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Eventos de branqueamento de corais no Atlântico Sul: recifes marginais são possíveis refúgios climáticos?

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O presente trabalho em nível de mestrado foi avaliado e aprovado por banca examinadora composta pelos seguintes membros:

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Certificamos que esta é a **versão original e final** do trabalho de conclusão que foi julgado adequado para obtenção do título de mestre em ecologia.

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Prof.(a) Dr.(a) Bárbara Segal
Orientador(a)

Florianópolis, 2022.

As cores da vida

Presos em nossas ações, as convicções livres para o mercado
O consumo, o insumo é absorvido
Ainda ontem éramos mais cores, apesar das dores
Um respiro, um suspiro existia
Enquanto hoje sobram atores e rumores
E as cores da vida se perdem no mar azul, nos corais brancos
Que aos prantos clamam por cores a mais, graus a menos
Nesse planeta azul, nessa vida pretensa a rosa
Qual é a prosa que te convence?
Quem vence?
Precisamos colorir, mas antes descolorir
Para que muitos possam ver o que poucos sentem
Para que muitos chorem, implorem e entendam a razão
E a necessidade de muitos arco-íris
Filha minha, ilumina meu pesar
A teu favor, o amor
Aniquila minha agonia em não poder te ajudar
Defende o que acredita
Me empresta teu brilho, para que como um filho
Eu possa sem medo
Juntar o arremedo do que vai sobrar.

Paulo Ricardo Gaspar, 2022

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RESUMO

Eventos de estresse termal que desencadeiam o branqueamento de corais, são cada vez mais frequentes e intensos e ameaçam os recifes de coral de todo o mundo. Entretanto, os efeitos do aquecimento global se distribuem heterogeneamente, e assim, é emergente a busca de refúgios onde seja possível a sobrevivência e manutenção de ambientes recifais, para fins de planejamento de ações de gestão e conservação. O branqueamento pode ser potencializado pela alta incidência da radiação ultravioleta, a qual pode ser reduzida através da turbidez da água. Recifes localizados em águas turvas podem apresentar menor incidência de radiação, fornecendo assim, condições menos estressantes para os corais em comparação aos recifes de águas oligotróficas e transparentes durante eventos de estresse termal. Os recifes da província brasileira são os únicos recifes do Atlântico Sudoeste. Tais recifes lidam com condições ambientais adversas para a sobrevivência de corais, comparados aos recifes mais conhecidos, do Caribe e Indo Pacifico, e são considerados recifes marginais por tais características diferenciadas. Entretanto, o branqueamento de corais no Brasil é pouco investigado em comparação a recifes da Austrália e Caribe, e a relação entre os possíveis fatores que desencadeiam ou atenuam o branqueamento ainda é mal compreendida e impede o melhor entendimento do fenômeno e de seus efeitos nos ambientes recifais brasileiros. A fim de melhorar a compreensão sobre branqueamento de corais no Atlântico Sul, realizamos uma revisão dos eventos de branqueamento de corais no Brasil e investigamos condições oceanográficas de 2002 a 2020, de 23 recifes representativos distribuídos ao longo da costa brasileira. As condições investigadas foram: a temperatura superficial do mar (SST), anomalias da SST (aSST), ondas de calor marinhas (MHW do inglês Marine Heat Waves), coeficiente de atenuação da luz em 490 nanômetros (Kd_{490} como proxy de turbidez) e radiação fotossinteticamente ativa (PAR). Pretendemos responder às seguintes questões: 1) quais regiões historicamente sofreram mais ondas de calor? (2) quais regiões têm historicamente alta turbidez e, portanto, são potenciais refúgios? (3) há variação histórica na turbidez? (4) os episódios de branqueamento ocorridos corroboram (1) e (2)? Os recifes tropicais da região nordeste apresentam os maiores valores e menor variação de PAR (~50 Einstein m^{-2} d^{-1}) e SST (24 a 30°C) em comparação aos recifes tropicais da região leste e subtropicais da região sul (~40 Einstein m^{-2} d^{-1} e 16 a 30°C), com exceção das ilhas oceânicas de Trindade e Martim Vaz que apresentam alto PAR. As ilhas oceânicas e a região tropical nordeste se destacam pela baixa turbidez, ao apresentarem os menores valores de Kd_{490}. Contrário a SST e PAR, as MHW foram mais intensas (50°C) e frequentes (>70) nos recifes subtropicais do sul e sudeste brasileiro. Em comparação aos recifes austrais, a maioria dos recifes tropicais do nordeste apresenta baixos valores de turbidez, fornecendo menor proteção à alta irradiância desta região. Em contrapartida, nos recifes subtropicais do sul, como a Ilha Rasa de Fora no Espírito Santo, e Arraial do Cabo no Rio de Janeiro, os altos valores de turbidez poderiam servir de barreira à irradiância e fornecer refúgio ao branqueamento. Nesse sentido, vale mencionar que tais recifes apresentam espécies e cobertura coralínea diferentes, o que também pode alterar a resposta do recife aos eventos de estresse termal. Os eventos de branqueamento de corais registrados se concentram nos recifes tropicais do norte (50%), Abrolhos (25%) e na Baía de Todos os Santos (18%), o que não corrobora com a intensidade de MHW e turbidez da água desses locais, ambas menores que na região sudeste e sul. Tais regiões são as mais propícias para o desenvolvimento de ambientes recifais no Brasil, e por consequência as mais estudadas. Mesmo que recifes biogênicos tropicais tenham apresentado menores intensidades de MHW, suas águas naturalmente claras e quentes somadas ao aumento da frequência de MHW fruto do aquecimento global podem colocar estes ambientes em risco. Já para os recifes da região subtropical, embora sejam almejados como refúgios ao branqueamento, é necessário que esses ambientes forneçam e mantenham condições favoráveis à sobrevivência das espécies de corais. Nossos resultados sugerem que recifes não biogênicos no limite sul da região tropical e na região subtropical têm sofrido com ondas de calor marinhas intensas, o que pode superar a atenuação do branqueamento promovida pela turbidez e ultrapassar o limiar de branqueamento mesmo em ambientes antes almejados como refúgio. Manter o monitoramento contínuo e padronizado do branqueamento de corais em ambientes recifais é imprescindível para melhorar a compreensão da resposta destes ambientes às mudanças impostas pelo aquecimento global. Tais monitoramentos devem fomentar ações de preservação que sejam adaptativas e alteradas de acordo com diferentes respostas dos ambientes recifais ao longo do tempo.

Palavras chave: Mudanças climáticas. Recifes brasileiros. Turbidez. Ondas de calor marinhas.

ABSTRACT

Thermal stress events, which trigger coral bleaching, are increasingly frequent and intense and threaten coral reefs around the world. However, the effects of global warming are heterogeneously distributed, and thus, there is an emergent search for refugees where the survival and maintenance of reef environments is possible, for purposes of planning management and conservation actions. Bleaching can be enhanced by the high incidence of ultraviolet radiation, and this radiation can be reduced through the turbidity of the water. Reefs located in turbid environments may have a lower incidence of radiation, thus providing less stressful conditions for corals, compared to reefs in oligotrophic and transparent waters during extreme thermal events. Such reefs deal with adverse environmental conditions for the survival of corals, compared to the better known reefs of the Caribbean and Indo Pacific, and are considered marginal reefs due to such differentiated characteristics. However, coral bleaching in Brazil is little investigated compared to Australian and Caribbean reefs, and the relationship between the possible factors that trigger or attenuate bleaching is still poorly understood and prevents a better understanding of the phenomenon and its effects on environments. Brazilian reefs. In order to improve the understanding of coral bleaching in the South Atlantic, we performed a review of coral bleaching events in Brazil and investigated the oceanographic conditions from 2002 to 2020 of 23 representative reefs distributed along the entire Brazilian coast. The conditions investigated were: sea surface temperature (SST), SST anomalies (aSST), marine heat waves (MHW), light attenuation coefficient at 490 nanometers (Kd_{490} as turbidity proxy) and photosynthetically active radiation (PAR). We intend to answer the following questions: 1) which regions have historically suffered the most heat waves? (2) which regions have historically high turbidity and are therefore potential refuges? (3) is there historical variation in turbidity? (4) Do known bleaching episodes corroborate (1) and (2)? Northeastern reefs show the highest values and smallest variation in PAR (~50 Einstein m^{-2} d^{-1}) and SST (24 to 30°C) compared to eastern and southern reefs (~40 Einstein m^{-2} d^{-1}) and 16 to 30°C), with the exception of the oceanic islands of Trindade and Martim Vaz which have a high PAR. The oceanic islands and the northeast region stand out for their low turbidity, as they present the lowest values of Kd490. Contrary to SST and PAR, MHWs were more intense (50°C) and frequent (>70) in southern and southeastern Brazilian reefs. Compared to southern reefs, most northeastern reefs have low turbidity values, providing less protection from the high irradiance of this region. In contrast, on southern reefs, such as Ilha Rasa de Fora in Espírito Santo and Arraial do Cabo in Rio de Janeiro, the high turbidity values could act as a barrier to irradiance and provide refuge to bleaching. In this sense, it is worth mentioning that these reefs have different species and coral cover from other reefs in Brazil, which can also alter the reef's response to thermal stress events. Coral bleaching events recorded are concentrated in the northern tropical reefs (50%), Abrolhos (25%) and Todos os Santos Bay (18%), which does not corroborate the intensity of MHW and water turbidity in these locations, both smaller than in the southeast and south. Such regions are the most favorable for the development of reef environments in Brazil, and therefore the most studied. Even though tropical biogenic reefs have shown lower MHW intensities, their naturally clear and warm waters added to the increase in MHW frequency due to global warming can put these environments at risk. As for the reefs of the subtropical region, although they are intended as refuges for bleaching through tropicalization, it is necessary that these environments provide and maintain favorable conditions for the survival of coral species. Our results suggest that non-biogenic reefs at the edge of the tropical and subtropical regions have suffered from intense marine heat waves, which can overcome the bleaching attenuation promoted by turbidity and surpass the bleaching threshold even in environments previously targeted as a refuge. Maintaining continuous and standardized monitoring of coral bleaching in reef environments is essential to improve understanding of the response of these environments to changes imposed by global warming. Such monitoring should encourage conservation actions that are changeable according to different responses from reef environments over time.

Keywords: Climate change. Brazilian reefs. Turbidity. Marine heat waves.

LISTA DE FIGURAS

LISTA DE TABELAS

SUMÁRIO

1- INTRODUÇÃO GERAL

Comparados à florestas tropicais devido a sua elevada complexidade estrutural e biodiversidade (CONNEL, 1978; REAKA-KUDLA, 1997), ambientes recifais constituem ecossistemas-chave, que suportam uma extensa e complexa cadeia trófica, além de fornecer diversos bens e serviços ecossistêmicos aos seres humanos (HOEGH-GULDBERG, 1999). No entanto, além da pesca excessiva, poluição, destruição de habitat e introdução de espécies exóticas, as mudanças climáticas do Capitaloceno (MOORE, 2016) têm representado desafios nunca antes experimentados pelos ecossistemas recifais (HUGHES et al., 2018; WILLIAMS et al., 2019). Eventos climáticos extremos devido ao aquecimento global estão desencadeando episódios de branqueamento em massa em recifes de todo o mundo (HUGHES et al., 2018; DONNER et al., 2017). O branqueamento ocorre quando a relação entre os corais e seus simbiontes fotossintéticos (microalgas da família Symbiodiniaceae) é interrompida (GLYNN, 1993).

Através de um processo evolutivo estruturado em trocas bem sucedidas de compostos orgânicos e inorgânicos (MUSCATINE & HAND, 1958; DAVY et al., 2012), os simbiontes associados aos corais translocam produtos de fixação de carbono e assimilação de nitrogênio para o hospedeiro (GORDON & LEGGAT, 2010; KOPP et al., 2015), enquanto o hospedeiro fornece acesso a nutrientes inorgânicos dissolvidos (WANG & DOUGLAS, 1999; IMBS et al., 2014). Aspecto chave para a construção recifal por corais escleractínios em águas oligotróficas (MUSCATINE & CERNICHIARI, 1969), a simbiose pode ser flexível, com um único hospedeiro associado a vários clados de simbiontes, que podem se desenvolver sob diferentes ótimos ambientais. Todavia, mesmo adaptada a regimes térmicos relativamente amplos, esta relação vem sendo desafiada pelo aumento da temperatura da água do mar e eventos climáticos extremos cada vez mais frequentes (HOEGH-GULDBERG, 1999). O estresse térmico pode interromper a simbiose por meio da fotoinibição no simbionte, levando à produção excessiva de espécies reativas de oxigênio, o que resulta na interrupção da interação e expulsão da microalga (WEIS, 2008, CZIESIELSKI et al. 2019). Para atender suas necessidades energéticas, corais branqueados contam com fontes alternativas de carbono fixo, como reservas de energia, ou ainda, a heterotrofia (GROTTOLI et al., 2006; HUGHES & GROTTOLI, 2013). Corais branqueados são fisiologicamente danificados e nutricionalmente comprometidos e podem morrer se o branqueamento for severo e o tempo de recuperação de seus simbiontes for prolongado (BAKER et al., 2008).

Desde o século XX, o branqueamento de corais é relatado em todo o globo de maneira local e esteve relacionado a estressores de pequena escala, principalmente clima mais frio ou mais quente do que o normal, ou ainda sedimentação e descargas de água doce (VAUGHAN, 1914; GLYNN, 1993; HUGHES et al. 2003). Após a década de 1980, o branqueamento de corais se tornou mais frequente e intenso em todo o mundo (HUGHES et al. 2017), com três grandes eventos atingindo escala global: 1997-1998, 2010 e 2014-2017 (EAKIN et al. 2019; HUGHES et al., 2018). Além das previsões, no cenário moderado, de aumento de até 3°C da temperatura global do oceano (SSP2-4.5, IPCC 2021), que impõem condições fora do limiar fisiológico termal da maioria das espécies de corais (HOEGH-GULDBERG et al., 2007; FRIELER et al., 2013), anomalias térmicas positivas e fenômenos climáticos aumentaram significativamente em frequência, intensidade e duração desde o início do século XX (OLIVER et al., 2018). Neste cenário, torna-se fundamental a identificação de refúgios onde seja possível a manutenção de espécies construtoras de recifes de corais, paralela a adaptação dos sistemas de gestão que acompanhem o cenário de mudança.

Há ampla evidência de que diferentes distúrbios ambientais levam ao branqueamento, como a temperatura (TCHERNOV et al. 2004; TOLLETER et al. 2013; LEVIN et al. 2016), luz (LESSER e FARRELL, 2004; DOWNS et al. 2013), salinidade (GARDNER et al. 2016; OCHSENKÜHN et al. 2017; AGUILAR et al. 2019), bem como nutrientes inorgânicos (CRAWLEY et al., 2010), ferro e outros metais traço (SHICK et al., 2011; BISCÉRÉ et al. 2018; FERRIER & PAGÈS et al., 2018). Mesmo que diversos fatores possam levar ao branqueamento, os estresses térmicos ainda são a condição mais importante no desencadeamento do fenômeno, levando a eventos massivos em grande escala (HUGHES et al. 2018), ao contrário do branqueamento mais pontual e localizado causado por fatores locais (por exemplo, salinidade, metais traço). Além desses fatores agindo separadamente, a interação e eventual sinergia entre eles também podem ser prejudiciais ou até benéficas (por exemplo, ANTHONY et al. 2011; VEGA & THURBER et al. 2013; GRAHAM & CONNOLLY 2014), e a resposta do branqueamento ou mortalidade dependerá em partes das características do ambiente recifal.

Estudos experimentais evidenciam, assim como já é conhecido para a temperatura (GUSTAFSSON et al., 2014), secas e alta salinidade (POWLES, 1984; MURATA et al., 2007), a importância da alta incidência de luz no desencadeamento e intensificação da fotoinibição, que impulsiona o branqueamento (IGLESIAS-PRIETO et al., 1992; WARNER et al., 1999; LESSER & FARRELL, 2004). Ambientes com menor irradiância, como recifes turvos, podem desencadear menos fotoinibição durante eventos de estresse termal (IGLESIAS-PRIETO et al., 1992; TAKAHASHI et al., 2004; LESSER, 2019), fornecendo maior prevenção ao branqueamento de corais quando comparados com recifes de águas transparentes (IGLESIAS-PRIETO et al., 1992; WARNER et al., 1999). Condições naturais de baixa irradiância podem ocorrer onde a turbidez da água é elevada (ANTHONY & CONNOLLY, 2004; ANTHONY et al., 2004; VAN WOESIK et al. 2012), como em recifes marginais (PERRY & LARCOMBE, 2003).

Mesmo que o desenvolvimento de um recife biogênico seja limitado por fatores abióticos (e.g.: temperatura, salinidade, saturação de aragonita e penetração de luz, KLEYPAS et al. 1999), as comunidades coralíneas possuem a habilidade de se desenvolver quando essas condições se apresentam de maneira diferenciada do que conhecemos previamente como ótimas, e nessas circunstâncias os recifes são caracterizadas como “marginais” (PERRY & LARCOMBE, 2003). Localizado fora das áreas equatoriais de alta temperatura e baixa concentração de nutrientes, recifes marginais ocorrem perto de limites ambientais conhecidos para a sobrevivência de corais (KLEYPAS et al. 1999) ou em áreas caracterizadas por condições "sub-ótimas" ou flutuantes (PERRY & LARCOMBE, 2003). Tais condições abióticas resultam em diferenças na diversidade, composição e características da comunidade coralínea (SMITH et al. 2020), além do funcionamento e construção do ecossistema recifal (GUINOTTE et al. 2003), diferindo os recifes marginais dos “recifes clássicos” (e.g. da Austrália e Indo-Pacífico) localizados principalmente em águas oligotróficas da região tropical.

Apesar da perda massiva de corais em todo o mundo, recifes turvos em Palau e na Grande Barreira de Corais vêm apresentando relativamente baixas mortalidades em alguns episódios de branqueamento (VAN WOESIK et al. 2012, MORGAN et al, 2017), assim como recifes do Atlântico Sudoeste (BANHA et al. 2019, TEIXEIRA et al. 2019, GASPAR et al., 2020; MIES et al., 2020). Além disso, recifes marginais do Atlântico Sul apresentaram historicamente menos estresse térmico do que recifes no Caribe e Indo-Pacífico (SKIRVING et al. 2019; IPCC 2021), e seus corais escaparam de eventos que dizimaram recifes em outros lugares (MIES et al., 2020). Os impactos do branqueamento em massa de corais no ecossistema recifal têm sido bem documentados principalmente no Indo-Pacífico e Caribe (HUGHES et al. 2018; SULLY et al. 2019) mas os recifes no Atlântico Sul permanecem pouco investigados (MIES et al. 2020), e até negligenciados aos olhos da ciência internacional, como em recentes revisões globais (HUGHES et al. 2017), salvo exceção (SULLY & VAN WOESIK, 2020).

A província brasileira (CASTRO & PIRES, 2001; FLOETER et al., 2008) possui os únicos recifes marginais no Atlântico Sudoeste, historicamente sujeitos a vazões de volumosos rios, resultando em ambientes com alta turbidez e nutrientes na coluna d'água, além de baixa incidência de luz (LOIOLA et al., 2019; MIES et al., 2020). Os recifes brasileiros ocorrem de 6°N a 27°S de latitude e apesar de apresentarem predomínio de matriz de algas epilíticas (MAE, WILSON & BELLWOOD, 1997), possuem uma ampla variação na cobertura recifal (AUED et al., 2018) e na temperatura média anual da superfície do mar. O primeiro branqueamento massivo de corais no Brasil foi registrado em 1993/1994, quando anomalias positivas de temperatura levaram ao extenso branqueamento nas regiões de São Paulo (MIGOTTO, 1997) e Abrolhos (CASTRO & PIRES, 1999). Entre 1997 e 1998, um forte ENSO (do inglês El Niño Southern Oscillation) foi responsável pelo branqueamento em escala global e também atingiu corais do sudeste ao norte do Brasil (ACOSTA, 2001; PEREIRA et al., 2003; LEÃO et al., 2006; AMARAL et al., 2008). A partir de 2000, branqueamentos moderados foram registrados no Brasil com frequência, como em 2003, 2005 e 2008, cujos eventos se concentraram na região nordeste e foram associados ao aquecimento das águas (COSTA et al., 2001; FERREIRA et al., 2006; OLIVEIRA et al., 2007; LEÃO et al., 2008, 2009; AMORIM et al., 2011; KRUG et al., 2012, 2013). Em 2010, outro branqueamento em escala global relacionado ao ENSO (EAKIN et al., 2019) foi evidenciado com menor gravidade no Brasil, sendo registrado nas ilhas oceânicas do nordeste (FERREIRA et al., 2013) e na região de Abrolhos (TEIXEIRA et al., 2021). Quatro anos depois, recifes ao redor do mundo iniciaram o pior e mais duradouro branqueamento de corais, também relacionado ao ENSO, com altas taxas de mortalidade no Indo Pacífico (EAKIN et al., 2017, 2019; HUGHES et al., 2017), enquanto poucos recifes no Brasil apresentaram branqueamento severo e ainda menos apresentaram mortalidade (TEIXEIRA et al., 2019, 2021; BANHA et al., 2019; GASPAR et al., 2020; FERREIRA et al.., 2021).

Mesmo que hajam casos isolados de branqueamento desencadeado pela interação entre aquecimento da água e incidência luminosa (CASTRO E PIRES, 1999), pelo turismo

(BARRADAS et al., 2010) ou sedimentação (PEREIRA et al., 2003), a maioria dos episódios de branqueamento relatados até 2016 para os recifes do Atlântico sudoeste foram associados a eventos de ENSO (KELMO & ATRILL 2013, FERREIRA et al., 2013, MIRANDA et al., 2013, DIAS & GONDIM, 2016, LEÃO et al., 2016, LISBOA et al., 2018). No entanto, eventos recentes de branqueamento no Brasil mostram outros possíveis fatores que influenciam esse fenômeno, como em 2019, quando alguns recifes apresentaram o maior branqueamento já registrado (TEIXEIRA et al., 2019; BANHA et al., 2019; GASPAR et al., 2021, FERREIRA et al. 2021, SOARES et al., 2021), em um ano sem ENSO.

Considerando a variabilidade espacial do aquecimento global e dos eventos de branqueamento de coral e a chance de atenuá-los por meio de condições locais (por exemplo, alta turbidez e baixa incidência de luz) revisamos o registro histórico e atual (1993 a 2020) dos eventos de branqueamento de coral no Brasil (0° a 24° S) na literatura e investigamos condições ambientais de 23 recifes representativos da costa brasileira. Pretendemos responder às seguintes questões: (1) Quais regiões historicamente sofreram mais ondas de calor? (2) Quais regiões apresentam alta turbidez e, portanto, são potenciais refúgios? (3) Há variação histórica na turbidez? (4) Os episódios de branqueamento ocorridos corroboram (1) e (2)? Com essa abordagem, pretende-se melhorar o entendimento dos eventos de branqueamento de corais no Atlântico Sul, seus possíveis fatores atenuantes e exacerbantes, a fim de identificar áreas mais ou menos sujeitas ao fenômeno, subsidiando estratégias de manejo e prioridades de conservação dos recifes brasileiros. O desenvolvimento desta pesquisa está apresentado a seguir, em capítulo único e em língua inglesa, formatado para submissão ao periódico Coral Reefs.

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CAPÍTULO ÚNICO

Mapping coral bleaching and its drivers: insights from South Atlantic reefs to climate change

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Mapping coral bleaching and its drivers: insights from South Atlantic reefs to climate change

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ABSTRACT

In order to improve the understanding of coral bleaching in the South Atlantic, we carried out a review of its bleaching events, and investigated oceanographic conditions (sea surface temperature - SST, SST anomalies - aSST, marine heat waves -MHW, light attenuation coefficient - Kd_{490} as turbidity proxy, photosynthetically active radiation - PAR) of 23 Brazilian reefs (between 1°N - 28°S). We aimed to answer the following questions: 1) which regions have historically registered most heat waves? (2) which regions have historically high turbidity and therefore may represent potential refuges? (3) is there historical variation in turbidity? (4) do bleaching episodes corroborate (1) and (2)? Compared to high latitude reefs, most tropical reefs have low turbidity values, providing less protection from the high irradiance of this region. In contrast, extratropical reefs, such as Ilha Rasa de Fora in Espírito Santo and Arraial do Cabo in Rio de Janeiro, the high turbidity values could act as a barrier to irradiance and provide refuge to bleaching, related to thermal stress. Coral bleaching events recorded are concentrated in northern tropical reefs, Abrolhos complex and Todos os Santos Bay, which does not corroborate the MHW intensity and water turbidity in these locations, both lower than in the subtropical reefs. Even though tropical biogenic reefs have shown lower MHW intensities, their naturally clear and warm waters added to the increase in MHW frequency due to global warming can put these environments at risk. As for reefs in the Brazilian subtropical region, although they are intended as refuges for bleaching through tropicalization, it is necessary that these environments provide and maintain favorable conditions for the survival of coral species. Our results suggest that non-biogenic reefs at the edge of the tropical and subtropical regions have suffered from intense marine heat waves, which can overcome the bleaching attenuation promoted by turbidity and surpass the bleaching threshold even in environments previously targeted as a refuge.

1 - INTRODUCTION

Reef environments are one of the most diverse and valuable marine ecosystems in the world (Moberg and Folke 1999). However, in addition to local impacts, the ocean warming as a result of climate change has put these environments at risk (Hughes et al., 2003). The warming and thermal-stress events lead to the disruption of the symbiotic relationships between corals and dinoflagellates of the family Symbiodiniaceae, in a phenomenon known as “coral bleaching” (Glynn 1993). Even though we know that heat stress causes bleaching, its space-time variability still needs to be investigated, aiming to improve understanding about the environmental main drivers that trigger coral bleaching and mortality.

Experimental studies show, as is already known for temperature (Glynn 1993. 1996, Gustafsson et al. 2014), droughts and salinity (Powles, 1984; Murata et al., 2007), the importance of the high light incidence in inducing photoinhibition (Iglesias-Pietro et al. 1992; Warner et al. 1999; Lesser & Farrell 2004), resulting in disruption of symbiosis, microalgae expulsion and host bleaching (Weis 2008). Environments with reduced irradiance, such as turbid reefs, during temperature stress events may trigger less photoinhibition (Iglesias-Prieto et al. 1992; Takahashi et al. 2004; Lesser et al. 2019) and prevent coral bleaching, compared with oligotrophic environments (Iglesias-Prieto and Trench 1994; Warner et al. 1999).

Low irradiance conditions can occur where turbidity is elevated (Anthony and Connolly 2004; Anthony et al. 2004; Van Woesik et al. 2012), as seen on marginal reefs (*sensu* Perry and Larcombe 2003) in Brazil (Mies et al. 2020). Located outside equatorial areas of high temperature and low nutrient concentration, marginal reefs occur near known environmental limits for coral survival (Kleypas et al. 1999) or in areas characterized by "suboptimal" or fluctuating conditions (Perry and Larcombe 2003). Such conditions results in different compositions, diversity (Smith et al. 2020) and characteristics of the coral community (Smith et al. 2020), in addition to the functioning and construction of the reef ecosystem (Guinotte et al. 2003), differing the marginal reefs from those “classic ones" (eg from Australia and Indo-Pacific) of the tropical region.

Despite massive coral loss worldwide, Southwest Atlantic reefs have remained relatively stable in terms of mortality (Perry et al. 2013; Banha et al. 2019; Teixeira et al. 2019; Gaspar et al. 2019, Mies et al. 2020), particularly in the latest and worst bleaching events, as well as other turbid reefs in Palau and the Great Barrier Reef (Cacciapaglia et al. 2016; van Woesik et al. 2012; Morgan et al. 2017). Furthermore, marginal reefs in the South Atlantic had historically less heat stress than reefs in the Caribbean and Indo-Pacific (Skirving et al. 2019; IPCC 2021). However, coral bleaching in Brazil remains poorly investigated compared to Australia and the Caribbean, and the relationship between possible factors that trigger or mitigate the phenomenon of bleaching in Brazilian corals is still poorly understood.

The first mass coral bleaching recorded for Brazilian reefs was in 1993/1994, when positive temperature anomalies led to extensive bleaching in the regions of São Paulo estate (Migotto 1997) and Abrolhos (Castro and Pires 1999). Between 1997/1998, a strong ENSO was responsible for global scale bleaching and also took corals from southeast to northern Brazil to bleach (Acosta 2001; Pereira et al. 2003; Leão et al. 2006; Amaral et al. 2008). From 2000 onwards, moderate bleaching has been recorded in Brazil frequently, as in 2003, 2005 and 2008, whose events are concentrated in the Northeast region and were associated with warming waters due to ENSO (Ferreira et al. 2006; Oliveira et al. 2007; Leão et al. 2008, 2009; Amorim et al. 2011; Krug et al. 2012, 2013). In 2010 another global scale bleaching related to ENSO (Eakin et al. 2019) was evidenced with less severity in Brazil, being registered in the northeast oceanic islands (Ferreira et al. 2013) and in the Abrolhos region (Teixeira et al. 2021). Four years later, reefs around the world began the worst and long-lasting mass coral bleaching, also related to ENSO, which led to high mortality rates in Indo Pacific (Eakin et al. 2017, 2019), while few reefs in Brazil showed severe bleaching and even less mortality (Teixeira et al. 2019, 2021; Banha et al 2019; Gaspar et al. 2019, Mies et al. 2020; Ferreira et al. 2021).

Even though there are cases of bleaching triggered by the interaction between warming and light incidence (Castro and Pires 1999), tourism (Barradas et al. 2010) or sedimentation (Pereira et al. 2003), most of the episodes of bleaching reported through 2016 for southwest Atlantic reefs were associated with ENSO (Kelmo and Atrill 2013, Ferreira et al. 2013; Miranda et al. 2013; Dias and Gondim 2016; Leão et al. 2016; Lisboa et al. 2018). However, recent bleaching events in Brazil show other possible factors influencing this phenomenon, such as in 2019, when some Brazilian reefs showed the highest bleaching ever recorded (Banha et al. 2019; Teixeira et al. 2019; Gaspar et al. 2020), in a year without ENSO (Soares et al., 2019).

Considering the spatial variability of coral bleaching events and the chance of attenuating them through local conditions (e.g. high turbidity, low light incidence), we reviewed the historical and current record (1993 to 2020) of coral bleaching events in Brazil (1°N to 24°S) in the literature and investigated environmental conditions of 23 representative reefs off the Brazilian coast. We aim to answer the following questions: 1) which regions have historically suffered more marine heat waves? (2) which regions have historically high turbidity and therefore are potential refuges? (3) is there historical variation in turbidity? (4) do bleaching episodes corroborate (1) and (2)? With this approach, it is intended to improve the understanding of coral bleaching events in the South Atlantic, its possible mitigating and exacerbating factors in order to identify areas more or less subject to the phenomenon, supporting management strategies and conservation priorities for Brazilian reefs.

2 - MATERIAL AND METHODS

2.1 Study Area

The Brazilian Province encompasses a heterogeneity of abiotic conditions and reef structures, composing a diverse system (*sensu* Castro and Pires 2001; Floeter et al. 2008). Separated from the Caribbean province by the plume of the Amazon River, South Atlantic corals are mostly restricted to Brazil, but even though some species are still shared (Garcia et al. 2017), the province presents low diversity and a high proportion of endemic reef-building species (Leão et al. 2003). Distributed across approximately 3,000 km (Castro and Pires 2001; Leão et al. 2003, 2016; Pereira-Filho et al. 2019), these reefs are mostly coastal, except for the oceanic island reef systems: Rocas Atoll, Fernando de Noronha, Trindade and Martin Vaz Islands and Arquipélago de São Pedro e São Paulo. In addition to being significantly and historically influenced by river discharges (Leão et al. 2003, 2016; Moura et al. 2016), the large latitudinal extension of Brazilian reefs (6°N to 27°S) leads to diverse environmental conditions, such as temperature, salinity, turbidity and light incidence. The benthic community, despite the epilithic algal matrix (EAM, Wilson and Bellwood, 1997) predominance, presents a wide range in reef cover (Aued et al. 2018).

The main surface ocean currents on the Brazilian continental margin are the warmer Brazil Current flowing southwards (>20°C) and the colder Brazilian Northern Current flowing northwards (<16°C) (Castro and Miranda 1998; Prates et al. 2007; Palmeira et al. 2015). The southeastern coast is also influenced by upwelling events (Kampel et al. 1997), bringing colder and nutrient-rich waters into shallow water environments (Guimaraens et al. 2005). These peculiarities, and the lack of continuous monitoring, prevented a clear understanding of the Brazilian reef system in comparison to the models developed for

Caribbean and Indo-Pacific reefs, mainly about the impacts and responses to mass bleaching and climate change on reef-building fauna.

Coral bleaching in Brazil has been registered since the 1990s by localized efforts of research institutions and researchers, but without an incentive, support or federal recognition, mainly lately (Rodrigues, 2021) and, therefore, it does not present a standardized sampling effort, whether on a spatial, temporal or methodological scale. In order to build a monitoring network, the Coral Vivo project, a conservation movement founded in 2003 at the National Museum (Federal University of Rio de Janeiro), has joined efforts for the continuous and standardized monitoring of 14 representative reef environments of the Brazilian coast. To support this program, here we compiled environmental data not only from 14 of these sites, but from 23 reef environments in Brazil (Fig. 1). The main features and locations of Brazilian reef environments monitored in this study are summarized in Table 1 and supplementary material (Table S1 and Brazilian Reefs Description). The location of the sites and the entire study below follows the division of coral regions by Leao et al. (2003), presented in Figure 1.

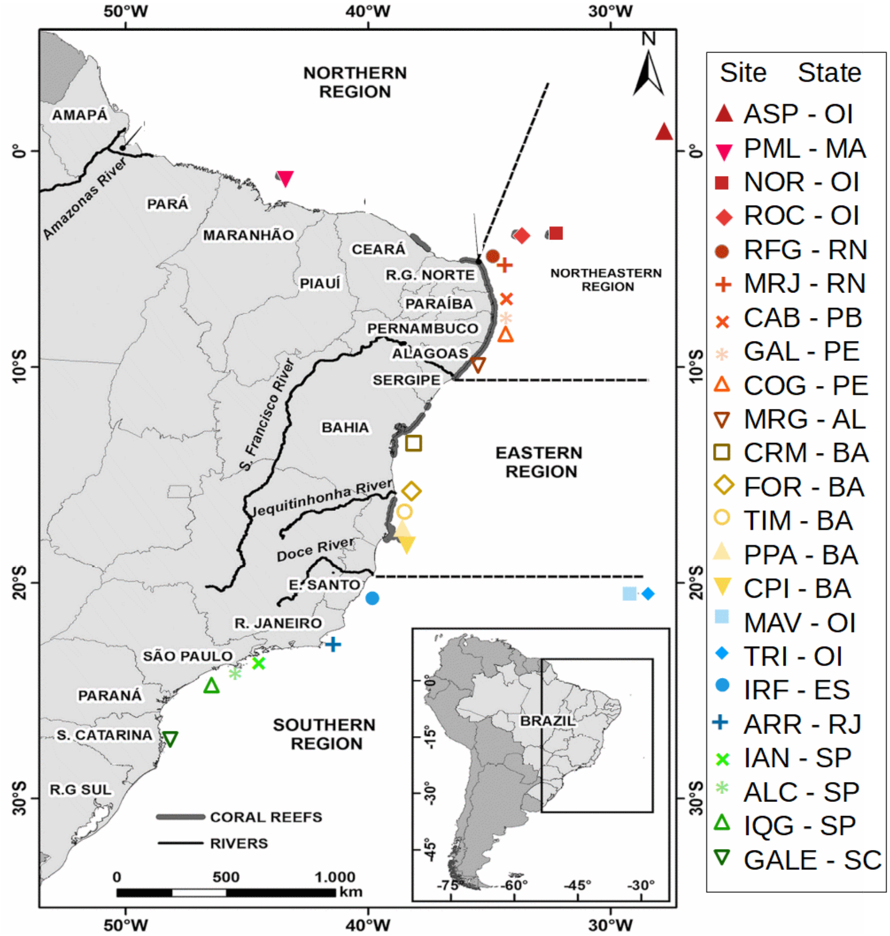

Figure 1: Location of the 23 reefs investigated (colored symbols) in this work and their identification code with their state. Table 1 shows the names of the sites. Adapted from Leão et al., 2003.

2.2 Brazilian Reefs

In the northern (0º30'S to 5º29'S) region (Leão et al. 2003, Fig. 1), characterized by patch and bank reefs, there is the Manuel Luis parcel, reefs that grow as pinnacles. The abundant reefs of the inner shelf of the northeast region (5º29' to 10º30'S) are characterized as patch or elongated banks reefs and are located close to the coastline or parallel to the beach. In addition to the coastal reefs, the northeast region also encompasses 3 of 5 oceanic islands investigated here (Fig. 1). The eastern region (10º30'S to 19º40'S) is the largest area of coral reefs on the entire Brazilian coast and presents several reef forms. In this region there are isolated shallow bank reefs and continuous shallow fringing reefs bordering the coasts of the islands. Also in the eastern region are the richest and most well-known coral reefs in eastern Brazil, the Abrolhos complex, which has fringing reefs and characteristic structures of the area, the chapeirões. The southern (19º30’ to 27º30’S) region presents the growth limit of hermatypic corals, where there are almost no more biogenic reefs and corals are found mainly in rocky reefs, but some with relatively high coral cover (Aued et al. 2018; Pereira-Filho et al. 2019). At the northern limit of the southern region there are two more oceanic islands monitored in this study (Fig. 1)

Table 1 - Name, code, latitude, longitude and main characteristics of the reefs evaluated in this study. Region is according to Leão et al. (2003) (Figure 1). Location means oceanic or coastal systems and the shortest distance to shore in kilometers. Marine Protected Areas (MPA) refers to the presence or not (-) and their category, NT = No Take (few restrictions to human presence and fisheries), NE = No Entry (access restricted for research). Finally, the approximate percentage of coral cover, based on the most recent literature cited in parentheses.

Site	Code	Lat	Long	Region	Location	MPA	Coral Cover
Arquipélago de São Pedro e São Paulo	ASP	0.92	-29.35	NE	Oceanic (1000)	NE	≤1% (Reis et al. 2013)
Parcel do Manuel Luis	PML	-0.94	-44.25	N	Coastal (60)	NE	≤ 1 % (Cordeiro et al. 2021)
Fernando de Noronha	NOR	-3.85	-32.49	NE	Oceanic (360)	NT	≤ 12 % (Matheus et al. 2019)
Atol das Rocas	ROC	-3.96	-33.90	NE	Oceanic (280)	NE	≤ 8% (Longo et al. 2015)
Rio do Fogo	RFG	-5.20	-35.38	NE	Coastal (0)	NT	≤ 5 % (Aued et al. 2018)
Maracajaú	MRJ	-5.40	-35.20	NE	Coastal (0)	NT	≤ 5 % (Aued et al. 2018)
Cabedelo	CAB	-7.02	-34.71	NE	Coastal (0)	-	≤ 4 % (Morais and Santos 2018)
Porto de Galinhas	GAL	-8.78	-35.10	NE	Coastal (0)	-	≤ 8 % (Aued et al. 2018)
Coroa Grande	COG	-8.90	-35.14	NE	Coastal (0)	NT	≤ 8 % (Aued et al. 2018)
Maragogi	MRG	-9.01	-35.12	NE	Coastal (0)	NT	≤ 8 % (Aued et al. 2018)
Recife de Caramuanas	CRM	-13.11	-38.65	E	Coastal (2)	NT	≤ 18 % (Aued et al. 2018)
Recife de Fora	FOR	-16.41	-39.02	E	Coastal (6)	NT	≤ 7 % (Costa Jr et al. 2005)
Recife de Timbebas	TIM	-17.47	-39.02	E	Coastal (18)	NT	≤ 10 % (Aued et al. 2018)
Parcel das Paredes	PPA	-17.80	-38.93	E	Coastal (25)	NT	≤ 10 % (Aued et al. 2018)
Chapeirão do Pierre	CPI	-17.97	-38.71	E	Coastal (62)	NT	≤ 10 % (Aued et al. 2018)
Ilha Martin Vaz	MAV	-20.48	-28.86	S	Oceanic (1140)	NE	≤ 9 % (Aued et al. 2018)

Ilha Trindade	TRI	-20.49	-29.32	S	Oceanic (1200)	NE	≤ 9 % (Aued et al. 2018)
Ilha Rasa de Fora	IRF	-20.68	-40.37	S	Coastal (2)	-	≤ 2% (Aued et al. 2018)
Arraial do Cabo	ARR	-22.76	-41.88	S	Coastal (0)	-	≤ 7 % (Aued et al. 2018)
Ilha Anchieta	IAN	-23.53	-45.08	S	Coastal (1)	NT	≤ 3 % (Aued et al. 2018)
Ilha Alcatrazes	ALC	-24.09	-45.69	S	Coastal (40)	NT	≤ 3 % (Aued et al. 2018)
Ilha Queimada Grande	IQG	-24.49	-46.67	S	Coastal (30)	NE	≤ 6% (Pereira-Filho et al. 2019)
Ilha Galé	GALE	-27.17	-48.41	S	Coastal (7)	NE	≤ 1 % (Aued et al. 2018)

2.3 ENVIRONMENTAL VARIABLES

Monthly remote-sensing data was derived at each of 23 investigated reefs, from July 2002 to December 2020. Irradiance was assessed as photosynthetically available radiation (PAR) (i.e., downwelling irradiance between 400 and 700 nm; Gove et al. 2013) and turbidity as the diffuse attenuation coefficient at 490 nm (Kd_{490}) and were obtained with 4 km^2 resolution from the Moderate Resolution Imaging Spectroradiometer (MODIS) (available at http://oceandata.sci.gsfc.nasa.gov/). Turbidity was considered to be positively related to the diffuse attenuation coefficient of light at the 490 nm wavelength (Kd_{490}), or the rate at which light at 490 nm is attenuated with depth (Office for Coastal Management, 2019). Image processing was performed in the SeaWiFS Data Analysis System (SeaDAS, Baith et al. 2001) and when data was not available for the investigated location, it was obtained from the nearest reliable pixel.

Following the standardized MHW definition (Hobday et al. 2016), a MHW event occurs when the SSTs exceed a seasonally varying 90th percentile for a minimum of five consecutive days. According to this methodology, an event is considered continuous even if gaps of 2 days or less occur between events. In this study, to identify the MHW following Hobday et al. (2016), we used daily gridded SST data, with a horizontal resolution of 1/4° for the period 1982–2020, obtained from the National Oceanic and Atmospheric Administration

Optimum Interpolation Sea Surface Temperature V2.0 (Reynolds et al. 2007). Sea surface temperature anomalies were calculated using the 1998–2002 daily climatology.

2.4 HISTORICAL BLEACHING DATASET

We assembled a dataset on coral, hydrocorals, and zoanthids bleaching occurrences by searching information published in journal articles and reports on Scielo, Web of Science, SCOPUS, ScienceDirect and PubMed. We used the keywords "coral bleaching" and "cnidaria bleaching" plus the names of countries with coastlines in the South Atlantic, both in the South American and African continents. In the survey, bleaching or non-bleaching responses were not obtained for different species, but for the entire reef system. This survey was conducted in four languages (English, Portuguese, French and German) in order to search for information regarding the reefs on the eastern edge of the Atlantic ocean. In addition, we searched for the keywords plus the name of the oceanic islands (including Brazilian ones: Rocas Atoll, Fernando de Noronha, Arquipélago de São Pedro e São Paulo, Trindade and Martin Vaz), since when we searched only the term coral bleaching and brazil, these oceanic environments did not appear.

The search resulted in almost 1000 articles that were first filtered according to the theme of publication, restricted to bleaching reports and excluding related subjects. We subsequently filtered the articles according to the location of the record, aiming to compile only bleaching events in the South Atlantic. From the remaining articles, bleaching reports not associated with temperature and natural conditions (e.g.: experiments) were excluded, as well as those related to local stressors (eg: sedimentation and tourism). To avoid possible species sampling bias, only mass bleaching events in the studied reef system were considered, excluding punctual events. Finally, articles whose data on bleaching could not be extracted were also excluded. After this procedure, we obtained the occurrence of cnidarians (i. e. corals, hydrocorals and zoanthids) mass bleaching and/or mortality in 29 articles.

From each publication, the location and month in which the bleaching occurred or not was extracted, resulting in a total of 319 monthly records, between August 1993 and January 2020. Monthly mean environmental variables were obtained for the publications sampled location and period, from July 2002 onwards due to the availability of remote-sensing data, for each sampling period reported by the articles, in the same manner described above, in 2.1 - Environmental Variables. The variables compiled with the review were specific to the place and time sampled by the publications and are: sea surface temperature (SST); temperature anomaly (aSST); light attenuation coefficient (Kd_{490}); photosynthetically active radiation (PAR) and; cumulative intensity of marine heat waves (MHW).

2.5 Data Analysis

In order to explore the distribution of environmental data over time (between July 2002 and December 2020) and space, boxplots were generated with the monthly abiotic variables in the R software (R Core Team 2018). The monthly variables were then condensed into summer (November to April) and winter (May to October) semesters, in order to reduce the data volume and proceed with the analyses. In order to evaluate significant differences according to reef areas, years and season, we run an analysis of similarities (ANOSIM). Principal coordinate analysis (PCO) was used to summarize spatio-temporal similarities (Euclidean distance) between reefs, years and seasons. The Spearman nonparametric correlation coefficient (based on ranks) was used to investigate the relationship between variables and the PCO axes, with results illustrated as superimposed vectors in the PCO diagrams. The correlation between environmental variables was verified using the variance inflation factor (VIF) in the R software (R Core Team 2018). All variables were maintained since the VIF value was less than 5 for all. Both PCO and ANOSIM were realized using PRIMER 6 with PERMANOVA software (Clarke and Gorley 2006).

To understand whether bleaching records corroborate turbid refugia or marine heatwave hotspots among the sites studied, boosted regression trees were built following the procedures of Elith et al. (2008). Due to the availability of abiotic data through MODIS, the bleaching and mortality records used for the BRT analysis were only from 2002 onwards. Thereby, bleaching BRT analyses were made with 24 publications and 280 records on a monthly scale, while, for mortality BRTs, 16 publications that monitored the phenomenon for 231 months were used. Different from traditional regression methods that produce a single 'better' model, BRT is based on the boosting of a large number of simple regression trees (e.g. Elith et al. 2006). There are three most important attributes of BRT models: 1) Bag fraction determines the proportion of data selected to fit a tree at each step. 2) The learning rate is the contribution of each tree to the overall model explanation. 3) Tree complexity represents the number of nodes (splits) of each tree (Elith et al. 2008). To attain the highest accuracy and avoid model overfit (i. e. lowest values of cross-validation deviance and standard error), optimal BRT models were selected by examining all possible combinations of values for bag fraction 0.5 and 0.75, learning rate 0.001, 0.005, 0.01, and 0.05, and tree complexity 1–5 (cf. Elith et al. 2008). To assess the relative strength of interaction effects, Friedman's H statistic, which varies from 0 to 1, with higher values indicating the strongest interactions, was used. All models were fitted based on a Bernoulli distribution using the packages gbm (version 1.5–7) and gbm.step in the R software (R Core Team 2018).

3- RESULTS

3.1 ENVIRONMENTAL VARIABLES

The boxplots of photosynthetically active radiation, light attenuation coefficient, sea surface temperature, and marine heat waves intensity (Fig. 2A, 2B, 2C and 2D, respectively) confirm the heterogeneity of the studied sites. The temperature range (Fig. 2C) follows the expected latitudinal distribution, with the sites in the north, northeast and east (from ASP to CPI in Fig. 1) showing the highest temperatures and lowest SST variations, compared to the sites in the southern region (from MAV to GALE, from 20°S onwards). While temperatures vary between 24 and 30°C in the east, north and northeast regions, the south region sites experience sea surface temperatures from 16 to 30°C.

The variability of PAR follows a pattern similar to temperature, where the northernmost sites present the highest values (medians close to 50 Einstein m^{-2} d^{-1}) and the smallest variations, while from 20°S onwards the median approaches 40 Einstein m^{-2} d^{-1} and the variation ranges from 20 to 60 Einstein m^{-2} d^{-1} (Fig. 2A). As expected, the northernmost locations (from ASP to TRI) have the warmest and clearest waters, the opposite from the southernmost locations with colder and turbid waters (IRF to GALE), with the exception of Trindade and Martin Vaz, that even at limit of the south region, as oceanic environments have high light incidence.

Light attenuation measured by Kd_{490} (Fig. 2B) show a lower water turbidity at the five oceanic sites (Atol das Rocas, Fernando de Noronha, São Pedro and São Paulo, Trindade and Martin Vaz) whose mean values are much lower than other sites and do not exceed 0.1 m^{-1} (Fig. 2B). Excluding Rio do Fogo and Recife de Fora, whose Kd_{490} are greater than 0.2 m^{-1}, all the sites in the north, northeast and east regions have Kd_{490} mostly below this value, which demonstrates the relatively higher transparency of their waters. On the other hand, the southernmost sites presented the highest Kd_{490}, which may exceed 0.2 m^{-1}, demonstrating the higher water turbidity from 20°S onwards.

Marine heat waves were more intense in subtropical reefs (>20°S, Fig 2D), reaching cumulative intensities of up to 50°, except Ilha Rasa de Fora (IRF) which, like tropical reefs, did not experience MHW with cumulative intensity higher than 40°C. In terms of frequency, reefs such as PML and MRJ are the only ones in the north and northeast region to present more than 60 marine heat waves between 2002 and 2020, while the other reefs are between 35 and 59 marine heat waves and the subtropical ones (IAN, ALC, IQG, GALE) presented more than 70 in the same period.

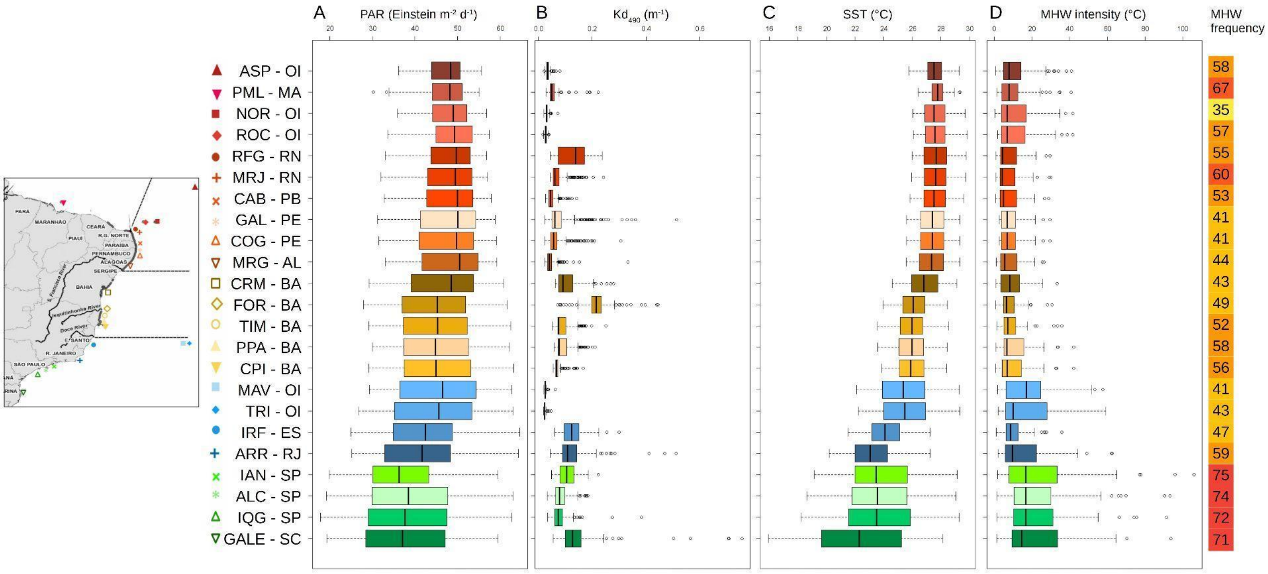

Figure 2: Boxplot illustrating the photosynthetically active radiation (A), light attenuation coefficient (B), sea surface temperature (C) and marine heat wave intensity and frequency (D) as a function of the studied sites. The northern region (PML) site is presented in pink, the northeast sites in shades of red and orange (APS, NOR, ROC, RFG, MRJ, CAV, GAL, COG, MRG), in the eastern region in shades of yellow (CRM, FOR, TIM, PPA, CPI) and southern (MAV, TRI, IRF, ARR, IAN, ALC, IQG, GALE) sites in shades of blue and green. Box plot center = median, outerlimit = 75% percentile, and range is shown by the whiskers. In each site, monthly data from August 2002 to December 2020 are shown. MHW frequency refers to the total number of marine heat waves on reefs between 2002 and 2020.

Axis 1 and 2 of the PCO explained 42.8 and 35.6% of total variation data, respectively (Fig. 4). The most notable difference between sites is on the axis 1, with more turbid sites on the left side (Galé - GALE, Queimada Grande - IQG, Anchieta - IAN, and Alcatrazes Islands - ALC) and oceanic islands and sites in the east, north and northeast regions to the right on the x-axis with clear and warm water (high values of PAR and SST). In axis 2, some reefs such as TRI, MAV, IAN, ALC and IQG stand out, presenting a high cumulative intensity of MHW.

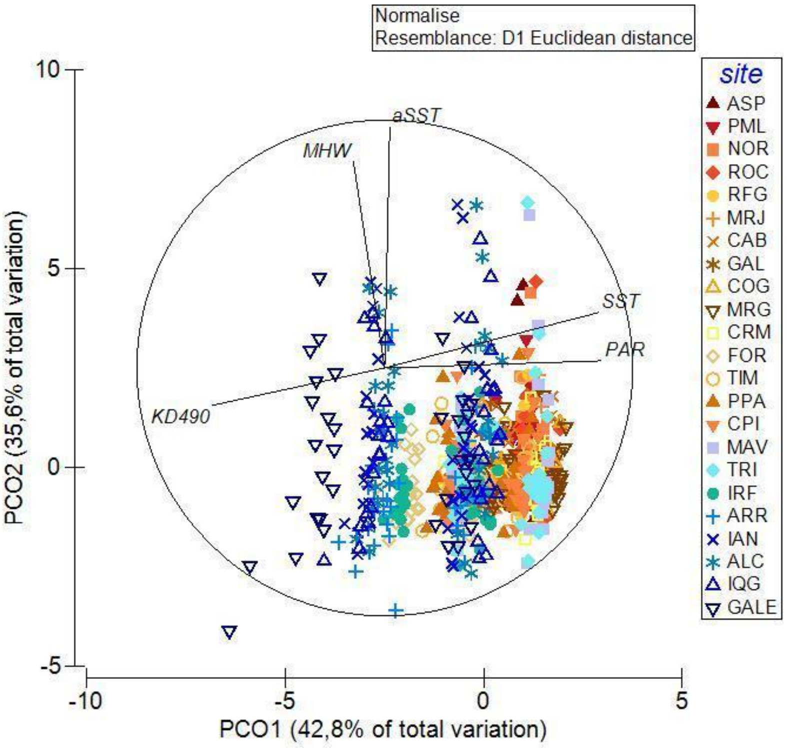

Figure 3: Principal coordinate analysis (PCO) summarizing differences between reefs according to their biotic factors (SST, Kd_{490}, PAR, aSST, MHW intensity). Variables with Spearman correlation with a given PCO axis are illustrated as superimposed vectors.

Between seasons semesters (Fig. 5A), winter is clearly the turbid one, even though it is also subject, sporadically, to warm and clear water, which is likely to occur at sites above 20°S. In relation to years (Fig. 5B) most are concentrated in conditions of high SST and PAR, with little presence of MHW or aSST, except 2009 and 2018 standing out with high values of SST, PAR, MHW and aSST. The most recent years, excluding 2009, are shown in the upper part of the PCO space, revealing the increase in the frequency of thermal stresses over time. The ANOSIM shows significant differences between sites (R=0.191; P=0.001), years (ANOSIM: R=0.065, P=0.001) and seasons (ANOSIM: R=0.268; P=0.001).

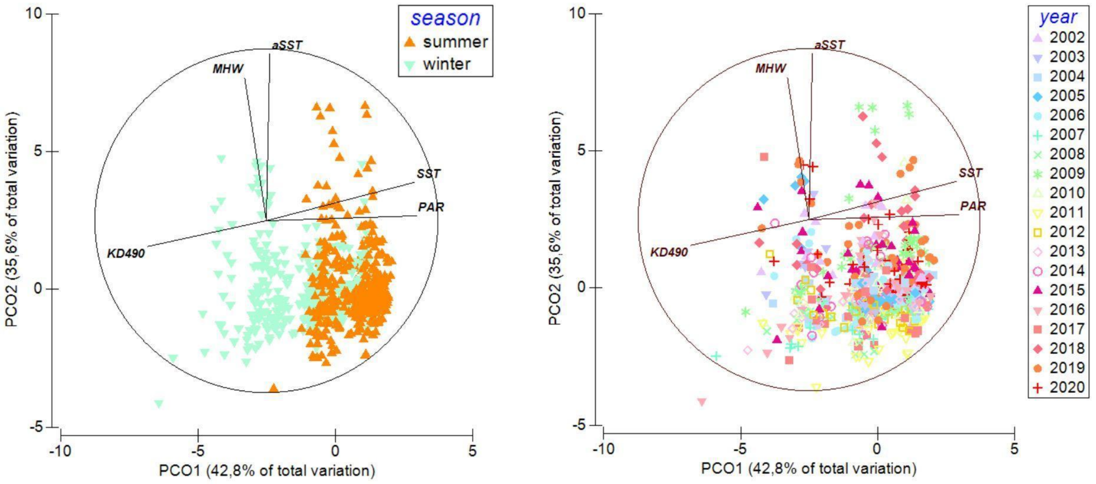

Figure 4: Principal coordinate analysis (PCO) summarizing differences between seasons semesters (A) and years (B) according to their biotic factors (SST, Kd490, PAR, aSST, MHW intensity). Variables with Spearman correlation with a given PCO axis are illustrated as superimposed vectors.

3.2 BLEACHING HISTORY

No records of bleaching or mortality of cnidarians were found for the African coast of the South Atlantic Ocean. For Brazilian reefs, the literature review resulted in 29 publications, which registered bleaching in different locations during 319 moments (on a monthly scale), from October 1993 to January 2020. Of the monitored period by the articles, corals were bleached 56.9% of the time and in just over 20% of the records there was coral mortality. Hydrocorals were sampled in 13 publications covering 75 months of investigation, of which presented bleaching and mortality in 70% and 18% of the period, respectively. Bleaching in zoanthids was investigated by only 6 publications which covered a sample period of 130 months, of which 90% of the time zoanthids showed no bleaching, and in less than 1%, mortality. The coralline region (Leão et al. 2003) mostly represented in the bleaching records is the north, with almost 50% of the studies, followed by the east and northeast regions (~25 and ~18% respectively), and finally only 5% of the studies were carried out in the South region. When analyzing the spatial distribution of all bleaching records (Fig. 6), the concentration of studies near the Abrolhos complex and the Todos os Santos Bay is noticeable.

Turbidity and PAR were the variables that most contributed to the BRT bleaching model, with 30.2% and 30%, respectively (Fig. 6A). Turbidity followed the expected pattern, showing more bleaching at lower Kd_{490} values and less bleaching at high turbidity values, evidencing its role in attenuating bleaching. In contrast, in relation to PAR, bleaching is high up to approximately 40 Einstein m^{-2} d^{-1}, decreases between 40 and 60 and then increases from 60 Einstein m^{-2} d^{-1} onwards (Fig. 6A). In relation to temperature, which explains 19% of the model, as expected, bleaching increases with increasing SST. On the other hand, temperature anomalies explain 13.9% of the model and reveal a decrease in bleaching with an increase in the anomaly (Fig. 6A). The intensity of marine heat waves explains 6.9% of the model and follows the expected pattern of increased bleaching with increasing MHW (Fig. 6A). A median interaction (interaction size 0.49) was recorded between turbidity and PAR, and between PAR and SST (interaction size 0.44, Fig. S1).

Light incidence was the most important variable for coral mortality, explaining 37.2% (Fig. 6B). As for bleaching, PAR was the opposite of the expected pattern, with high mortality in the lowest PAR values, and while light increases, mortality decreases. Turbidity explained 31.7% of the model and its increase means a decrease in mortality (Fig. 6B), as well as for bleaching. Similar to PAR, SST, which explains 19.9%, presented a pattern contrary to what was expected in relation to mortality, which decreases with increasing temperature (Fig. 6B). Explaining 10.4% of mortality, temperature anomaly promotes mortality when it increases, but in a smooth way and is almost indifferent to mortality at non-anomalous temperatures (Fig. ¨B). A median interaction (interaction size 0.54) was recorded between PAR and SST, and between turbidity and PAR (interaction size 0.46, Fig. S1).

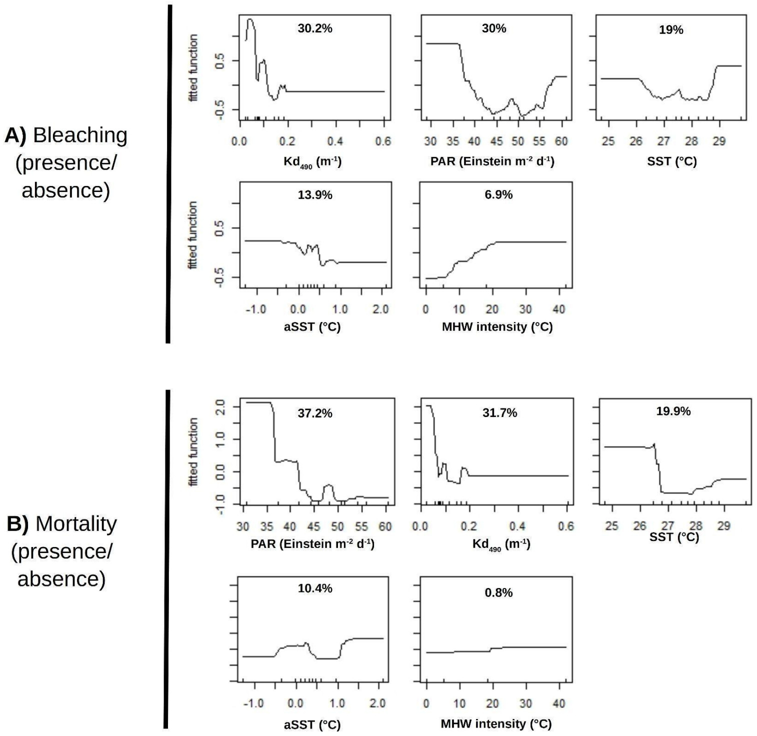

Figure 5: Partial dependence plots for influential variables predicting: A) bleaching, B) mortality.Y axes are centered to have zero mean over the data distribution

Bleaching records used for BRT modeling encompass events mostly monitored in the north and northeastern regions (45 and 39% respectively), and then in the eastern and southern region (10 and 6% respectively). Some of the bleaching records analyzed in this review match reef locations also monitored by the project cora vivo and this study,, such as Parcel do Manuel Luis (PML), Cabedelo (CAB), Timbebas (TIM), Parcel da Paredes (PPA), Anchieta Island (IAN), Porto de Galinhas (GAL), Oceanic Islands (NOR, ROC, ASP, TRI, MAV), Arraial do Cabo (ARR) and Todos os Santos Bay, whose Caramuanas reef (CRM) (Fig 1 and 7), besides all the oceanic islands. From all of these monitored reefs, the ones with the highest bleaching frequencies were in the Abrolhos and Cabedelo region. For mortality, the studied reefs presented similar trends, but are concentrated in the northeast region, Todos os Santos Bay, Abrolhos and some Oceanic Islands.

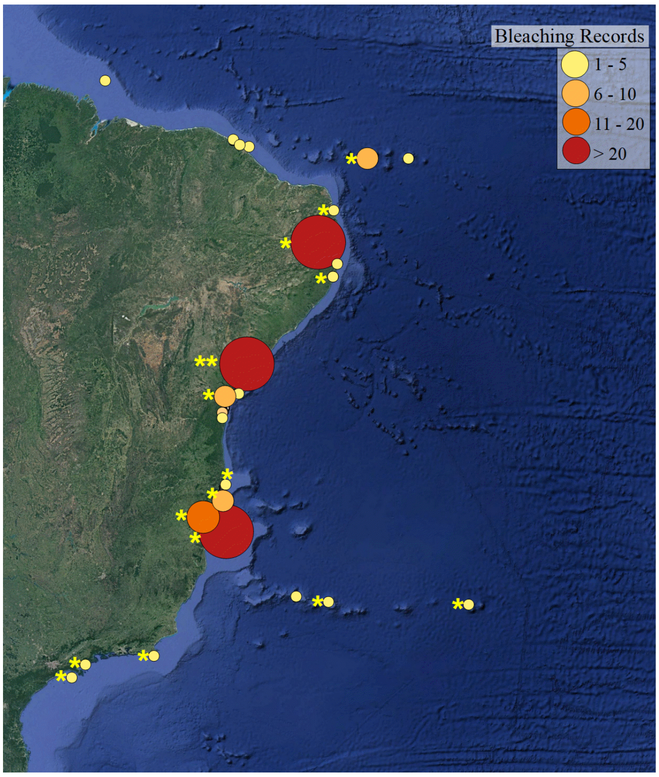

Figure 7: Geographical distribution of all documented episodes of bleaching and coral mortality in the South Atlantic between 2002 and 2020. Circle size refers to the number of bleaching records, and the yellow asterisks represent records with mortality. South Atlantic bleaching episodes references: 24, in Supplementary Material Reference List S1.

4 - DISCUSSION

Here we investigate the possible attenuating and triggering factors of cnidarian bleaching and mortality in the South Atlantic by analyzing conditions of sea surface temperature and anomalies (e.g. marine heat wave intensity and frequency), turbidity and light incidence in 23 representative reefs in the Brazilian coast since 2002, in addition to a review of cnidarian bleaching and mortality records in the South Atlantic. No bleaching or mortality records were found for the South African Atlantic coast, which, despite the different representation of the reef environments in each region, raises the alarm of inequality in scientific development. In the global review of bleaching events by Sully et al. (2019), this discrepancy in reef investigation is quite evident, where only one record was found for the African continent, in the northern Atlantic, while Indo-Pacific concentrates most efforts. Although less understood about the impacts of climate change, reefs in Brazil and on the African continent represent an ecosystem support base for coastal populations, whether through economic development or livelihoods and food security by fisheries (Begossi et al. 2000, Chuenpagdee et al. 2006, Carneiro 2011).

In the portion of the South American continent surrounded by the Atlantic, different from what we expected, the records of bleaching do not correspond to regions that suffered most from marine heat waves (e.g. subtropical reefs), but mainly to naturally higher background temperatures regions (e.g. tropical reefs from east and northeastern region), interacting with high variability of PAR and turbidity. The regions that present higher frequency of bleaching records, such as the Todos Santos Bay and Abrolhos are the best known coral regions of the Brazilian coast (Leão et al. 2003) and, consequently, the most studied locations in this regard, which may have influenced this result. For mortality, records are distributed from 3° to 24°S but are much milder than bleaching itself, or even less than the mortality reported in other reefs around the world in the same sampled periods (De'ath et al. 2012; Eakin et al. 2019). In addition, many mortality records are in Todos os Santos Bay, a region under the influence of several aggravating factors for the reef maintenance, such as overfishing (Cruz et al. 2009), invasive species (Miranda et al. 2016) and sewage (Roth et al. 2016).

It’s worth mentioning that coral communities in Brazilian reefs have different species composition along their latitudinal distribution, which can alter the response of corals to thermal stress (Brown et al. 1990, Glynn 1996, Smith et al. 2014). Even though we have been working with large scale bleaching records to avoid differentiating between species responses, for mortality the species composition greatly changes the reef response even when bleaching affects all species (Ferreira et al., 2021). Reefs in southern Brazil have greater coverage of massive corals (Leão et al. 2003, 2016), including species thermal tolerants (e.g.: *Mussismilia* sp. and *Siderastrea* sp., Loya et al. 2001, Schlöder & D’Croz 2004), then branched ones (e.g.: *Millepora* sp., Ferreira et al. 2021) than some reefs in the north. Reefs with higher mortality frequency in the reported bleaching events, such as Abrolhos and the northeast region, have greater coverage of branched corals compared with the southern reefs (Leão et al. 2003, 2016), which may have influenced the reef's response in terms of mortality. However, the lack of standardized monitoring leads to limited review data, and therefore it was not possible to compare the response of different species to bleaching or mortality.

The Indo-Pacific and Caribbean coral bleaching intensification (Hughes et al. 2017) does not seem to happen in the South Atlantic, which historically presents fewer thermal stress events (Skirving et al. 2019), bleaching (Sully et al. 2019) and coral mortality (Mies et al. 2020; this paper). Some characteristics of Brazilian reefs support their lower prevalence and severity of bleaching, such as corals' massive morphology, tolerance to high turbidity and nutritional enrichment, in addition to flexible and tolerant symbiotic associations (Mies et al. 2020). Such conditions, added to the wide latitudinal distribution of the reefs of the southwest Atlantic, have imposed the hope of Brazilian reefs as climate refuges for the maintenance of some reef building species in a warm future (Vergés et al. 2014; Mies et al. 2020; Bleuel et al. 2021).

As in other coral regions of the world, in Brazil, bleaching and mortality were more intense in reefs between 5 and 20 °S, in the tropical region (Sully et al. 2019), where most coral reefs are found. Such environments within the Brazilian coast are considered as transparent water reefs, but they are characterized by higher turbidity in relation to Pacific and Caribbean reefs. In fact, South Atlantic tropical reef bleaching records are less intense compared to reefs elsewhere, possibly due, in part, to the attenuation promoted by turbidity, and also due to species composition, since Caribbean and Indo Pacific reefs have several branching species not found in the Brazilian province (Mies et al., 2020).

Corals are expected to follow an extratropical migration (Yamano et al. 2011; Vergés et al. 2014) that several organisms have already done, expanding their distribution towards the poles in response to warming (Sunday et al. 2012; Cheung et al. 2013). Bleuel et al. (2021) predicted the possible expansion of tropical Brazilian reefs towards extratropical and mesophotic reefs, but also warned about the increased probability of bleaching and vulnerability, challenging their role as a refuge. In fact, Brazilian subtropical reefs had low mortalities in the last mass bleaching event, but also had the highest bleaching rate ever recorded (Banha et al. 2019, Gaspar et al., 2019). Besides that, low mortality rates can be associated with characteristics other than turbidity and the region, such as the composition of monitored assembly.

We found that Brazilian subtropical reefs present, historically, more turbid waters than tropical ones, at the same time they have been the most affected by marine heat waves since 2002. As in tropical reefs, higher turbidity conditions occur mostly in winter at subtropical reefs, as well, the coldest conditions, while marine heat waves occur regardless of seasonality.

Furthermore, subtropical reefs in the austral summer can have sea surface temperatures as high as tropical ones, which in interaction with the incidence of MHW and the low turbidity characteristic of the season, can lead corals to exceed the bleaching threshold. So, it is possible that even in the environment previously intended as a refuge, such as subtropical regions, the interaction between certain environmental conditions can still lead to coral bleaching, as occurred in southeastern Brazil in 2019 (Banha et al. 2020). In this sense, the subtropical oceanic islands, Trindade and Martin Vaz, stand out, which, as well as the other reefs in this region, present intense MHW, however, as they are oceanic systems, their low turbidity is not able to attenuate the incidence of light or bleaching.

Unlike tropical biogenic reefs, extratropical reefs in the southwest Atlantic are mostly characterized as rocky (Floeter et al. 2006) and presents extremely low coral cover (Leão et al. 2003; Aued et al. 2018), with the exception of a recent discovery (Pereira-Filho et al. 2019). These reefs are even more turbid and experience temperatures below the physiological threshold of several coral species. Such reefs are even less studied, noticed or understood than tropical reefs and this can undermine the hope that they can serve as a refuge, since the lack of knowledge of the system hinders the understanding of its response to these stressful conditions. It is worth mentioning that until 2019, the limit of the distribution of biogenic reefs in Brazil went as far as the abrolhos bank (19°30'S), but it expanded to 24°S with the discovery of coral reef on the Queimada Grande Island (Pereira Filho et al. 2019). In 2018 most of the coral reefs in the Caribbean and Indo-Pacific were already known and even monitored, while in Brazil we were still discovering biogenic coral reefs. This scenario partly justifies a lack of understanding of the responses to bleaching and mortality of the southwest Atlantic reefs compared to other reefs and demonstrates the need and importance of continuous and standardized monitoring in order to improve the understanding of Brazilian reef systems.

In this study, the use of BRT models supported the hypothesis that turbidity attenuated the bleaching and mortality of Brazilian reefs in the events reported between 2002 and 2020. However, other factors must be evaluated for such assertion, such as species composition and associated microbiome, in addition to local environmental conditions. Therefore, there remains a need to understand how these reefs will respond to excessive and rapid ocean warming. The BRT models responded contrary to what was expected for light incidence, which may have been a result of the naturally varied PAR conditions of the monitored reefs, or atmospheric conditions such as clouds. In addition, the bleaching records in Brazil are in naturally more turbid environments with low PAR values, presenting different taxonomic composition and biogeochemical conditions compared to reefs in the Caribbean and Indo Pacific.

Another important feature that is reflected in the uncertainty of the factors that lead Brazilian corals to bleaching is the lack of systematic and regular sampling of reef environments. Unfortunately, due to discontinuation of financing, sampling in Brazil is still carried out when there is an opportunity, and this depends on the availability of resources, which has suffered several interruptions currently (Rodrigues, 2021). Systematic and long-term sampling would allow the best understanding of the response of reef systems to stressful conditions, its sporadic nature impairs the understanding of ecosystem changes and impacts on human well-being. Therefore, it is urgent to improve and activate monitoring programs, in addition to using the knowledge generated for adaptive management in relation to climate change in coastal and reef areas.

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6 SUPPLEMENTARY MATERIAL

Table S1 - Name, code, latitude, longitude and environmental variables of the reefs evaluated in this study. The summarized environmental conditions correspond to the monthly mean and standard deviation (mean ± sd) of the variables compiled between July 2002 and December 2020: sea surface temperature (sst in °C), light attenuation coefficient at 490 nanometers wavelength (kd_{490}in m^{-1}), photosynthetically active radiation (par in Einstein m^{-2} day^{-1}), accumulated marine heat wave intensity (mhw intensity in °C) and SST anomaly (aSST in °C).

Site	Code	Lat	Long	sst	kd_{490}	par	mhw intensity	aSST
Arquipélago de São Pedro e São Paulo	ASP	0.92	-29.35	27.56 ± 0.69	0.036 ± 0.007	47.14 ± 4.64	3.14 ± 7.45	0.18 ± 0.41
Parcel do Manuel Luis	PML	-0.94	-44.25	27.77 ± 0.55	0.056 ± .024	47.29 ± 5.03	3.13 ± 6.74	0.28 ± 0.32
Fernando de Noronha	NOR	-3.85	-32.49	27.59 ± 0.85	0.031 ± 0.005	47.93 ± 4.8	3.24 ± 7.53	0.24 ± 0.34
Atol das Rocas	ROC	-3.96	-33.90	27.63 ± 0.83	0.028 ± 0.004	48.65 ± 5.17	2.92 ± 7.06	0.24 ± 0.33
Rio do Fogo	RFG	-5.20	-35.38	27.64 ± 0.92	0.128 ± 0.052	48.15 ± 5.83	1.96 ± 4.85	0.17 ± 0.29
Maracajaú	MRJ	-5.40	-35.20	27.62 ± 0.90	0.074 ± 0.032	48.01 ± 6.33	2 ± 4.81	0.17 ± 0.28
Cabedelo	CAB	-7.02	-34.71	27.58 ± 0.90	0.050 ± 0.018	48.02 ± 6.57	1.93 ± 4.79	0.15 ± 0.28
Porto de Galinhas	GAL	-8.78	-35.10	27.42 ± 0.97	0.087 ± 0.069	48.01 ± 7.27	1.65 ± 4.38	0.14 ± 0.3
Coroa Grande	COG	-8.90	-35.14	27.42 ± 0.97	0.068 ± 0.038	47.70 ± 7.38	1.65 ± 4.38	0.14 ± 0.3
Maragogi	MRG	-9.01	-35.12	27.39 ± 0.97	0.046 ± 0.026	48.64 ± 7.24	1.66 ± 4.38	0.14 ± 0.3
Recife de Caramuanas	CRM	-13.11	-38.65	26.89 ± 1.08	0.106 ± 0.04	46.83 ± 8.73	1.95 ± 5.29	0.12 ± 0.38
Recife de Fora	FOR	-16.41	-39.02	26.13 ± 0.98	0.217 ± 0.048	44.96 ± 8.69	1.95 ± 4.73	0.10 ± 0.39
Recife de Timbebas	TIM	-17.47	-39.02	25.98 ± 1.03	0.102 ± 0.394	45.45 ± 8.7	2.32 ± 5.61	0.12 ± 0.43
Parcel das Paredes	PPA	-17.80	-38.93	25.99 ± 1.08	0.096 ± 0.033	45.25 ± 8.83	2.78 ± 6.49	0.14 ± 0.42
Chapeirão do Pierre	CPI	-17.97	-38.71	25.99 ± 1.08	0.072 ± 0.016	45.52 ± 8.89	2.63 ± 6.43	0.14 ± 0.39

Ilha Martin Vaz	MAV	-20.48	-28.86	25.44 ± 1.66	0.025 ± 0.004	45.99 ± 9.83	3.44 ± 9.65	0.11 ± 0.54
Ilha Trindade	TRI	-20.49	-29.32	25.50 ± 1.66	0.024 ± 0.003	45.12 ± 9.84	3.52 ± 9.83	0.11 ± 0.54
Ilha Rasa de Fora	IRF	-20.68	-40.37	24.25 ± 1.26	0.127 ± 0.039	42.64 ± 8.87	2.36 ± 5.7	0.02 ± 0.54
Arraial do Cabo	ARR	-22.76	-41.88	23.14 ± 1.44	0.122 ± 0.058	41.39 ± 9.05	4.5 ± 10.72	0.05 ± 0.71
Ilha Anchieta	IAN	-23.53	-45.08	23.87 ± 2.23	0.107 ± 0.033	36.61 ± 8.23	8.21 ± 17.37	0.351 ± 1
Ilha Alcatrazes	ALC	-24.09	-45.69	23.74 ± 2.33	0.084 ± 0.028	39.06 ± 10.08	7.93 ± 16.13	0.36 ± 0.99
Ilha Queimada Grande	IQG	-24.49	-46.67	23.72 ± 2.58	0.080 ± 0.033	38.3 ± 10.31	7.78 ± 15.46	0.37 ± 0.96
Ilha Galé	GALE	-27.17	-48.41	22.27 ± 3.1	0.145 ± 0.089	37.42 ± 11.02	7.1 ± 14.97	0.24 ± 0.92

Figure S1:

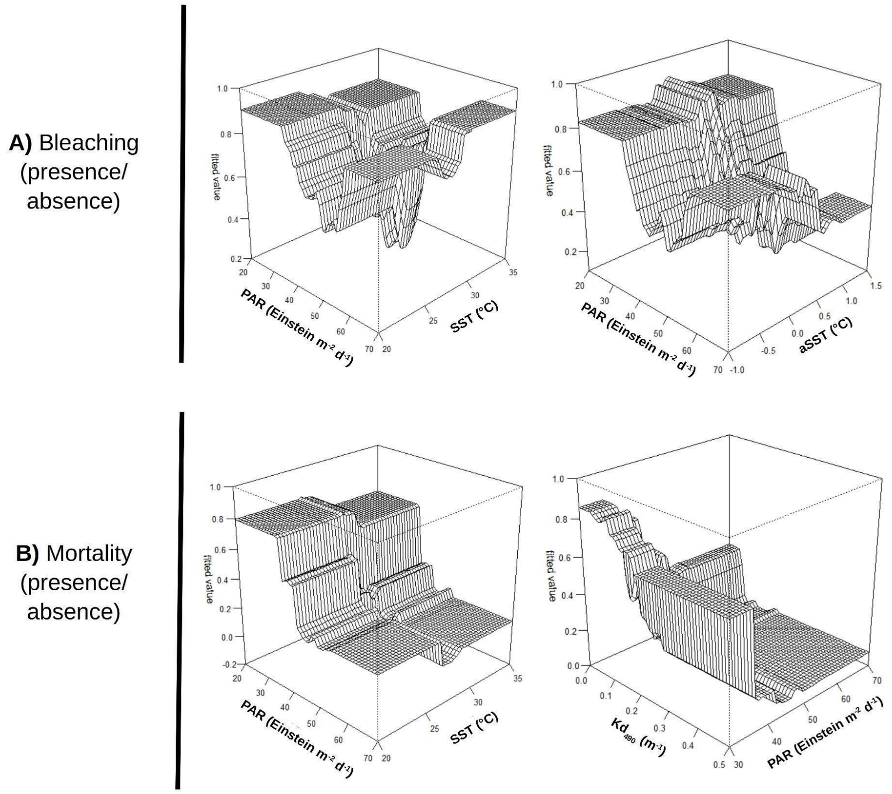

Figure S1: Three-dimensional partial dependence plots for the strongest interaction in the models for predicting: A) bleaching, B) mortality All variables except those graphed are held at their means.

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Brazilian Reefs Description

The Brazilian northern (0º30’ to 5º29’S) region (Leão et al. 2003, Fig. 1) encompasses the recently described Amazon plume reefs (Collette and Rutzler 1977; Moura et al. 2016; Francini-Filho et al. 2018). In the southernmost and shallowest part of the Amazonian Reef System is the Parcel do Manuel Luis (PML, Fig. 1), a no-take and no-entry marine area due to its unique reef formations (Rocha and Rosa 2001) that represent the reef shallows further north of the Brazilian coast (Rocha 2003; Floeter et al. 2006). These reefs grow as pinnacles in depths of 25 to 30 m and the top of the pinnacles reach up to 2 m water depth during spring low tides. The PML benthic community is diverse and even dominated by macroalgae (Aued et al. 2018), also presenting less coverage of algal turfs, corals (Cordeiro et al. 2021), coralline algae, sponges and ascidians (Rocha and Rosa 2001).

The northeastern (5º29’ to 10º30’S) region comprises the coastline from Rio Grande do Norte to Alagoas states and includes three out of five oceanic islands monitored here (Fig. 1): Fernando de Noronha (NOR), Rocas Atoll (ROC) and São Pedro e São Paulo Archipelago (ASP). The only atoll in the South Atlantic, Rocas (ROC) is the first no-entry marine protected area in Brazil, created in 1979. The reef substrate is mainly formed by coralline algae, vermetid gastropods and encrusting foraminifera (Kikuchi and Leão 1997), but seven species of scleractinian corals and one hydrocoral occur there, with *Siderastrea stellata* dominance (Leão et al. 2016). The Fernando de Noronha (NOR) archipelago is composed of a main island, with reefs at depths up to 60m mostly constituted by volcanic rocks. Reef benthic community is mainly composed of turf algae (Zamoner et al. 2021), brown macroalgae (Aued et al. 2018; Matheus et al. 2019), and articulated and crustose coralline algae (Eston et al. 1986). Coral cover in NOR is generally low in the shallows and increases with depth, with 22 coral species described (Pires et al. 1992), the most abundant being *Montastraea cavernosa* (Eston et al. 1986; Pires et al. 1992; Ferreira et al. 2006; Krajewski and Floeter 2011; Matheus et al. 2019). The São Pedro and São Paulo Archipelago (ASP) is a remote group of rocks lying on the mid-Atlantic ridge located approximately 1100 km off the coast of Rio Grande do Norte state, the largest being the Belmonte Islet (Vaske et al. 2010). Nineteen coral species have been reported on the rocky shores of these islets, lower in richness than NOR and comparable with PML and ROC. All of these three oceanic sites are subjected to intense wave action in comparison to coastal systems and are characterized by a semi-diurnal and mesotidal regime.

The northeast region still encompasses six coastal reefs monitored here: Rio do Fogo (RFG), Maracajaú (MRJ), Cabedelo (CAB), Porto de Galinhas (GAL) Coroa Grande (COG) e Maragogi (MRG). At the northern coastal end are the Rio do Fogo and Maracajaú reefs, which are part of an extensive offshore reef formation, where the "APA dos Recifes de Corais", a marine protected area (MPA) established in June 2001. These sites are characterized by coral knolls and patch reefs parallel to the coast (Leão et al. 2003) and restricted to a sublittoral turbid zone (Testa and Bosence 1999). These reef systems are mostly built by calcareous algae, vermetids and corals (Maida and Ferreira 1997; Castro and Pires 2001), but the benthic community is dominated by turf and macroalgae (Roos et al. 2019). Cabedelo Reef (CAB) is considered to be the richest in faunal terms and more differentiated in structure than those further north. Described as plateau reefs, with an abundance of cracks, calcareous algae and corals, *Siderastrea sp.* still plays a predominant role, supported by millepores (Mendes & Pinheiro, 2019). Located on the bank of a river, CAB reefs are subject to high sedimentation and tourism, with literature mentioning impacts on reef zones (Costa et al. 2007; Debeus and Crispim 2008).

The predominance of macroalgae and zoanthids and low cover of corals and calcified hydroids characterize the reef environment of Porto de Galinhas Beach (GAL), one of the most visited beaches in Brazil. These reefs are in the form of blocks in front of the beach and close to the reef crest there is a direct impact from tourists who walk on the reefs (Sarmento and Santos 2012). In the extreme south of the State of Pernambuco, is the Coroa Grande (COG) reef. Characterized as coastal patch reefs, nine zooxanthellate corals and four zoanthids are found in the benthic community, with *Siderastrea stellata* and *Palythoa caribaeorum* being the dominant species (Neves et al. 2003). The Maragogi reef (MRG) comprises a sandstone bank with a thin framework formed by corals (mainly *Porites* species), calcareous algae and vermetid molluscs (Laborel-Deguen et al., 2019). Inserted in the MPA (Marine Protected Area) Protected Area of Costa dos Corais (APACC), even with the turf-dominated community (Aued et al. 2018), they have relatively high biodiversity (Maida and Ferreira 2003), with *Millepora alcicornis* domain between millepores (Ferreira et al. 2006). However, tourist exploitation also introduces direct sources of impact on the reefs (e.g. trampling, waste and garbage, artificial food offered to fish by tourists).

In the eastern region (10º30’ to 19º40’S), in the State of Bahia, is located the Caramuanas reef (CRM), which comprises three main flat reef banks. This reef complex is within the MPA Todos os Santos Bay Environmental Protection Area (APA BTS), where the "fanustical core" of Brazilian corals that extends to the Abrolhos archipelago begins (Laborel 1970). The benthic community of the CRM is dominated by encrusting and articulating calcareous algae, but has up to 18% coral cover, being *Mussismilia hispida*, *M. braziliensis*, *Porites branneri*, and *Siderastrea* sp. the most common (Cruz et al. 2009; Aued et al. 2018). Further south in the state of Bahia is Recife de Fora (FOR), an extensive coralline plateau, with elliptical shape and *Mussismilia braziliensis* being the essential building species (Calderon et al. 2019) but *Siderastrea sp.* are the most abundant, followed by *Porites astreoides*. In the extreme south of the state of bahia, the continental shelf widens forming the Abrolhos (MPA National Marine Park) bank that comprises the largest and richest reefs of the South Atlantic, with at least 20 species of coral, including all that are endemic to Brazil (Leão et al. 2003). The Abrolhos complex is formed by two arches, the coastal one consisting of reefs with different shapes and sizes (TIM and PPA) while the outer arch, which borders the eastern part of the Abrolhos Islands, is formed by isolated “chapeirões” in waters with depth greater than 20m (CPI). Timbebas (TIM) benthic community is represented by crustose coralline algae, vermetid, gastropods and *Zoanthus* sp. (Villaça and Pitombo 1997), which *M. braziliensis* as the most abundant coral species (Francini-Filho et al. 2008). Parcel das Paredes (PPA) is a huge elliptical plateau emerging from almost its entire surface, where frondose fleshy macroalgae are very abundant (Coutinho et al 1993), as well as turf algae and zoanthids

(*Palythoa caribeorumm*; Segal and Castro 2011). The Chapeirão do Pierre reef (CPI) is part of the Abrolhos's offshore arch and has a benthic cover dominated by turf and soft and hard corals.

The southern (19º30' to 27º30'S) region presents the growth limit of hermatypic corals, where there are almost no more biogenic reefs and corals are found mainly in rocky reefs, but some with relatively high coral cover (Aued et al. 2018; Pereira-Filho et al. 2019). The Trindade and Martim Vaz Island complex encompasses two oceanic islands monitored here (TRI and MAV), which are the most isolated and the newest (Cordani, 1970) oceanic islands in the south-western tropical Atlantic Ocean. The marine biodiversity of TRI and MAV is remarkably low, with benthic assemblages considered one of the poorest among tropical islands in the world (Floeter et al. 2008). Its benthic covers are dominated by sand, green algae and coralline crustose algae, while corals are less representative, and more common in MAV (Pereira-Filho et al. 2011). On the coast of Espírito Santo there is a rocky reef, Reef Ilha de Fora (IRF), 6 km away from the coast, up to 20 m in depth and the bottom includes rock formations covered by cnidarians. Arraial do Cabo, in the state of Rio de Janeiro, is considered a transitional zone between the tropical and subtropical province, called "coral oasis" where the coral species *Siderastrea stellata* and *M. hispida* occur (Laborel 1970). At Arraial do Cabo, the monitored reef, Praia do Forno (ARR), has a benthic community dominated by calcareous articulated algae and turf filaments (Ferreira et al. 1998a, b, 2001; Mendes et al. 2009), and among the cnidarians *Palythoa caribaeorum* is the most abundant, followed by *Millepora alcicornis*, octocorals and scleractinian corals.

The first site monitored in the state of São Paulo is Ilha Anchieta (IAN), 1 kilometer from the coastline. This reef is characterized by algae dominance, but with the presence of *M.. hispida* (Pereira 2007). Still in São Paulo, we monitored the island of Alcatrazes (ALC), 30 km off the coast, a no-take Marine Protected Areas (MPAs) whose rocky reef is dominated by turf algae (Aued et al. 2018). Queimada Grande Island (IQG) is located approximately 30 km off the coast of the State of São Paulo and has a structure built mainly by colonies of *M. decactis* that were cemented in place by crusty coralline algae (Capel et al. 2019). The benthic community of IQG is dominated by turf geniculate coralline algae, followed by fleshy algae, the zoantharian *Palythoa caribaeorum* and the scleractinian coral *M. hispida* (Pereira-Filho et al. 2019). The last and southernmost monitored site is Galé Island (GALE), approximately 7 km off the coast, which is a no-entry marine protected area within a Marine Biological Reserve that is characterized by turbid and cold waters. In this site is the southern distribution limit of the *Madracis decactis* coral, which on the island forms a unique formation of free-living colonies (Capel et al. 2012). The benthic community is dominated by turf , macroalgae and coralline crustose algae (Aued et al. 2018).

2 CONCLUSÃO GERAL

Nesse estudo, investigamos os possíveis fatores atenuantes e desencadeadores do branqueamento e mortalidade de cnidários no Atlântico Sul através de uma revisão bibliográfica dos registros de branqueamento e mortalidade. Além disso, analisamos as condições de temperatura e anomalias da superfície do mar, turbidez, incidência de luz e intensidade e frequência de ondas de calor marinhas em 23 recifes representativos da costa brasileira entre 2002 e 2020. Não foram encontrados registros de branqueamento ou mortalidade para a costa oeste da África o que, apesar da diferente representatividade dos ambientes recifais em cada região, ressalta a desigualdade no desenvolvimento científico a este respeito (SULLY & VAN WOESICK, 2019). Embora menos compreendidos quanto aos impactos das mudanças climáticas, os recifes no Brasil e no continente africano representam uma base ecossistêmica para as populações costeiras, seja por meio do desenvolvimento econômico ou da subsistência e segurança alimentar através da pesca (BEGOSSI et al. 2000, CHUENPAGDEE et al. 2006 , CARNEIRO 2011).

Para a costa brasileira, diferente do esperado, os registros de branqueamento não correspondem às regiões que mais sofreram com as ondas de calor marinhas (e.g.: recifes subtropicais), mas principalmente a regiões naturalmente mais quentes (por exemplo, recifes tropicais), em sinergia com alta variabilidade de PAR e turbidez. As maiores frequências de branqueamento foram relatadas nos recifes mais conhecidos da província brasileira, na região de Abrolhos e da Baía de Todos os Santos (LEÃO et al., 2003), o que pode ter influenciado este resultado. Os registros de mortalidade são bem distribuídos latitudinalmente (3°S a 24°S), e sua frequência é muito menor do que a dos eventos de branqueamento relatados, assim como a mortalidade reportada para recifes de outros locais nos mesmos períodos amostrais (EAKIN et al. 2019; DE'ATH et al. 2012. Para a Baía de Todos os Santos, local com mais registros de mortalidade, vale mencionar outros fatores agravantes à saúde recifal como sobrepesca (CRUZ et al., 2009), descarga de efluentes (MIRANDA et al., 2016) e espécies invasivas (ROTH et al., 2016).

Além de possíveis fatores locais agravantes, a diferente composição das comunidades bentônicas recifais ao longo da costa brasileira também pode influenciar a resposta dos corais ao estresse termal, principalmente em relação à mortalidade (BROWN et al. 1990, GLYNN 1996, FERREIRA et al., 2021). Os recifes no sul do Brasil apresentam maior cobertura de espécies de corais de formato massivo (LEÃO et al., 2003, 2016), incluindo espécies com resistência ao estresse termal (LOYA et al. 2001, SCHLÖDER & D'CROZ, 2004), do que de formato ramificado, em comparação com alguns recifes do norte e nordeste. A região de Abrolhos por exemplo, foi uma das que concentrou os registros de mortalidade encontrados neste estudo, e apresenta maior cobertura de corais ramificados do que recifes da região subtropical (LEÃO et al., 2003, 2016), o que pode ter influenciado a resposta do recife em termos de mortalidade.

O branqueamento de corais no Indo-Pacífico e no Caribe tornou-se mais frequente, intenso e duradouro, a exemplo de branqueamentos em escala global que resultaram em altas taxas de mortalidade (HUGHES et al., 2018). No entanto, essa intensificação não parece ocorrer no Atlântico Sul, que historicamente apresenta menos eventos de estresse térmico (SKIRVING et al., 2019), branqueamento (SULLY et al., 2019) e mortalidade de corais (BANHA et al. 2019; MIES et al., 2020; GASPAR et al., 2019). Algumas características dos recifes brasileiros suportam sua menor prevalência e severidade de branqueamento, como morfologia maciça dos corais (GATES & EDMUNDS, 1999; LOYA et al., 2001; SCHLÖDER & D'CROZ, 2004; MIES et al., 2020), tolerância à alta turbidez e enriquecimento nutricional da coluna d'água (MORGAN et al., 2017; KUTA & RICHARDSON, 2002; MIES et al., 2020), além de associações simbióticas flexíveis e tolerantes (MIES et al., 2020). Tais condições, somadas à ampla distribuição latitudinal dos recifes do Atlântico sudoeste, têm imposto aos recifes brasileiros a esperança de refúgios para a manutenção de ambientes recifais em um futuro e rápido aquecimento (VÉRGES et al., 2014; MIES et al., 2020).

Assim como em outras regiões de corais do mundo, no Brasil o branqueamento e a mortalidade foram mais intensos nos recifes entre 5 e 20°S, na região tropical (SULLY et al., 2019), onde se encontram a maioria dos recifes de corais. Tais recifes, dentro da costa brasileira, são os que apresentam águas mais transparentes, mas são considerados relativamente turvos em comparação aos recifes do Indo Pacífico e Caribe. De fato, os registros de branqueamento dos recifes subtropicais e tropicais do atlântico sul são menos intensos em comparação com outros recifes no mundo (MIES et al., 2020), possivelmente devido à atenuação promovida pela turbidez, assim como, à composição da comunidade bentônica majoritariamente massiva, uma vez que recifes do Caribe e Indo Pacífico apresentam altas coberturas de corais ramificados que não ocorrem na costa brasileira.

Espera-se que os corais sigam uma migração extratropical (Yamano et al. 2011; Vergés et al. 2014) que vários organismos já fizeram, expandindo sua distribuição em direção aos pólos em resposta ao aquecimento (SUNDAY et al. 2012; CHEUNG et al. 2013). Bleuel et ai. (2021) previram a possível expansão de recifes tropicais brasileiros em direção a recifes extratropicais e mesofóticos, mas também alertaram para o aumento da probabilidade de branqueamento e vulnerabilidade, desafiando seu papel como refúgio. De fato, os recifes subtropicais brasileiros tiveram baixas mortalidades no último evento de branqueamento em massa, mas também tiveram a maior taxa de branqueamento já registrada (BANHA et al. 2019, GASPAR et al., 2019). Além disso, baixas taxas de mortalidade podem estar associadas a outras características além da turbidez e da região, como a composição do ambiente recifal.

Nesse estudo mostramos que os recifes subtropicais brasileiros apresentam águas mais turvas do que os tropicais, mas têm sido os mais afetados pelas ondas de calor marinhas desde 2002. Como nos recifes tropicais, as condições de maior turbidez ocorrem principalmente no inverno bem como as condições mais frias, enquanto as ondas de calor marinhas ocorrem independentemente da sazonalidade. Além disso, os recifes subtropicais no verão austral podem ter temperaturas da superfície do mar tão altas quanto os tropicais, o que em interação com a incidência de MHW e a baixa turbidez característica da estação, pode levar os corais a excederem o limiar de branqueamento nos recifes subtropicais. Assim, é possível que mesmo em ambientes anteriormente almejados como refúgios (regiões subtropicais), a interação entre determinadas condições ambientais ainda pode levar ao branqueamento de corais, como ocorreu no sudeste do Brasil em 2019 (BANHA et al. 2020). Nesse sentido, destacam-se as ilhas oceânicas subtropicais, Trindade e Martim Vaz, que, assim como os demais recifes subtropicais, apresentam MHW intensas e frequentes, porém, por se tratarem de sistemas oceânicos, sua baixa turbidez não é capaz de atenuar a incidência de luz. Como essa condição de estresse térmico na região subtropical deve aumentar (IPCC, 2021) é possível que o aquecimento e incidência de MHW decorrente das mudanças climáticas atuando nos recifes extratropicais ultrapasse o limiar térmico fisiológico dos corais, levando-os ao branqueamento mesmo em seus refúgios termais.

Ao contrário dos recifes biogênicos tropicais, os recifes extratropicais no Atlântico sudoeste são caracterizados principalmente como rochosos (FLOETER et al. 2006), têm cobertura de coral extremamente baixa (LEÃO et al. 2003; AUED et al. 2018), com exceção de uma descoberta recente (PEREIRA-FILHO et al. 2019). Tais recifes são ainda menos estudados e compreendidos que os recifes tropicais e isso pode minar a esperança de que possam servir de refúgio, uma vez que a falta de conhecimento do sistema dificulta o entendimento de sua resposta a condições estressantes. Vale ressaltar que até 2019, o limite de distribuição dos recifes biogênicos no Brasil ia até o banco de abrolhos (19 ° 30'S), mas se expandiu para 24 °S com a descoberta do recife de coral na Ilha da Queimada Grande (PEREIRA-FILHO et al. 2019). Ou seja, em 2018 a maioria dos recifes de corais do Caribe e do Indo-Pacífico já eram conhecidos e até monitorados, enquanto no Brasil ainda estávamos descobrindo recifes de corais biogênicos. Este cenário justifica em parte a falta de compreensão das respostas ao branqueamento e mortalidade dos recifes do Atlântico sudoeste em comparação com outros recifes e demonstra a necessidade e importância do monitoramento contínuo e padronizado para melhorar o entendimento dos sistemas recifais brasileiros.

Outra característica importante que se reflete na incerteza dos fatores que levam os corais brasileiros ao branqueamento é a falta de amostragem sistemática e regular dos ambientes recifais. Infelizmente, devido à descontinuação do financiamento, a amostragem no Brasil ainda é feita quando há oportunidade, e isso depende da disponibilidade de recursos financeiros, que tem sofrido várias interrupções atualmente (RODRIGUES, 2021). A amostragem sistemática e de longo prazo permitiria o melhor entendimento da resposta dos sistemas de recifes a condições estressantes, sua natureza esporádica prejudica a compreensão das mudanças do ecossistema e impactos no bem-estar humano. Portanto, é urgente aprimorar e ativar programas de monitoramento, além de utilizar o conhecimento gerado para uma gestão adaptativa em relação às mudanças climáticas em áreas costeiras e recifais.

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APÊNDICE A - Nota publicada pela autora e colaboradores no periódico Biota Neotropica

Severe coral bleaching of *Siderastrea stellata* at the only atoll in the South Atlantic driven by sequential Marine Heatwaves

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Abstract

Threatened by global warming and extreme climatic events, such as El Niño Southern Oscillation (ENSO) and Marine Heatwaves (MHW), coral reefs worldwide faced the worst bleaching and mortality event between 2014 and 2017, induced by the 2015/2016 ENSO. We evaluated the impacts of ENSO and MHW episodes on bleaching and mortality frequencies of *Siderastrea stellata* at Rocas Atoll, Southwestern Atlantic, using visual censuses conducted in 2016, 2017 and 2019. Bleaching rate varied significantly along the sampling period (11.71% in 2016, 1.52% in 2017, and 88% in 2019), but mortality was always less than 4%. Bleaching events in Atlantic reefs have been constantly associated with ENSO, until these recent events of the last two years. We suggest that MHW were probably the primary driver of the observed bleaching, especially in 2019, when much higher bleaching rates were observed, than in ENSO periods. Although Southwestern Atlantic massive corals are considered more resistant to thermal stress than reefs corals worldwide, the strong events registered since 2019 highlight the need for continuous monitoring to better understand coral bleaching dynamics and improve predictions on the effects of global change in the region.

Key words: Climate change; coral mortality; El Niño Southern Oscillation (ENSO); Brazilian reefs; Rocas Atoll.

Branqueamento severo de *Siderastrea stellata* no único atol do Atlântico Sul impulsionado por ondas de calor marinhas sequenciais.

Resumo

Ameaçados pelo aquecimento global e eventos climáticos extremos, como El Niño Oscilação Sul (ENSO) e Ondas de Calor Marinhas (MHW), os recifes de coral em todo o mundo enfrentaram o pior evento de branqueamento e mortalidade entre 2014 e 2017, induzido pelo ENSO 2015/2016. Nesse estudo, avaliamos os impactos dos episódios de ENSO e MHW nas frequências de branqueamento e mortalidade de *Siderastrea stellata* no Atol de Rocas, Atlântico Sudoeste, a partir de censos visuais realizados em 2016, 2017 e 2019. O branqueamento variou significativamente ao longo do período de amostragem (11,71% em 2016, 1,52% em 2017, e 88% em 2019), mas a mortalidade não, sendo sempre inferior a 4%. Eventos de branqueamento em recifes do Atlântico têm sido constantemente associados ao ENSO, até os eventos recentes dos últimos dois anos. Nós sugerimos que as MHW foram provavelmente o principal impulsionador do branqueamento observado, especialmente em 2019, quando as taxas de branqueamento observadas foram maiores do que nos períodos de ENSO. Embora os corais massivos do Atlântico Sudoeste sejam considerados mais resistentes ao estresse térmico quando comparados com corais recifais de outros oceanos, os fortes eventos registrados desde 2019 destacam a necessidade de monitoramento contínuo para entender melhor a dinâmica do branqueamento de corais e melhorar as previsões sobre os efeitos das mudanças globais na região.

Palavras-Chave: Mudanças climáticas; Mortalidade de corais, El Niño (ENSO); Recifes brasileiros; Atol das Rocas.

Introduction

Coral reefs are among the most diverse and economically important environments on the planet, as they harbor most of the marine biodiversity and provide a large number of ecosystem services (Graham & Nash 2013). Consequently, these systems face a number of local and global anthropogenic impacts, such as overfishing, pollution, habitat destruction, introduction of exotic species, and ocean acidification (Hughes et al. 2003). However, global warming is undisputedly the biggest threat to coral reefs worldwide, especially taking into account that global climate models predict an average increase in sea surface temperature (SST) of 0.027 °C per year from 1990 to 2090 (Bopp et al. 2013). The major negative effect caused by the increase in SST on coral reefs is the disruption of the symbiotic relationships between corals and dinoflagellates of the family Symbiodiniaceae, in a phenomenon known as “coral bleaching” (Glynn 1993). In this relationship, microalgae can provide most of the energy requirements of the coral host (Muscatine et al. 1984), and its disruption damages the physiology and energy budget of the coral (Lesser 2011). If prolonged, this disruption may lead to high levels of coral mortality (Berkelmans et al. 2004, Oliver et al. 2009, Eakin et al. 2019). Since the twentieth century, coral bleaching has been reported in scattered localities and was related to small-scale stressors such as sedimentation, freshwater supply, and colder or hotter than normal weather (Vaughan 1914, Glynn 1993, Hughes et al. 2003). However, after the 1980s coral bleaching became more frequent worldwide (Hughes et al. 2017), with three major global scale coral bleaching events: 1997-1998, 2010 and 2014-2017 (Eakin et al. 2019).

The average annual global temperatures of the ocean and atmosphere of 2015, 2016, and 2017 were the highest ever recorded since the 1800s (Hughes et al. 2017). During 2015/2016 a strong and prolonged ENSO (El Niño Southern Oscillation) raised the global mean SST at 0.5 °C, and remarkably, 2017 was the warmest non-El Niño year ever registered (Eakin et al. 2019). This severe warm period sparked the most intense massive bleaching of corals worldwide and became known as the third global coral bleaching event (GCBE) (Hughes et al. 2018, Eakin et al. 2019). During this event, the highest incidence of coral bleaching and mortality in the Atlantic was recorded in the Caribbean (Hughes et al. 2017). In Brazil, some reefs showed up to 73% bleaching for some coral species, but mortality was overall lower than 3% (Teixeira et al. 2019). In addition, Southwestern Atlantic reefs faced a record-breaking heatwave event in 2019, which, together with the ENSO positive phase, increased SST and triggered mass coral bleaching (Banha et al. 2019, Duarte et al. 2020). These bleaching episodes have been reported in the Southwestern Atlantic reefs since 1993 (Migotto 1997), but while most of them have been related to ENSO (Kelmo & Atrill 2013, Ferreira et al. 2013, Miranda et al. 2013, Dias & Gondim 2016, Leão et al. 2016, Lisboa et al. 2018), there is still no consensus about the main drivers generating recent thermal anomalies that trigger coral bleaching in the region (Soares et. al. 2019).

Besides ENSO, another climatic factor that has impacted the Brazilian marine ecosystem are the Marine Heatwaves – MHW – (Rodrigues et al. 2019), which probability of occurrence has already increased more than

20 times due to global warming (Laufkötter et al. 2020). Defined as a period of at least five days wherein the temperature is above the 90th percentile of the values historically observed for a given location and at a certain time of the year, the MHW are extreme climatic events in oceanic systems (Hobday et al. 2016). The impacts of MHW on marine ecosystems reported so far include, for example, mass mortality of seabirds in the Northeast Pacific (Jones et al. 2018), biomass decrease, and shifts in the distribution of fish stocks (Cheung & Frölicher 2020). However, the relationship between MHW and coral bleaching has been only recently reported (Fordyce et al. 2019, Smale et al. 2019), with MHW promoting immediate mortality and microbial biofilm formation over dead coral skeletons (Leggat et al. 2019). In view of all the impacts to coral reefs, studies that evaluate the effects of thermal anomalies on coral communities, whether by ENSO or MHW, are key to understand the dynamics of coral bleaching and to predict these impacts (Hughes et al. 2017). This is especially critical in the Southwestern Atlantic, where bleaching studies are still scarce, endemism in reef corals is high (Leão et al. 2016) and unprecedented thermal stresses have been reported (Rodrigues et al. 2019). Thus, we assessed the frequency of bleaching and mortality of the coral *Siderastrea stellata* Verrill, 1868 at the Rocas Atoll from 2016 to 2019, and evaluated its relation with the 2015/2016 ENSO and other climatic events, such as MHW. Rocas is potentially one of the most "pristine" areas of the Southwest Atlantic, and figures as a natural laboratory to understand the effect of thermal stress on corals, since it is not directly exposed to other anthropogenic impacts, such as pollution, urbanization and fishing (Longo et al. 2015).

Material and Methods

1. Study area

Located 230 km off the northeastern coast of Brazil, Rocas Atoll (03°50’S, 33°49’W, Figure 1a) is the only atoll in the South Atlantic, and is the first no-entry marine protected area in Brazil, created in 1979. The biological reserve encompasses about 360 km^2 of strictly protected area managed for research, where fishing activities and tourism are not allowed, leading to low human impact (Kikuchi & Leão 1997, Soares 2018). The reef substrate is mainly formed by coralline algae, vermetid gastropods and encrusting foraminifera (Kikuchi & Leão 1997), but seven species of scleractinian corals and one hydrocoral occur there (Leão et al. 2016). The atoll is subjected to intense wave action in comparison to coastal systems and is characterized by a semi-diurnal and mesotidal regime (Kikuchi & Leão 1997). During the low tide, two main habitats can be distinguished, open pools that constantly communicate with the exterior of the atoll and are more exposed to wave action than closed pools, which remain completely isolated from the exterior area of the atoll during low tides (Figure 1b). The benthic community in Rocas is dominated by the abundant reef-building coral *Siderastrea stellata* (Echeverria et al. 1997, Longo et al. 2015). This species is highly tolerant to thermal stress and widely distributed and common on Brazilian coastal reefs (Leão et al. 2016, Garcia et al. 2017).

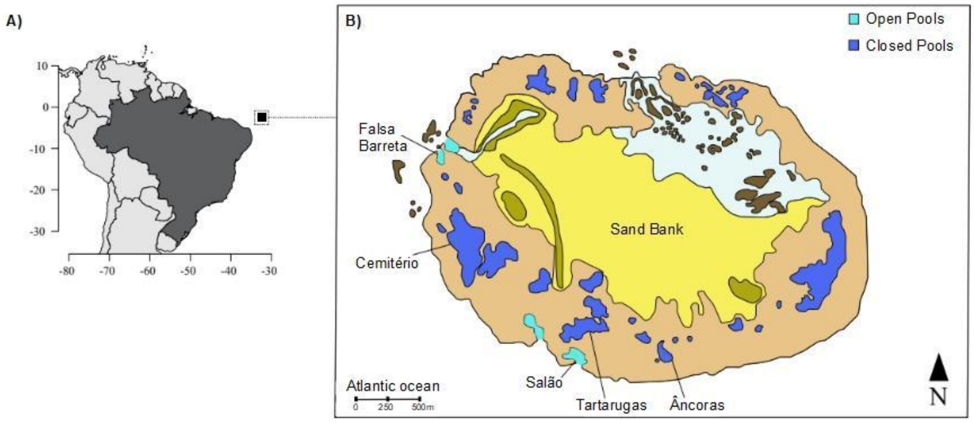

Figure 1: A) Geographic location of the Rocas Atoll and B) Position of study sites, at the tide pools: Falsa Barreta, Cemitério, Salão, Tartarugas, and Âncoras. Adapted from Longo et al. (2015).

2. Data collection

We conducted the sampling in four tide pools (Cemitério, Tartarugas, Âncoras and Falsa Barreta; Figure 1b) during low tides in May 2016 and 2017, and in June 2019. In each pool, we performed five visual censuses along 20 x 1 m (20m^2) belt transects, at depths up to 5 m, to estimate the frequency of bleaching and dead corals, according to ReBentos Protocol (Leão et al. 2015). All colonies of *S. stellata* with more than 3 cm in diameter within transect area were visually counted (Nmin = 1533; Nmax = 1791) and classified into three categories: (1) no bleaching = with no sign of affected color, (2) bleached = lighter in color than normal, with different degrees of discoloration, including patches of bleaching and whiteness, and (3) recently dead = bare skeleton without living tissue and minimal algal overgrowth.

3. Abiotic factors

To examine the effect of thermal stress events on *S. stellata* bleaching and mortality, we compiled a set of ocean temperature data during the sampling period at Rocas Atoll, and analyzed the coral's response considering these thermal stresses in the four months prior to the surveys. This 4 months-period was previously indicated as the time of response seen in Rocas Atoll corals (Ferreira et al. 2013). We collected the daily mean SST between 2016 and 2019 from the US National Oceanic and Atmospheric Administration - Advanced Very High Resolution Radiometer (NOAA - AVHRR) (http://www.esrl.noaa.gov/psd/). Then, we obtained the Monthly Multivariate ENSO Index (MEI) values (Wolter & Timlin 1993) from NOAA's Earth System Research Laboratory (esrl.noaa.gov/psd/enso/mei) from January 2015 to December 2019 to evaluate the effect of ENSO phases on the bleaching observed at Rocas Atoll. Considering the SST and MHW, we built an event curve between 2016 and 2019 with the Marine Heatwave Tracker, which uses the daily Optimally Interpolated Sea Surface Temperature (OISST) from the NOAA, available at http://www.marineheatwaves.org/tracker.html, (Schlegel 2018). To assess cumulative intensity, we obtained the maximum degree heating week (DHW) value during each time interval of 4 months before sampling, from NOAA Coral Reef Watch (CRW's), available at https://coralreefwatch.noaa.gov/product/vs/gauges/fernando_de_noronha.php. These values, based on CRW's Regional Virtual Station time series data, reflect the observed and forecasted bleaching alert level surrounding Rocas Atoll.

4. Data analysis

To examine whether the bleaching and mortality frequencies varied among 2016, 2017 and 2019, we performed two Kruskal-Wallis tests. We transformed the bleaching and mortality frequencies using the arcsine square root transformation before the analyses. We used this approach because bleaching and mortality data are percentages with a non-normal distribution, thus precluding the use of parametric tests. Additionally, we used Dunn tests for testing the difference observed in Kruskal-Wallis tests. All the analyses were performed with the R software (R Core Team 2018).

Results and Discussion

We observed a significant difference in the bleaching frequency among years (Kruskal-Wallis test: $X^2 = 47.7$, df = 2, p-value < 0.01), in contrast to the mortality frequency (Kruskal-Wallis test: $X^2 = 0.51$, df = 2, p-value = 0.77; Figure 2). During all sampled years, bleaching episodes were underway, which may underestimate mortality. In 2016, average bleaching (11.71% ± SD 13.81) and mortality (0.97% ± SD 2.39) frequencies at Rocas Atoll (Figure 2b and 2c, respectively) were small compared to the severe global trend observed during the 2015/2016 ENSO (Hughes et al. 2017). This pattern was also observed in another less abundant coral species (e.g. *Favia gravida*, *Montastraea cavernosa* and *Porites astreoides,*), which presented few signs of bleaching during this year (authors pers. obs.). In 2017, average bleaching frequency (1.52% ± SD 1.89) was almost eight times smaller than 2016 (Dunn test: z = 2.30, p-value < 0.01; Figure 2b), but the number of dead colonies was three times higher (3.2% ± SD 6.6), despite no significant difference (Figure 2c).

Average bleaching frequency in 2019 was 88.01% (± SD 8.97), almost sixty times higher than 2016 (Dunn test: z = -4.68, p-value < 0.01) and 2017 (Dunn test: z = -6.82, p-value < 0.01) (Figure 2b). Unlike the upward trend in bleaching frequency, the number of dead colonies has halved (1.31% ± SD 4.12) when comparing 2017 to 2019, despite the lack of statistically significant difference (Figure 2c). Although 2019 was a non-El Niño year, the most severe bleaching event to date at the Southwestern Atlantic was recorded at that time, with high bleaching but low coral mortality (Banha et al. 2019, Duarte et al. 2020, Mies et al. 2020), similar to Rocas Atoll. The bleaching history at Rocas Atoll coincides with the ENSO years, such as the 2003 event that caused bleaching in less than 4% of the colonies studied by Ferreira et al. 2006, while during ENSO 2010, less than 20% of the colonies bleached, but up to 60% showed signs of disease (Ferreira et al. 2013).

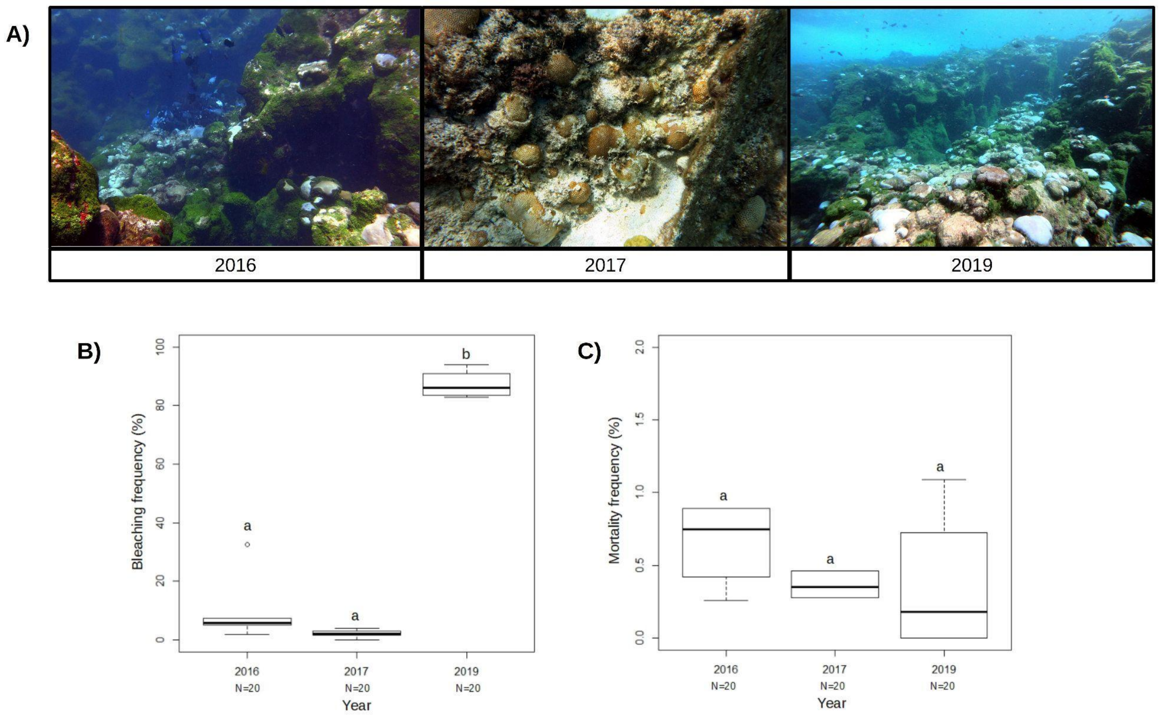

Figure 2: A) Coral communities at Rocas Atoll over the sampling period (2016, 2017 and 2019), at the sampled areas. Note a few bleaching colonies of *Siderastrea stellata* in 2016, and several bleached colonies in 2019, while 2017, colonies were mostly healthy. B) Bleaching frequency of *Siderastrea stellata* at Rocas Atoll, as a function of sampling years: 2016, 2017 and 2019. Box plot center = median, outerlimit = 75% percentile, and range is shown by the whiskers. In each case, data from N=20 belt transects are shown. C) Mortality frequency of *Siderastrea stellata* at Rocas Atoll, as a function of sampling years: 2016, 2017 and 2019. Box plot center = median, outerlimit = 75% percentile, and range is shown by the whiskers. In each case, data from N=20 belt transects are shown.

In 2016, thermal stress events in the four months preceding the survey reached a maximum SST of 29.5 °C and a high frequency of positive thermal anomalies that did not exceed 1 °C (Figure 3a), with a maximum DHW value less than 1 °C-week. In the same period, there were three moderate MHW (Figure 3b) with an average duration of 6.6 days and average intensities, maximum and cumulative averages of 0.85 °C, 1.06 °C and 5.67 °C, respectively. Therefore, coral bleaching at Rocas Atoll in 2016 may not have been triggered only by ENSO (Figure 3c), but also by MHW that occurred before the sampling period. Soares et al. (2019) highlighted a bleaching event in the Southwestern Atlantic triggered by anomalous SST in 2010 that was not correlated with the ENSO, but with lower wind speeds and water turbidity.

In 2017, the daily average SST during the four months prior to the survey was similar to that observed in 2016, with maximum DHW value less than 1 ° C-week, and a maxim.um SST of 29.5 °C (Figure 3a), characterizing a hot year even without ENSO (Figure 3c). However, during this period a lower frequency of positive thermal anomalies was observed, with two episodes reaching 1 °C (Figure 3a). Two moderate MHW occurred before sampling in 2017, with an average duration of 12 days, mean accumulated intensity of 10.57 °C, average intensity of 0.89 °C, and maximum average of 1.04 °C. The MHW events during the pre-sampling period in 2017 were less frequent and more interspaced, despite being longer, than the pre-sampling period in 2016 (Figure 3b), which may have influenced the low bleaching frequency in 2017.

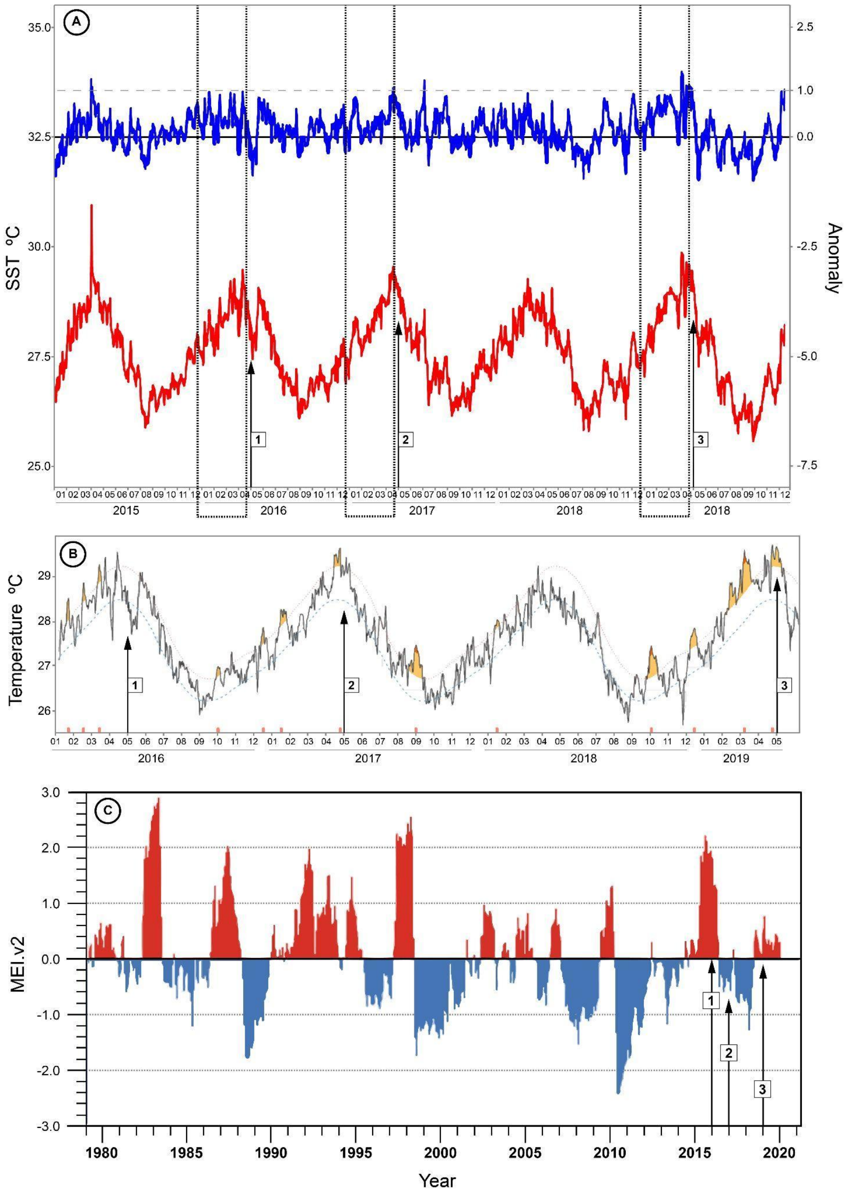

Figure 3: Temporal thermal series. A) Daily mean values of sea surface temperature (red line) and thermal anomaly (blue line) reported for Rocas Atoll. Numbers (1-3) within a small square indicate the sampling moment in each year and the big dashed square shows the four months prior to the survey, when thermal stresses were analyzed. The x-axis represents time, with monthly intervals, from January 2016 to June 2019. The main y-axis represents the SST (°C) and the secondary the anomaly (°C). Data extracted from the satellite (AVHRR) and made available by NOAA (http://www.esrl.noaa.gov/psd/). B) Marine Heatwaves at Rocas Atoll, between 01/01/2016 and 05/31/2019. The red dotted line is the threshold value for each location for each day of the year and is defined based on the 90th percentile value. A thermal stress event that is at least five days or more above this threshold value represents a MHW (orange areas). The lightest orange areas represent moderate MHW, and the darkest strong events. The dashed blue line represents the climatological mean. Numbers (1-3) within a small square indicate the sampling moment in each year. The x-axis represents time, with monthly intervals, and the y-axis

represents the SST (°C). Available at http://www.marineheatwaves.org/tracker.html. C) Multivariate ENSO indices (y-axis) from 1979 to 2020 (x-axis). El Niño (positive phase) in red; La Niña (negative phase) in blue. Numbers (1-3) within a small white square next to the arrows indicate the sampling years (1 = 2016; 2 = 2017; 3 = 2019). Data source: (esrl.noaa.gov/psd/enso/mei).

In 2019, SST reached a maximum of 30.0 °C, and presented higher frequency and intensity (1.5 °C) of positive anomalies than in 2016, with more thermal anomalies than 2017 (Figure 3a). The maximum DHW value in the period was higher than previous years, reaching 7.5 ° C-week. Two MHW were registered in 2019, with an average duration of 31.5 days and a cumulative intensity of 31.51 °C, both three times higher than in previous years (Figure 3b). The intensity and maximum averages of MHW were similar to those of previous years: 1.02 °C and 1.46 °C, respectively. A much lower ENSO index was detected in 2019 compared to 2016 (Figure 3c). Regarding the three sampling years, 2019 reached the highest SST, presented larger and more frequent thermal anomalies, as well as more intense MHW, which may explain the severe bleaching frequency (i.e. >50% of bleached colonies, according to Donner et al. 2017) in 2019 (Figure 2a and 2b).

Bleaching events may have distinct 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 the overall health state of the ecosystem (Hoegh-Guldberg 1999). Thermal stress in the South Atlantic has historically been lower than in other regions such as the Caribbean and the Indo-Pacific (Skirving et al. 2019), and its reefs have escaped multiple thermal stress events which have plagued reefs elsewhere. Despite the massive coral loss observed around the world, Southwestern Atlantic reefs have remained relatively stable in terms of mortality (Perry et al. 2013, Banha et al. 2019, Teixeira et al. 2019). Between 2014 and 2017, when the most severe, widespread, and longest-lasting global-scale coral bleaching event was recorded (Eakin et al. 2017, 2019), Abrolhos reef, in Brazil, suffered less than 3% of coral cover loss due to bleaching and mortality (Teixeira et al. 2019).

Coral species from the Southwestern Atlantic, including *S. stellata*, have been considered highly resistant to thermal stress, which is possibly related to associations with thermotolerant endosymbionts (Marshall & Baird 2000, Loya et al. 2001, Costa et al. 2004, 2008). Colonies of *S. stellata* from the Northeastern Brazilian reefs harbors mainly symbionts from genus *Cladocopium* (Costa et al. 2008, Monteiro et al. 2013), a genus whose lineages most frequently found on corals are thermotolerant (Swain et al. 2017). Coral colony morphology is also often related to bleaching susceptibility, with massive forms less susceptible to bleaching (Brown et al. 1990, Gleason 1993). Most Brazilian coral species, such as *S. stellata*, have a massive growth form (Leão et al. 2003), that is also associated with a higher thermal stress tolerance (Loya et al. 2001, Schlöder & D'Croz 2004) in comparison to branching corals (Brown et al. 1990, Glynn 1996, Smith et al. 2014). These traits of Brazilian coral may drive the higher resistance during thermal stress events registered so far, especially for *S. stellata* at Rocas Atoll, due to its massive morphology, possible thermal tolerant symbiont diversity (Costa et al. 2008) inhabiting shallow and warm tide pools (Echeverria et al. 1997). In addition, Rocas Atoll is isolated from the mainland and is the most effective marine protected area in Brazil, lacking local stressors (Brandão et al. 2017) that could act in concert with global drivers that promote coral bleaching. On the other hand, Rocas Atoll is a shallow and non-turbid reef, therefore more susceptible to bleaching due to thermal stress than coastal ones (Glynn 1996, Takahashi et al. 2004).

This scenario may have started to change from 2019, when the incidence of severe MHW in some reefs, such as at Rocas Atoll, Abrolhos coral reefs and São Paulo rocky reefs, triggered the highest bleaching events registered so far in the Southwestern Atlantic (Banha et al. 2019, Duarte et al. 2020). Impacts of MHW on coral reefs have been reported in Australia (Le Nohaïc et al. 2017, Clarke et al. 2019) and some Pacific islands, with different coral species being affected (Rubio-Portillo et al. 2016, Falter et al. 2016, Couch et al. 2017). Unlike large spatial and temporal scale ENSO events, MHW represents the most extreme and "rare" incidences of thermal stress relative to a seasonally dependent historical baseline (Hobday et al. 2016). However, similarly to ENSO, the duration and frequency of MHW has increased significantly since the early twentieth century (Oliver et al. 2018, Laufkötter et al. 2020). It is worth mentioning that the effects of MHW on coral reefs are distinct from how coral bleaching has been understood to date, resulting in an immediate heat-induced coral mortality, rapid dissolution of the coral skeleton, and loss of the three-dimensional reef structure (Leggat et al. 2019).

This work highlights the need to re-think our understanding of coral bleaching events in Southwestern Atlantic reefs, its drivers and the immediate impact on corals, especially in Brazilian reefs whose responses to thermal stress are still poorly understood (Mies et al. 2020). Maintaining time series for monitoring coral population parameters and environmental drivers is crucial for understanding coral bleaching phenomena in the Southwestern Atlantic and better addressing the coral reef crisis. Rocas Atoll is one of the most effective marine protected areas in Brazil, with minimal local anthropogenic impacts and may be used as a natural model system for evaluating global impacts on its reef community. Indeed, a better understanding of what are the main drivers of coral bleaching in Southwestern Atlantic can be useful to improve predictions and anticipate impacts on Brazilian reefs related to global change.

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Authors' Contributions

Tainá Gaspar and Juan Quimbayo: substantial contribution to the concept and design of the study; contribution to the data collection; contribution to the data analysis and interpretation; contribution to manuscript preparation.

Renan Ozekoski and Lucas Nunes: substantial contribution to the concept and design of the study; contribution to the data collection; contribution to manuscript preparation.

Amana G. Garrido and Thiago C. Mendes: contribution to the data collection; contribution to manuscript preparation.

Anaide W. Aued and Bárbara Segal: substantial contribution to the concept and design of the study; contribution to manuscript preparation; contribution to critical revision, adding intellectual content.

Conflict of interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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