprises one of the most abundant species on pinnacles' tops (Francini-Filho et al. 2008, 2013), and was one of the less susceptible species. This massive species with a thick soft tissue layer presents an extremely narrow geographic (13-20^{o}S) and depth range (1-15 m) and seems to be highly adapted to the local conditions of the Abrolhos' pinnacles' tops (Pires et al. 2011), akin to some abundant coral species in the Great Barrier Reef (GBR), Australia (e.g. *Cyphastrea* spp., *Turbinaria* spp.). However, most other Abrolhos' coral species presented significant between-habitat

differences in abundance and bleaching prevalence. Although shading may provide protection against thermal stress (e.g. Coelho et al. 2017), we found that species typical of pinnacles' walls, such as *M. cavernosa* and *Agaricia* spp. (the 1st and 2nd most abundant corals in this habitat), presented lower bleaching prevalence in the tops, where they are less abundant. Therefore, under extreme scenarios, the few survivors in habitats where abundance and growth rates are low may be a critical component in reef resilience, especially when mortality is high (Hoogenboom et al. 2017; Hughes et al. 2018b). The relationship between coral abundance and bleaching prevalence is a poorly explored topic that deserves further research efforts, especially in marginal reefs with low richness and high coverage of a few endemic species.

Depth and cross-shelf trends of bleaching prevalence and severity may also be variable. For instance, during the 1997-98 anomaly in the GBR, Marshal and Baird (2000) recorded inverse patterns of bleaching at the Palm (negative association with depth) and Magnetic (positive) islands. The Magnetic islands are within a region chronically subjected to more thermal stress, and these authors remarked on the potential role of coral acclimatization in this location. The general trend for the GBR (1997-98 and 2002) seems to be increased bleaching levels in inshore reefs (Berkelmans et al. 2004), but novel data from turbid-zone reefs (Le Nohaïc et al 2017; Morgan et al. 2017) indicates high bleaching tolerance in these poorly sampled systems. In Abrolhos, with the exception of low bleaching levels in the deeper mesophotic reefs, we did not find a cross-shelf trend in bleaching prevalence, and interactions between arc and habitat effects were overall weak (see Table 3). Contrasting with the GBR, where there are higher inshore temperatures during thermal anomalies (Berkelmans et al. 2004), we did not record significant temperature differences between the coastal and offshore arc reefs (Fig. 3), and the strong habitat effect due to the oddly-shaped pinnacles' morphology seems to overwhelm the weaker cross-shelf effect.

Quadrat data is limited for spatial comparisons, but bleaching prevalence in the deeper mesophotic California Reef tended to be lower than 10%, i.e. less than in the emerging reefs (>30%). Offshore, water column stratification seems to intensify in the summer, and our *in situ* temperatures from the California Reef measured at 20m depth indeed deviate sharply from SSTs. Mesophotic reefs can be a thermal refuge, with low bleaching and bleaching related mortality, but less than half of the species recorded in the pinnacles' reefs also occur in the deeper mesophotic California reef, which also presented more limited coral cover. In addition, bleaching threshold temperatures are likely lower than in shallow reefs (Smith et al. 2016). Therefore, the Abrolhos' deeper reefs only provide a partial refuge to climate changes (Bongaerts et al. 2010; Smith et al. 2016).

The 2014-16 global anomaly resulted in moderate to severe bleaching in 75% of the 100 localities studied by Hughes et al. (2017) across the Indo-Pacific and the Caribbean, but the consequences of the TGBE, in terms of coral mortality and ecosystem-level effects, will only be fully understood as more detailed reports accumulate (e.g. Hoogenboom et al. 2017; Le Nohaïk et al. 2017; Morgan et al. 2017; Rodgers et al. 2017; Sheppard et al. 2017; Hughes et al. 2018b). Bleaching levels in Abrolhos were high (up to 73% of colonies bleached in offshore arc pinnacles tops), but overall mortality was low (<3% of total coral cover) as of March 2017, contrasting with the high mortality rates recorded in the Indo-Pacific and the Caribbean, with >80% coral mortality even in undisturbed Central Pacific Reefs (Rodgers et al. 2017).

Zooxanthellate reef-building corals occur in a wide range of temperatures, from Southern Africa and Australia to the Persian Gulf (cold and hot extremes, respectively), but most species occur under relatively narrow tropical or equatorial conditions. Within species-specific and regional limits some corals may acclimate, and even adapt, to more extreme conditions (McClanahan 2017). Accordingly, thermal thresholds to bleaching differ regionally (Jokiel and Brown 2004; Krueger et al. 2017), ranging from 27 to 35°C (Central Pacific and Persian Gulf, respectively), and are also dependent on the duration of the thermal stress (Liu et al. 2014). Most corals live dangerously close to their upper thermal threshold and tend to bleach when temperature remains 1-2°C above local summer maxima for more than a month (Coles et al. 1976; Glynn and D'Croz 1990). However, turbid-zone reefs dominated by stress-tolerant species may function as climate-change refugia (van Woesik et al. 2012; Morgan et al. 2017), either due to reduced irradiance or local adaptation/acclimation to higher disturbance levels. However, these "nearshore climate-change refugia" are not immune to bleaching (Le Nohaïc et al. 2017; Morgan et al. 2017), especially under the disturbing scenario forecasted for the 21st Century (Hughes et al. 2018a). Indeed, the loss of a few coral species that are more susceptible to thermal anomalies (e.g. *Millepora* spp.) may have deep consequences in such low diversity systems with low functional redundancy.

4.5 CONCLUSION

Five bleaching episodes were documented in scattered SWA localities since 1993-94. Branching hydrocorals *Millepora* spp. were among the most affected species in Abrolhos, and also in northern Bahia during the 1997-98 event. The Brazilian-endemic and endangered coral *M. braziliensis* and was one of the less susceptible species. Although shading may provide protection against thermal stress we found that species typical of pinnacles' walls presented lower bleaching prevalence in the tops, where they are less abundant. The strong habitat effect

due to the oddly-shaped pinnacles' morphology seems to overwhelm the weaker cross-shelf effect. The Abrolhos' deeper reefs only provide a partial refuge to climate changes due to lower species richness and lower cover. Eventhough, bleaching levels in Abrolhos were high, overall mortality was low, contrasting with the high mortality rates recorded in the Indo-Pacific and the Caribbean. Our results, besides providing a detailed account of the TGBE effects in the largest SWA reef system, add to the recent evidence that low-diversity turbid-zone reefs may be less susceptible to climate stress than the high-diversity reefs that dwell in clear oligotrophic waters.

5 CONCLUSION

According to the results presented in this study, which are derived from a long-term high-resolution time series and empirical data from replicated bioessays, both ratified by field data, add to the growing evidence that turbid zone reefs present unique functional properties that challenge the current models explaining the global decline of coral reefs. The endemic reef builder of the Abrolhos reefs, *M. braziliensis* was found to be tolerant towards turbidity, which confirms previous evidence found in the literature, with the addition of increased resilience from competition and thermal stress. Filamentous cyanobacteria supress *M. braziliensis* tissue, most likely through the production of allelochemicals, what makes periodic outbreaks potentially harmful to corals in the Abrolhos Bank area. Increased frequency of blooms may be related to environmental conditions, probably correlated with the eutrophication of coastal waters, increased sea water temperature, low wind and low wave energy periods. Coral bleaching events are recurrent in SWA since 1993-1994, but overall mortality is considerably lower than tropical sites within the Indo Pacific and the Caribbean. The oddly-shaped pinnacles of Abrolhos seem to influence the bleaching trends. The generality of coral-algae competition models was not verified for Abrolhos Bank, given the evidences of better fitness in corals from turbid sites with higher algal cover relative to offshore conspecifics. Avoiding coral decline goes well beyond no-take zoning and shall include a longer road that includes water quality control, assurance of connectivity among associated habitats and climate change mitigation.

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7 SUPPLEMENTARY MATERIAL

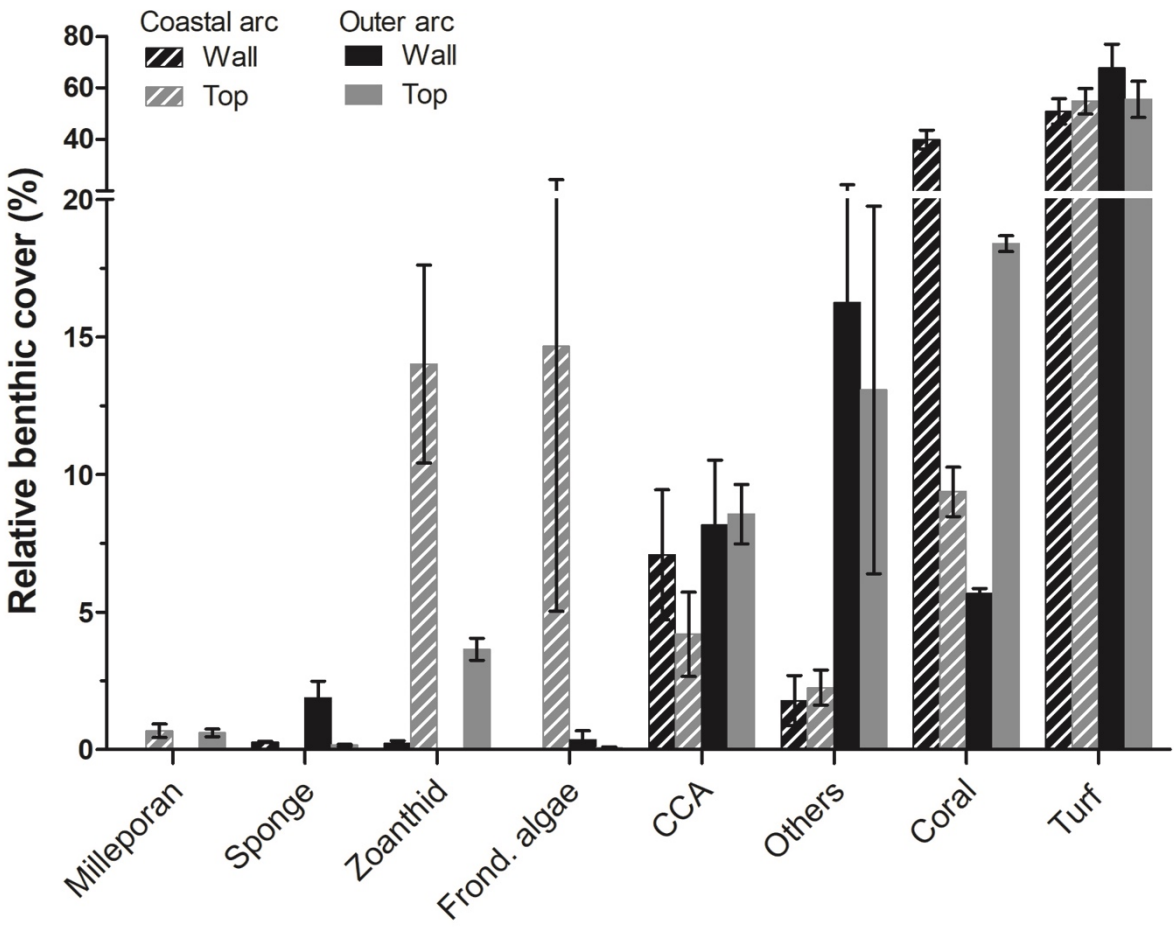

Figure 20 Relative benthic cover (mean ± SE) in the Abrolhos reefs. Others include black coral, octocoral, sea urchin, calcareous articulated algae, *Halimeda*, non-biotic and unidentified organisms.

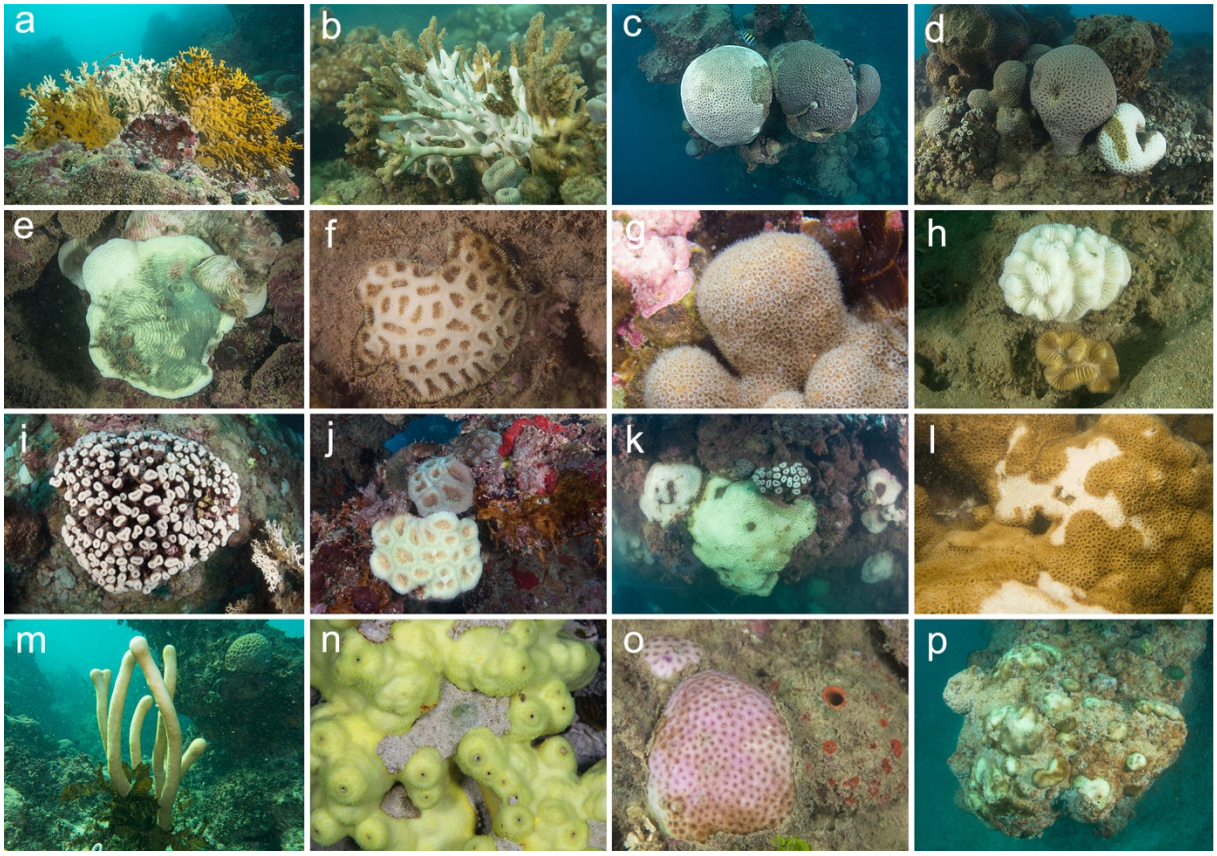

Figure 21 Bleached corals recorded during the Third Global Bleaching Event in the Abrolhos reefs, Brazil. **a**= *Millepora alcicornis* (from the left to the right: PB, HB and H); **b**= *Millepora alcicornis* (BM); **c**= *Mussismilia braziliensis* (left colony: HB, center and right colonies: PB); **d**= *M. hispida, M. hartii and M. lepthophylla* (PB)*, M. braziliensis* (H)*, M. braziliensis* (HB and BM) (colonies from the left to the right); **e**= *Agaricia fragilis* (HB); **f**= *Favia gravida* (HB); **g**= *Madracis decactis* (PB); **h**= *Meandrina braziliensis* (HB and PB); **i**= *Mussismilia hartii* (HB); **j**= *M. hispida* (PB and HB); **k**= *Montastraea cavernosa* (HB, two larger colonies), *Madracis decactis* (H, between *M. cavernosa* colonies), *Mussismilia hispida* (H and PB, in the left, above *M. cavernosa* colonies), *M. hartii* (above *M. cavernosa*, to the right of *M. hispida*), *Agaricia* sp. (HB, three colonies in the right); **l**= *Palythoa caribaeorum* (H and HB); **m**= *Plexaurella grandiflora* (HB); **n**= *Porites astreoides* (HB); **o**= Siderastrea stellata (HB); **p**= *Stephanocoenia intersepta* (HB, several colonies), *Porites astreoides* (HB, small colony, upper right), *Scolymia* sp. (H, solitary, upper right). PB= Partially Bleached, HB= Heavily Bleached, BM= Bleaching and Mortality (see Methods). Photos by Leo Francini, Athila Bertoncini, Fernando Moraes and Rodrigo Moura.

Tabela 5 Results of pairwise tests contrasting between-year changes in the area of live coral tissue.

PAB (offshore site)		
Year	t	p
2008, 2009	1.1555	0.2713
2008, 2012	0.9671	0.3498
2008, 2013	1.4535	0.1707
2008, 2014	0.858	0.3967
2008, 2015	1.458	0.1621
2008, 2016	2.0453	0.0623
2009, 2012	0.0004	0.9977
2009, 2013	0.9286	0.4272
2009, 2014	1.9859	0.071
2009, 2015	0.6805	0.5228
2009, 2016	1.5429	0.1559
2012, 2013	0.8645	0.4312
2012, 2014	1.7547	0.1042
2012, 2015	0.528	0.6062
2012, 2016	1.2212	0.2312
2013, 2014	2.0087	0.0564
2013, 2015	0.5646	0.6041
2013, 2016	0.126	0.9058
2014, 2015	2.1859	0.0448
2014, 2016	2.6795	0.0121

PLES (coastal site)		
Year	t	P
2009, 2012	3.0073	0.017
2009, 2013	1.5085	0.176
2009, 2014	1.8853	0.098
2009, 2015	2.1628	0.042
2009, 2016	2.6358	0.023
2012, 2013	2.2437	0.04
2012, 2014	1.4436	0.173
2012, 2015	1.5861	0.139
2012, 2016	0.3372	0.726
2013, 2014	0.6868	0.514
2013, 2015	0.8225	0.458
2013, 2016	2.071	0.062
2014, 2015	0.0318	0.974
2014, 2016	1.5336	0.155
2015, 2016	1.589	0.137
2009, 2012	3.0073	0.017

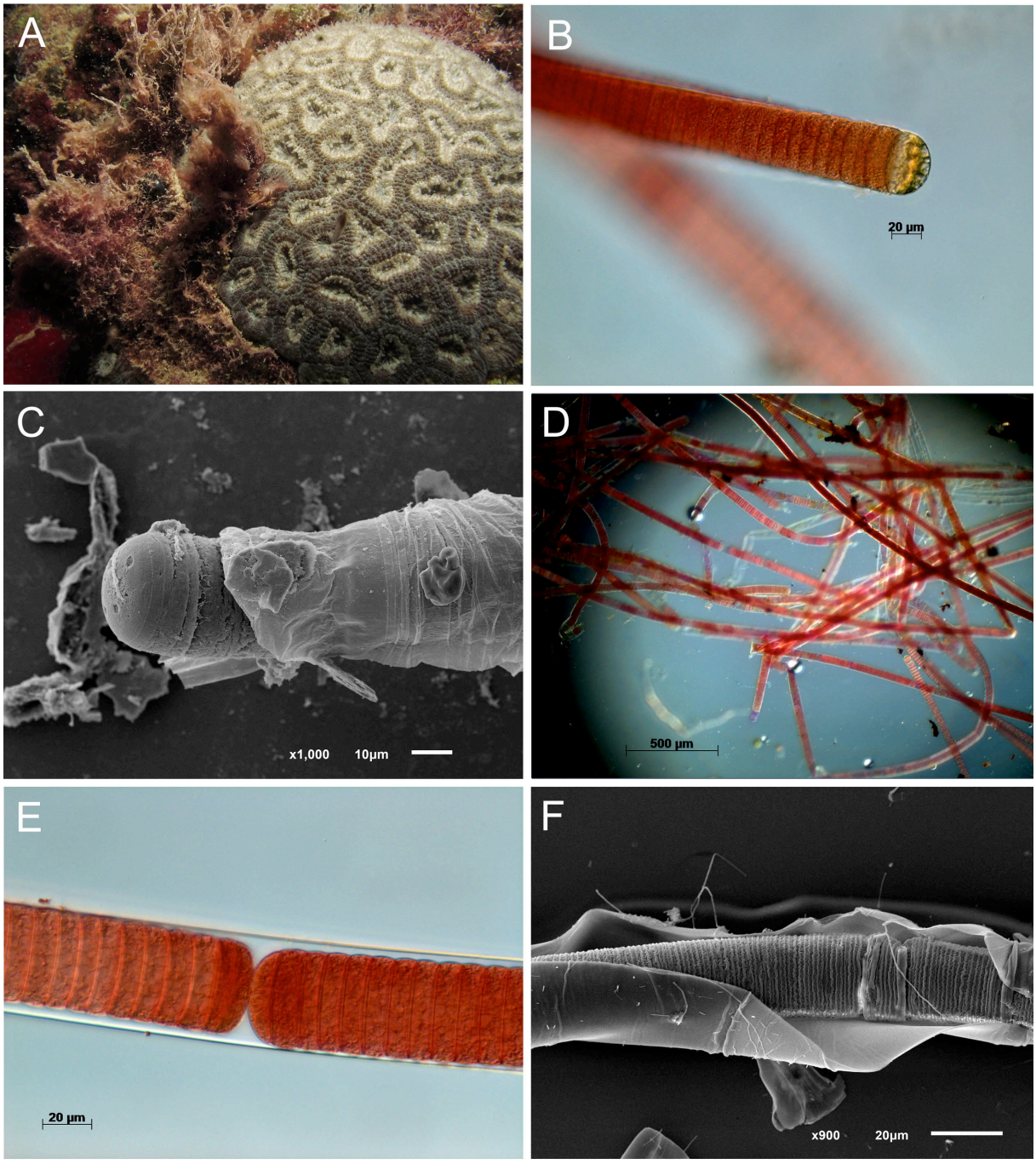

Figure 22 Benthic filamentous cyanobacteria from Abrolhos Bank, *in-vivo* as upright tuft bordering *M.braziliensis* colony (A); filament with spherical terminal cell under DIC microscopy (B); non-ramified cyanobacterial filament, with spherical terminal cell, enclosed in exopolysaccharide sheaths in MEV microscopy (C); interwoven trichomes before isolation (D); discoid cells enclosed in exopolysaccharide sheaths under DIC (E); discoid cells enclosed in exopolysaccharide sheaths in MEV (F). Photography: Felipe Ribeiro (A); Inacio Neto (B-F).