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CAROLINE COSTA LUCAS

BLEACHING AND TROPHIC ECOLOGY OF CORALS ON MARGINAL REEFS (EQUATORIAL SOUTHWESTERN ATLANTIC)

FORTALEZA

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Tese submetida à Coordenação do Curso de Pós-Graduação em Ciências Marinhas Tropicais, da Universidade Federal do Ceará, como requisito parcial para obtenção do grau de Doutor em Ciências Marinhas Tropicais.

Área de concentração: Utilização e Manejo de Ecossistemas Marinhos e Estuarinos.

Orientador: Prof. Dr. Marcelo de Oliveira Soares.

Coorientador: Prof. Dr. Sergio Rossi

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RESUMO

Os recifes de corais são importantes ecossistemas com alta biodiversidade e produtividade nos oceanos tropicais. Além disso, oferecem serviços à sociedade, como a proteção à linha de costa, renovação dos estoques pesqueiros e beleza cênica que promove o turismo. A região do Atlântico Sudoeste Equatorial possui um perfil único quanto aos níveis de turbidez e a alta e estável temperatura da água do mar, o que é relevante para estudos que avaliam o efeito de fatores ambientais sobre as comunidades recifais como os corais escleractíneos e zoantídeos. Nesta tese são abordados o branqueamento e a ecologia trófica de corais nessa região equatorial utilizando como modelo de estudo ecossistemas recifais da costa semiárida do Nordeste do Brasil. No capítulo I avaliamos o branqueamento de *Siderastrea stellata* e investigamos os fatores ambientais que poderiam ter causado o branqueamento. Observou-se que entre fevereiro e junho de 2020, os recifes da costa cearense passaram por dois eventos de *marine heatwaves* (MHW) em um intervalo de tempo de 8 dias e com intensidade máxima acima da média de temperatura de, aproximadamente, 1,9 °C e 1,25 °C. O *degree heating week* (DHW) durante o período do branqueamento foi de 17,6 °C/semana, o maior registro nos últimos 17 anos para a região do Atlântico Sudoeste Equatorial. Logo, sugerimos que estes fatores, em conjunto com a baixa turbidez e velocidade dos ventos, podem ter provocado o branqueamento. No capítulo II analisamos o branqueamento durante 2013-2015, na espécie tolerante *S. stellata,* e a relação com as condições climáticas e oceanográficas do período. Constatamos que houve um déficit de chuva entre anos de 2013 e 2015. A baixa pluviometria do período diminuiu a nebulosidade e a turbidez, o que deixou as colônias de corais em águas rasas desprotegidas contra a irradiação solar e ocasionando o branqueamento em determinados períodos do ano. No terceiro e último capítulo, a ecologia trófica dos zoantídeos *Palythoa caribaeorum, Palythoa variabilis* e *Zoanthus sociatus* foram abordados por meio de uma revisão de literatura integrativa. *Z. sociatus* é uma espécie de natureza autotrófica e parece ter afinidade por matéria orgânica particulada como alimento externo. *P. caribaeorum e P. variabilis* parecem usar mais a via heterotrófica que a autotrófica. *P. caribaeorum* parece ter preferência por fitoplâncton na sua alimentação. As diferentes estratégias tróficas auxiliam em explicar a abundância, resistência e ampla distribuição destes zoantídeos em ecossistemas recifais no Atlântico Equatorial. As comunidades recifais do Atlântico Sudoeste Equatorial e suas respostas a fatores ambientais podem dar novas e intrigantes explicações para o entendimento da resistência dos corais às mudanças ambientais globais em recifes marginais.

Palavras-chave: corais; zoantídeos; temperatura; ecologia trófica; ambiente recifal.

ABSTRACT

Coral reefs are important ecosystems with high biodiversity and productivity in the tropical oceans. Besides that, offer services to society, such as coastal protection, maintenance of fish stocks, and scenic beauty that promotes tourism. The Equatorial Southwestern Atlantic region has a unique profile in terms of turbidity levels and high and stable seawater temperature, which is relevant for studies that assess the effect of environmental factors on reef communities such as scleractinians and zoantharians corals. Thus, this work was designed to understand the bleaching and trophic ecology of corals in the Equatorial Southwestern Atlantic using as a study model the reef ecosystems of the semiarid coast in northeastern Brazil. In Chapter I, we reported the bleaching of *Siderastrea stellata* and investigated the environmental factors that could have caused mass bleaching. It was observed that between February and June 2020, the reefs on the coast of Ceará State underwent two marine heatwaves (MHW) events in an interval of 8 days and with maximum intensity above the average temperature of approximately 1.9 °C and 1 .25°C. The degree heating week (DHW) during the bleaching period was 17.6 °C/week, the highest record in the last 17 years for the Equatorial Atlantic region. Therefore, we suggest that these factors, together with low turbidity and wind speeds, may have caused the bleaching together with meteorological variables. In chapter II we analyze the bleaching, along 3 years (2013-2015), of tolerant specie *S. stellata* and the relationship with the climatic and oceanographic conditions of the period. We found that there was a deficit in rainfall between 2013 and 2015. The low rainfall of the period may have reduced cloudiness and turbidity, which left the coral colonies in shallow-water unprotected against solar radiation and occasioned bleaching in certain periods of the year. In the third and last chapter, the trophic ecology of zoanthid corals *Palythoa caribaeorum*, *Palythoa variabilis,* and *Zoanthus sociatus* was addressed through an integrative review. *Z. sociatus* is an autotrophic species and seems to have an affinity for particulate organic matter as an external food source. *P. caribaeorum* and *P. variabilis* seem to use more of the heterotrophic pathway. *P. caribaeorum* seems to have a preference for phytoplankton in its diet. The different trophic strategies help to explain its abundance, resistance, and wide distribution in reef communities in the Equatorial Atlantic. Reef communities in the Equatorial Southwestern Atlantic and their responses to environmental factors may provide new and intriguing answers to help understand coral resistance to global environmental changes.

key-words: coral; temperature; trophic ecology; reef environment.

LISTA DE ILUSTRAÇÕES

LISTA DE TABELAS

LISTA DE ABREVIATURAS E SIGLAS

TSM	Temperatura da Superfície do Mar
SST	Sea Surface Temperature
SSTA	Sea Surface Temperature Anomaly
DHW	Degree Heating Weeks
MHW	Marine Heating Waves
BT	Bleaching Treshold
OISST	Optimally Interpolated Sea Surface Temperature
BDMET	Base de Dados Meteorológicos Brasileiros
ENSO	EL Niño – Southern Oscillation
PRESS	Peer Review of Eletronic Search Strategies
PRISMA	Principais itens para relatar Revisões Sistemáticas e Meta-Análises
Kd490	Coeficiente de atenuação da luz difusa a 490 nm
SFA	Saturated fatty acids
MUFA	Monounsaturated Fatty Acids
HUFA	Highly Unsaturated Fatty Acids
PUFA	Polyunsaturated Fatty Acids
GLM	Generalized Linear Model
GAM	Generalized Additive Model

SUMÁRIO

1 INTRODUÇÃO GERAL

Os ambientes recifais formam um importante ecossistema tropical por apresentarem alta produtividade e biodiversidade, sendo considerado o mais complexo e mais diverso nos oceanos (CONNELL, 1978). Em termos de diversidade e estrutura física básica, estes ecossistemas recifais tropicais são comparados, em terra, às florestas úmidas dos trópicos pois ambos ecossistemas apresentam configurações tridimensionais, abrigando uma rica variedade de organismos (REAKA-KUDLA, 1997). A importância dos recifes de corais é demonstrada pelo fato de corresponderem a menos de 1 % do substrato costeiro e oceânico e abrigarem pelo menos 25 % das espécies marinhas já descritas (SHEPPARD, DAVY e PILLING, 2009). Os ambientes recifais também atuam no ciclo biogeoquímico do carbonato e carbono, sendo ambos importantes serviços de regulação no âmbito das mudanças climáticas (ROSSI *et al.*, 2017). A retenção de carbono (C) e carbonato de cálcio ($CaCO_3$) em animais bentónicos suspensívoros diminui o fluxo de dióxido de carbono (CO_2) para a atmosfera, diminuindo a quantidade desse gás no ar e seu efeito para o aquecimento global (ROSSI e RIZZO, 2020).

Acredita-se que 500 milhões de pessoas residentes em países costeiros e insulares sejam dependentes dos bens e serviços ecossistêmicos fornecidos por recifes tropicais saudáveis, como renovação da pesca, atração do turismo pela beleza cênica, produção de fármacos em organismos e proteção à costa pela dissipação de energia das ondas (COSTANZA *et al.*, 2014). Somente no Havaí, benefícios econômicos produzidos pelos recifes foram estimados em 360 milhões de dólares por ano, com potencial para quase 10 bilhões de dólares (HERMAN e VAN BEUKERING, 2004). Assim, pode-se dizer que os ecossistemas recifais disponibilizam valores culturais, biológicos, sociais e econômicos extremamente relevantes para a sociedade.

No Atlântico Sudoeste, os recifes brasileiros apresentam diferentes formas, ampla distribuição geográfica e ocorrência em diversas profundidades, ocorrendo de forma descontínua por mais de 4.000 km desde o estado do Amapá até o estado de São Paulo (SOARES *et al.*, 2021b). Há ocorrência de ambientes recifais nas ilhas oceânicas do Atol das Rocas, Arquipélago de Fernando de Noronha, Arquipélago de São Pedro e São Paulo e no Arquipélago de Abrolhos, sendo este último o maior, mais estudado e mais diverso banco recifal no Atlântico Sudoeste Tropical (MAIDA e FERREIRA, 1997). Em termos de profundidade, esses ecossistemas ocorrem comumente em ambientes rasos e na zona entremarés (LEÃO *et al.*, 2010; LEÃO, KIKUCHI e TESTA, 2003; RABELO *et al.*, 2015).

Contudo, também já foram encontrados em áreas mais profundas, como o Sistema de Recifes da Amazônia, descrito como um extenso e heterogêneo ecossistema mesofótico (70-220 m de profundidade) entre os limites da Guiana Francesa e do Brasil até o estado do Maranhão (MOURA *et al*., 2016). Também no Atlântico Sudoeste equatorial, os recifes da costa semiárida brasileira são encontrados em zonas entremarés, em ambientes rasos e mesofóticos (RABELO, SOARES e MATTHEWS-CASCON, 2013; SOARES *et al*., 2016; SOARES *et al*., 2017).

A costa equatorial semiárida Brasileira (por exemplo, no estado do Ceará) é caracterizada por uma diversidade de ambientes marinhos, incluindo recifes. Em especial, são comuns os recifes entremarés que têm formação sedimentar principalmente de arenitos e possuem semelhanças quanto às espécies bentônicas que ocupam este tipo de recife (SOARES, RABELO e MATTHEWS-CASCON, 2011; DE MACÊDO CARNEIRO *et al*., 2021). Essa região apresenta um clima tropical semiárido e demonstra uma variabilidade intra-anual acentuada na precipitação (CAVALCANTI *et al*, 2009). O primeiro semestre tem um regime de chuvas concentradas no período entre fevereiro e maio e com ventos de baixa velocidade. Já o segundo semestre tem ventos mais intensos, sendo estes os alísios que predominam do sentido leste-oeste. Assim, esse litoral possui características definidas como o alto suprimento de sedimentos siliciclásticos próximo a costa, águas moderadamente turvas devido a resuspensão de sedimentos e temperaturas estáveis e altas, entre 26 e 30 °C (PORTELA, 2009; SOARES *et al*., 2019; MORAIS *et al*., 2020). Essas características peculiares desses recifes marginais a tornam interessante para estudos sobre branqueamento e ecologia trófica dos cnidários (corais escleractíneos e zoantídeos) no Atlântico Sudoeste Equatorial (SOARES e RABELO, 2014).

Os corais escleractíneos e zoantídeos (corais moles) são componentes dos recifes tropicais e apresentam importantes funções ecológicas. Os zoantídeos podem se tornar os principais componentes bentônicos nos recifes expostos a fatores ambientais que dificultam o assentamento de corais escleractíneos (FAUTIN, 1988; CRUZ *et al*., 2015a; MENDONÇA-NETO *et al*, 2008) e também, atuar como habitat para outras espécies de invertebrados (PÉREZ, VILA-NOVA e SANTOS, 2005). Esses são fortes competidores nos ambientes recifais e, portanto, podem alterar a distribuição e abundância das espécies recifais (RABELO *et al*, 2015; BELFORD e PHILLIP, 2012). Nos recifes entremarés, os zoantídeos podem até serem mais abundantes que os corais escleractíneos que são bioconstrutores (BELFORD e PHILLIP, 2012; SOARES, RABELO e MATTHEWS-CASCON, 2011). Os zoantídeos apresentam características evolutivas que permitem a ocupação de ambientes com intensas

flutuações diárias em parâmetros como a temperatura da água do mar, salinidade e dessecação como nos recifes entremarés. Por isso, eles são considerados importantes componentes bentônicos em ecossistemas recifais (SEBENS, 1982; RABELO *et al.*, 2015; DURANTE, CRUZ e LOTUFO, 2018).

Com o aumento da temperatura da água do mar e acidificação dos oceanos, estima-se uma mudança de cobertura (e.g., mudança de fase) nos recifes em escala global com predomínio de zoantídeos e diminuição de escleractíneos em alguns sítios (BELFORD e PHILLIP, 2012). Entretanto, diversos fatores ambientais como o pH, a salinidade, estresse térmico e variação na concentração de clorofila-*a* também podem influenciar a distribuição desse grupo de cnidários, levando a modificações nos limites de ocupação dos zoantídeos em recifes no Oceano Atlântico (DURANTE, CRUZ e LOTUFO, 2018). Portanto, esses organismos desempenham um papel importante na dinâmica dos ambientes recifais e podem alterar os serviços ecossistêmicos disponibilizados como a biodiversidade e menor proteção contra a erosão costeira (NORSTRÖM *et al.*, 2009).

Algumas espécies de cnidários apresentam uma relação simbiótica com microalgas dinoflagelados da família Simbiodinaceae, e essa associação é necessária tanto à vida da maioria dos corais como na formação biogênica dos recifes por escleractíneos e hidrocorais (VILLAÇA, 2002). Essa relação permite que as microalgas e o coral troquem moléculas energéticas através da fotossíntese colaborando para o funcionamento metabólico e fisiológico de ambos (SUTTON e HOEGH-GULDBERG, 1990; WEIS, 2008). O branqueamento é caracterizado pela perda da cobertura viva e colorida composta pelas algas. A saída das algas expõe a cor do esqueleto calcário das colônias, que é de cor branca (GLYNN, 1993). Eventos de branqueamentos em massa estão relacionados, geralmente, ao aumento anormal da temperatura na superfície do mar (TSM) e ondas de calor (*Marine Heatwaves* - MHWs), podendo causar desde a morte da colônia até a degradação do ecossistema recifal (BAKER e CUNNING, 2015).

O branqueamento é uma resposta a algum estresse na relação simbiótica coral-alga que pode ser causado por um único fator ou por sinergia de vários fatores ambientais, como: anomalias térmicas tais como as MHWs (BROWN, 1997; HOEGH-GULDBERG, 1999), radiação solar intensa (HOEGH-GULDBERG e SMITH JASON, 1989), turbidez (CACCIAPAGLIA e WOESIK, 2015), microrganismos patogênicos (BEN-HAIM e ROSENBERG, 2002) e microplásticos (SYAKTI *et al.*, 2019). Além disso, existem fatores que podem influenciar na intensidade dos eventos de branqueamento como a história térmica local (KLEYPAS, DANABASOGLU e LOUGH, 2008; THOMPSON; VAN WOESIK, 2009),

o tipo e diversidade das algas simbiontes presentes na relação simbiótica (BERKELMANS e VAN OPPEN, 2006), as características ambientais locais (cobertura por nuvens, turbidez, ventos, efluentes) (MUMBY *et al*., 2001; DUNNE e BROWN, 2001, biodiversidade do sistema coralíneo (MARSHALL e BAIRD, 2000; TEIXEIRA *et al*., 2019) e aumento da temperatura da água do mar (HOEGH-GULDBERG *et al*., 2007; BAKER *et al*, 2004).

Os danos causados nos cnidários como escleractíneos e zoantídeos devido ao branqueamento são diversos. As consequências podem ser vistas por meio da possível alteração das espécies de microalgas no tecido animal (PANITHANARAK, 2015), de mudança na densidade da fauna associada (STELLA, MUNDAY e JONES, 2011), da redução de parâmetros reprodutivos (HAGEDORN *et al*., 2016), do maior perigo de ingestão de microplásticos (AXWORTHY e PADILLA-GAMIÑO, 2019), do aumento de doenças em corais (MULLER *et al*., 2008) e da diminuição do crescimento e mortalidade parcial ou total das colônias (CANTIN e LOUGH, 2014; CANTIN *et al*., 2010). Esses prejuízos podem levar a degradação e diminuição da biodiversidade recifal a longo prazo, com a consequente perda de bens e serviços ecossistêmicos (WILKINSON *et al*., 1999).

Perturbações nos sistemas recifais são capazes de mudar a complexidade, a diversidade e os serviços fornecidos (NORSTRÖM *et al*., 2009). Assim, entender os fatores que influenciam e determinam o branqueamento nos corais se torna um recurso valioso para compreender os processos e a dinâmica que levam a sua formação, como também, a sua degradação (AERTS e VAN SOEST, 1997; NIEDER *et al*., 2019; CORREIA *et al*., 2018; CASSATA e COLLINS, 2008). Mudanças na biodiversidade e composição bentônica dos recifes de corais já são percebidas devido ao aquecimento e anomalías das águas do mar, o que pode afetar o crescimento larval, a proliferação de doenças nos corais e a diminuição de cobertura por corais bioconstrutores e aumento de cobertura por algas, esponjas, zoantídeos e octocorais que podem reduzir o processo da fábrica carbonática e acresção recifal (FRANCINI-FILHO *et al*., 2010; ANTHONY *et al*., 2008; MIES *et al*., 2018a, CRUZ *et al*., 2015b).

A mudança de fase, com dominância de zoantideos, em recifes do Atlântico Sudoeste vem sendo documentada nos últimos anos (CRUZ *et al*., 2015ab; CRUZ *et al*., 2016). Possivelmente existe uma relação entre o comportamento alimentar dos zoantideos, sua resistência e a estabilidade/aumento desse grupo de organismos recifais. O domínio de zoantideos pode estar associado a sua ecologia trófica, devido o uso de matéria orgânica e plâncton presentes na coluna de água e que podem ser utilizados na sua alimentação, e a predominância da heterotrofia de algumas espécies de zoantideos (*Palythoa* spp.) (DE

SANTANA *et al.*, 2015; ROSA *et al.*, 2016; VINAGRE *et al.*, 2018). Além disso, os fenômenos de ressurgência que ocorrem em alguns recifes brasileiros também favorecem a maior quantidade alimento particulado e carbono dissolvido que podem ser utilizados como fonte de energia pelos zoantídeos (VALENTIN, 2001: EÇA *et al.*, 2014).

O estudo de padrões alimentares nos corais escleractíneos e zoantídeos é uma ferramenta que vem sendo utilizada para entender a sobrevivência, resistência e resiliência durante distúrbios ambientais e para os que vivem em condições extremas. A forma de obtenção de energia parece ser uma característica que garante uma ampla distribuição e sucesso em ocupar vários habitats (ROSA *et al.*, 2016). Os cnidários podem estabelecer uma entrada de energia via mista de autotrofia e heterotrofia, o que é chamado de mixotrofia. Em cnidários saudáveis, a via autotrófica pode atender de 65 a 100 % de suas necessidades energéticas (MUSCATINE, MCCLOSKEY e MARIAN, 1981; FALKOWSKI *et al.*, 1993). Em cnidários branqueados, a via heterotrófica pode passar a ser responsável por 100 % da demanda metabólica em algumas espécies que tem essa potencialidade (HOULBRÈQUE e FERRIER-PAGÈS, 2009) o que pode explicar a resistência e estabilidade das suas populações apesar do aumento de branqueamento. Portanto, compreender as variações na autotrofia e heterotrofia pode ajudar a estabelecer as respostas para o comportamento desses organismos durante o branqueamento e às condições ambientais a que eles estão expostos (TOLOSA *et al.*, 2011; LEAL *et al.*, 2013).

Nos últimos anos, esforços científicos têm sido aplicados para entender a região do Atlântico Sudoeste Equatorial (Brasil) e campos de estudo como a oceanografia (BRANDT, 2016; DIAS, CASTRO e LACERDA, 2013), geomorfologia (GOMES *et al.*, 2014; MORAIS *et al.*, 2020), distribuição e ecologia de peixes (KRAJEWSKI e FLOETER, 2011), os aspectos das comunidades planctônicas (OLIVEIRA-SANTOS, GARCIA e SOARES, 2016; EICHLER e MOURA, 2020; COSTA *et al.*, 2020) e fatores climáticos (DA SILVA et *al.*, 2017; CAVALCANTI, 2009) já são mais compreendidos. Entretanto, estudos sobre padrões de branqueamento e características da ecologia trófica e as respostas das espécies de corais e zoantídeos às condições locais ainda são escassos. Assim, a proposta dessa tese de doutorado é contribuir para o esclarecimento das lacunas que envolvem processos ecológicos e fisiológicos de corais escleractineos e zoantídeos que ocorrem na costa do Atlântico Sudoeste Equatorial específicamente na costa semiárida brasileira (a região menos estudada). Nesse contexto, destaca-se que essa região é pouco abordada, mas que tem tido uma produção científica crescente na última década e que as características da costa semiárida equatorial são ímpares, o que permite a produção de conhecimento inédito sobre as comunidades recifais, em

especial de corais escleractíneos e zoantídeos. Portanto, é necessário aplicar um esforço científico para compreender melhor os processos regionais e promover informações que possam ser utilizadas para a proteção dos ambientes recifais em escala local e global.

Esta tese se concentra em uma pesquisa desenvolvida em três capítulos em língua inglesa, prevendo futura publicação em periódicos internacionais. O primeiro capítulo aborda um evento de branqueamento ocorrido em 2020 e que demonstra ser o mais intenso fenômeno de branqueamento no coral *Siderastrea stellata* da costa semiárida do Atlântico Sudoeste Equatorial. O segundo apresenta outro evento de branqueamento em *S. stellata* que ocorreu entre 2013 – 2015 e parece estar relacionado com modificações nos padrões de chuva, estiagem, irradiação solar e turbidez. Estes dois capítulos iniciais usaram com modelo de estudo o coral escleractíneo *S. stellata;* a qual é uma das espécies mais abundantes e resistentes no Atlântico Sul. O último (terceiro) trata de uma revisão integrativa sobre a ecologia trófica de corais zoantídeos *Palythoa caribaeorum*, *Palythoa variabilis* e *Zoanthus sociatus* com o objetivo de conhecer o comportamento alimentar destas espécies e relacionar com as mudanças climáticas na região do Atlântico Sul.

2 CHAPTER I

The perfect match: a severe heatwave and decrease in turbidity drive bleaching in marginal reefs (Equatorial Southwestern Atlantic)

Authors: Caroline Costa Lucas, Carlos Eduardo Peres Teixeira, Sandra Vieira Paiva, Marcus Davis, Anne Larisse Alves Rebouças Gurgel, Sergio Rossi, Marcelo de Oliveira Soares.

2.1 Hypothesis

In chapter 1, the coral bleaching event that occurred on the semi-arid coast of Brazil (State of Ceará) in 2020 was studied, evaluating the potential environmental drivers. We tested the hypothesis that intense thermal factors (an unprecedented heatwave), together with local factors such as low turbidity and changes in wind speed, provoked the bleaching phenomenon in low-latitude ecosystems.

2.2 Objectives

2.2.1 General objectives

- Measuring the percentage of coral bleaching and evaluating the climatic and oceanographic conditions on the coast of the Ceará State (Equatorial SW Atlantic) in 2020, comparing those data with previous records.

2.2.2 Specific objectives

- Reporting the coral bleaching that occurred in June and July 2020;

- Investigating the climatic and oceanographic factors potentially responsible for bleaching: surface sea temperature (SST), sea surface temperature anomaly (SSTA), degree heating weeks (DHW), marine heating waves (MHWs), maximum monthly mean of temperature (MMM), bleaching threshold (BT), attenuation coefficient of diffuse light at 490 nm (Kd490) and wind speed;

2.3 Abstract

Marginal reefs have been described as particular ecosystems in which the main reef-builders live under suboptimal environmental conditions. The Equatorial SW Atlantic (Brazil) has extreme conditions in terms of moderate turbidity levels and high and stable seawater temperature (26-30 ºC), which is significant for novel studies that assess the effect of environmental factors on marginal coral communities. A bleaching event that occurred in marginal reefs (~18m depth) in the Equatorial Southwestern Atlantic (July of 2020 in Brazil) was reported and environmental data were analyzed accordingly. Bleaching was observed in

91 % of the surveyed coral colonies (*Siderastrea stellata*). The sea surface temperature maximum (SST) was approximately 29.5 °C in March 2020. The reefs were hit by sea surface temperature anomalies, reaching a maximum of 0.7 °C above the SST means during the initial months of 2020. Degree heating weeks (DHW) showed that the year 2020 had the highest and longest heat stress recorded in this century for the marginal reef studied, May with 17.6 °C/week. In the first six months of 2020, the reef region underwent three marine heatwaves (MHWs) with 1.54, 1.99, and 1.25 °C above the mean temperature, respectively. The third MHW occurred before the bleaching record (July). Turbidity, represented by Kd490, ranged from 0.045 in May to 0.057/m in November. The lowest means of turbidity and wind speed were observed during the first half-year of 2020. We suggest that intense thermal factors, together with local conditions (lower turbidity and wind speed), triggered coral bleaching in low-latitude marginal reef ecosystems.

Keywords: bleaching; turbidity; coral; *S. stellata*; shallow reefs.

2.4 Highlights

- In 2020, Equatorial SW Atlantic recorded the highest DHW in this century for this study area (May with 17.6 °C/week);

- During the first semester of 2020, occurred three MHW events on low-latitude marginal reefs. The last MHW was immediately before the bleaching record (July);

- Environmental conditions show the first semester is more susceptible to bleaching events than the second semester;

- DHW, clear waters, and MHW may have resulted in *S. stellata* bleaching in 2020;

2.5 Introduction

Tropical reefs are threatened in multiple ways. Globally, climate change is a major cause of the decline of these unique ecosystems (HUGHES et al., 2017, 2018). Climate change with extreme, long-lasting, and intense events such as marine heatwaves (MHW) has caused a wide range of ecological damage, including coral bleaching (HUGHES et al., 2018). In general, stress-sensitive corals have a low resistance to and delayed recovery from heat stress

events (ENRÍQUEZ et al., 2017); therefore, they are among the organisms that have been harmed by variation in temperature patterns and other human impacts (HUGHES et al., 2018). However, some reef-building coral species (e.g., *Mussismilia braziliensis*, *Porites* sp.) have demonstrated quick recovery after bleaching events (LOYA et al., 2001; FERREIRA et al., 2021)

In the Indo-Pacific (i.e., Australia's Great Barrier Reef), five major mass bleaching events have been recorded (1998, 2002, 2016, 2017, and 2020) to date, all related to thermal stress (OLIVER et al., 2018; PRATCHETT et al., 2021). The most severe episode accounted for approximately 60% of bleached corals (HUGHES et al., 2017). In the South Atlantic, the first bleaching event was recorded in 1994 (MIGOTTO 1995); thereafter, bleaching events have been observed in 26 species (AMARAL et al., 1998; CASTRO and PIRES 1999; LEÃO et al., 2008; SOARES and RABELO 2014; TEIXEIRA et al., 2019; DUARTE et al., 2020; SOARES et al., 2021b). The South Atlantic reefs are considered marginal because they occur in moderately turbid waters with high sedimentation rates relative to clear-water coral reefs with less sedimentation, such as in several parts of the Indo-Pacific and Caribbean Sea (SEGAL and CASTRO, 2011). Their coral composition has low richness (23 scleractinian species) but high endemism of scleractinian species adapted to these suboptimal reef conditions. The key to potential responses of disturbance-tolerant species to bleaching is their tolerance to high light levels in high-temperature conditions (SCHEUFEN et al., 2017ab). In this regard, stress-tolerant corals in marginal turbid-zone reefs are considered more resilient to thermal stress than are Caribbean and Indo-Pacific reefs (MIES et al., 2020; SOARES et al., 2021b), but they can be affected by repeated and intense marine heatwaves (DUARTE et al., 2020; PEREIRA et al., 2022).

Marginal reefs are habitats in which environmental suboptimal conditions allow only the persistence and dominance of a few resistant species (SOARES et al., 2017; BOUWMEESTER et al., 2020; SOARES et al., 2020a). In particular, South Atlantic marginal reefs have been described as marine animal forests in which stable high temperatures combined with strong winds and turbidity allow only a few disturbance-tolerant species to conform to the seascape (SOARES et al., 2020a). These reef areas may resist bleaching events because of their lower light conditions (shading effect due to turbidity)(SULLY and van WOESIK 2020), even when temperatures rise above the mean (SOARES et al., 2021b). This is crucial to understanding bleaching events in other tropical coral reefs where water transparency is much higher (HUGHES et al., 2003).

The bleaching events in the South Atlantic marginal reefs are related to high values of accumulated temperature per week (degree heating week, DHW), El Niño/South Oscillation (ENSO), marine heatwaves (MHW), and sea surface temperature anomalies (SSTA) (LEÃO et al., 2008; TEIXEIRA et al., 2019; BANHA et al., 2020; DUARTE et al., 2020, PEREIRA et al., 2022). A Percent number of bleaching of 1%–100% has been described in the last 26 years for species of hydrocorals, octocorals, scleractinians, and zoantharians (SOARES et al., 2021b). The variation in bleaching of different anthozoans is a result, besides others, of their photosynthetic performance and their ability to optimize light scattering (ENRÍQUEZ and PANTOJA-REYES 2005; ENRÍQUEZ et al., 2017), factors that must be considered when analyzing bleaching effects on animals other than scleractinians (SCHUBERT et al., 2017). In 2016, 2019 and 2020, the South Atlantic marginal reefs experienced the most intense heatwaves ever recorded, with significant coral bleaching in the turbid zone (TEIXEIRA et al., 2019; DUARTE et al., 2020; PEREIRA et al., 2022) and subtropical shallow reefs (BANHA et al., 2020). The Equatorial Southwestern Atlantic (SWA) harbors low-latitude turbid marginal reefs such as tide-pools, shallow, and mesophotic reefs dominated by few stress-tolerant scleractinians (e.g., *Siderastrea* and *Montastraea*) and zoantharians (e.g., *Zoanthus sociatus* and *Palythoa* spp.), and is the least studied coral reef region in the West Atlantic (RABELO et al., 2013; SOARES and RABELO, 2014; SOARES et al., 2019).

Moderate turbidity and wind intensity are also important protective factors for turbid-tolerant reef-building species in marginal SWA reefs (SOARES and RABELO 2014; SOARES et al. 2019; MIES et al., 2020). With an increase in wind velocity, vertical mixing of water layers intensifies and turbidity amplifies (KNOPPERS et al., 1999). This phenomenon is addressed by Ekman's Layer, in which, the wind stress drives movements on the water surface to 100 meters depth (PRICE, WELLER & SCHUDLICH, 1987). Therefore, this acts as a protective barrier against solar irradiation, reducing light-heat photosynthetic stress in stress-tolerant corals adapted to turbidity (BAKER et al., 2008; TEIXEIRA et al., 2019). There is information on the mechanism underlying the effect of turbidity on cnidarian bleaching; however, it can be deduced that light shadowing is a key factor in the resistance to the bleaching (BUDDEMEIER et al., 2004; MCCLANAHAN et al., 2007; van WOESIK & MCCAFFREY, 2017). Together with the high and stable seawater temperature, turbidity characterizes the low-latitude region and makes it a marginal reef environment with suboptimal conditions for corals (SOARES et al., 2019). Marginal reefs may provide climate-change refugia for some coral species adapted to extreme environmental conditions (e.g., depth and turbidity), but this

hypothesis is under intense debate (LOIOLA et al., 2019; TEIXEIRA et al., 2019; EVANS et al., 2020; SULLY and van WOESIK 2020; PEREIRA et al., 2022).

The objective of this short communication is to record the coral bleaching event that occurred in 2020 and investigate the climatic and oceanographic indicators during this phenomenon. We analyze crucial physical characteristics of the water column and suggest their potential impact on the bleaching of *S. stellata*. Notably, the Equatorial SWA is quite heterogeneous, and information about its low-latitude reefs, affected by bleaching is still insufficient; hence, there is a need to describe and understand this unique marginal reef ecosystem (CAMP et al., 2018; BURT et al., 2020).

2.6 Material and Methods

2.6.1 Study area

A survey was carried out on the Equatorial SWA coast (Ceará State, Brazil) in a marginal reef, at shallow depth (18 m) in 2020 (Figure 1). In this equatorial region, the low latitude geographic position and absence of upwelling and thermoclines result in little intra- and inter-annual temperature variation (DA SILVA et al., 2017; SOARES et al., 2019). Marginal reefs occur in a tropical semiarid climate characterized by two different seasons: rainfall (January to June) and drought (July to December), with average temperatures between 26 °C and 30 °C (CAVALCANTI, 2009). The winds are also differed between the seasons, with low-intensity winds from January to May (average monthly speed 5.1 m/s in April), and high-intensity winds from August to December (average monthly speed 8.8 m/s between August and September) (DA SILVA et al., 2017). East-west trade winds predominate most of the year in the reef region (CAVALCANTI, 2009). The sea surface temperature has an intra-annual variation of <4 °C, with an average of 26 °C (SOARES et al., 2019). The reef site is located within the legal area of the Pedra da Risca do Meio Marine Protected Area (PEMPRM). This Marine Protected Area (MPA) has 33,20 km², close to Fortaleza city, and is the first and only state MPA in this region.

Figure 1 - Study area (Equatorial Southwestern Atlantic coast, Brazil, Ceará State) with the localization of *Cabeço do Balanço* reef in *Parque Estadual Marinho da Pedra da Risca do*

Meio marine protected area (PEMPRM). Location of shallow reef utilized in this study, with their respective near city, recorded bleaching date, depth/zone, distance from the Southwestern Atlantic coast, and reef type (Ceará State, Brazil).
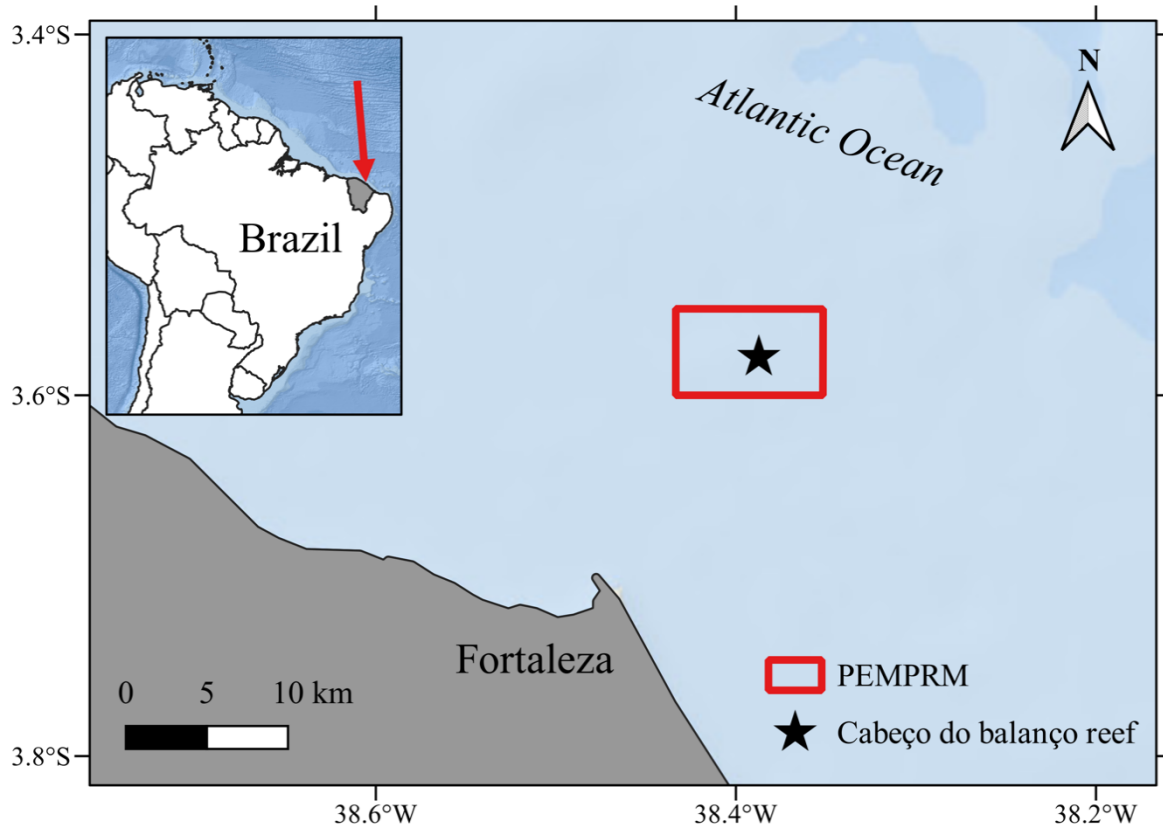
Source: author

2.6.2 Coral bleaching data collection

Sampling was carried out in a shallow turbid reef (Cabeço do Balanço), at depths of 18 m (Figure 1). This reef site could be accessed only by SCUBA diving. A systematic sampling design (e.g., transects and quadrats) assessment of bleaching was not feasible due logistical constraints. A record consisting of underwater photographs and videos recorded during citizen scientists' recreational activities was assembled (BEAR 2016; STUART-SMITH et al., 2017). Three dives were performed and recorded at the reef site, resulting in 6 videos. Approximately 16 photoquadrats were taken on this shallow reef. Corals were classified as "healthy" (no bleaching signal in the colony), "partially bleached" (when pigmentation was ≥50% of the colony covering), and "severely bleached" (when pigmentation was <50%). Through videos

and photos, the total number of colonies (109 colonies) was counted, and established the number of colonies bleached (99 colonies). The bleaching site was mapped using onboard vessel GPS, and bleached coral species was identified using scientific literature for the Brazilian reefs (SANTOS et al., 2016; LEÃO et al., 2016b).

2.6.3 Remote sensing analysis: Climate and oceanographical characteristics

Thermal stress was evaluated from indicators such as sea surface temperature (SST), sea surface temperature anomalies (SSTA), degree heating week (DHW), marine heatwaves (MHW), maximum monthly mean (MMM), and bleaching threshold (BT). To establish the BT, we identified the temperature of the warmest month in the seasonal cycle for this area, which is called the Maximum Monthly Mean (MMM) SST. The BT was 1 °C above the MMM. The time series used in this study was from 2003 to 2020. Other important environmental factors used in this research were Kd490 (scattered light attenuation coefficient at 490 nm) and wind speed. SST, SSTA, and Kd490 were obtained through the Giovanni Platform (MODIS sensor, 4 km spatial resolution). Kd490 has been used in coral reef studies to assess the transparency of water and thus its turbidity (SOARES et al., 2019; DUARTE et al., 2020; SULLY and van WOESIK 2020). The value of Kd490 (m-1) represents the rate at which light at 490 nm is attenuated with depth. A Kd490 of 0.1/meter means that light intensity will be reduced to one natural log within 10 meters of water. Thus, for a Kd490 of 0.1, one attenuation length is 10 meters. A higher Kd490 value means smaller attenuation depth and lower clarity of ocean water.

The DHW was extracted from the Global Coral Reef Watch (NOAA) at a resolution of 5 km and corresponded to the accumulation of heat over the previous 3 months. MHW is an indicator produced from NOAA's daily Optimally Interpolated Sea Surface Temperature (OISST) data and is available at http://www.marineheatwaves.org/tracker.html (SCHLEGEL and SMIT 2018). Wind speeds (m.s^{-1}) were obtained through the Brazilian Meteorological Database (BDMET) for an automatic meteorological station in the state of Ceará. We conducted the analysis using the average of each climate and thermal indicator included in this study.

2.6.4 Data analysis

We used statistical analysis of covariance to verify the relationship between the environmental factors evaluated in this study. Covariance measures the linear force between two numerical variables. After the use of covariance, we use Pearson's correlation (r) to indicate whether the relationship is strong or weak. In Pearson's correlation, the value of $r = -1$ suggests that the relationship between the analyzed variables is strong and inversely proportional, whereas the value of $r = +1$ indicates a strong and directly proportional relationship between the variables. We also used the determination coefficient to understand the variation between factors. Monthly data were used to perform statistical analyses. Statistical analyzes were executed in GraphPad Prism software version 8.2.0.

2.7 Results

2.7.1 Bleaching of Siderastrea stellata.

A bleaching event occurred in July 2020 on the Equatorial Atlantic coast (Brazil) (Figure 2). The severe bleaching was observed only in the major and dominant weedy reef-building scleractinian *S. stellata* on shallow reefs (18 m depth). This phenomenon affected 91 % of coral colonies, which corresponds to 99 fully bleached colonies (Figure 2).

Figure 2 - Scleractinian coral colonies bleached in July 2020 (Equatorial Southwestern Atlantic, Ceará coast, Brazil). A, B – *S. stellata* colony in the Cabeço do Balanço reef (18 m depth). C - Several colonies bleached of *S. stellata*.
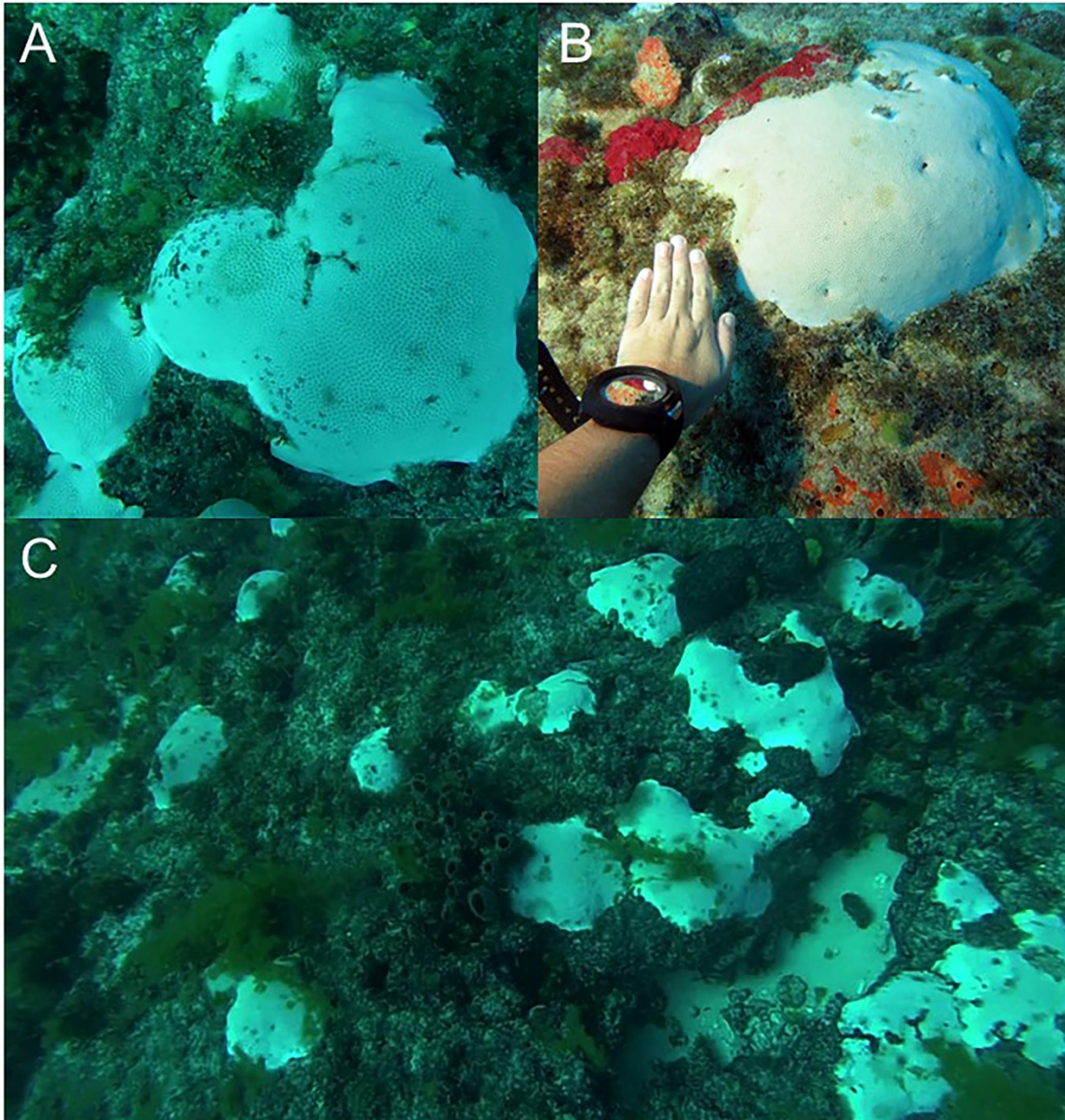
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2.7.2 Heat stress

The explanation for this coral bleaching in low-latitude marginal reefs in 2020 probably lies in some environmental factors related to changes in temperature (the most severe heatwave ever recorded in this equatorial region) and climatic-oceanographic characteristics. For the equatorial marginal reef region, March of 2020 presented the highest monthly averages of SST (Figure 3) (maximum of 29.5 °C) of the years evaluated in this study (2003–2020). The average annual temperature in 2020 was approximately 0.6 °C higher than the average annual

temperature in 2003, the beginning of the historical series in this equatorial coral reef region. The MMM temperature was 28.8 °C and occurred in March, indicating that the BT was 29.8 °C (Figure 3), 1 °C above the MMM. The average SST reached a maximum of 29.5 °C in March 2020, close to the BT; however, bleaching was only observed in July during reef surveys. February, March, April, and May had SST temperatures above 29 °C.

Figure 3 - Heat stress indicators for the Equatorial Southwestern Atlantic coast, Ceará coast, Brazil for the years 2003–2020. The solid, light blue line represents the monthly mean of sea surface temperature (Monthly SST). The dashed black line represents the maximum monthly mean (MMM) temperature. The solid black line represents the bleaching threshold (BT).
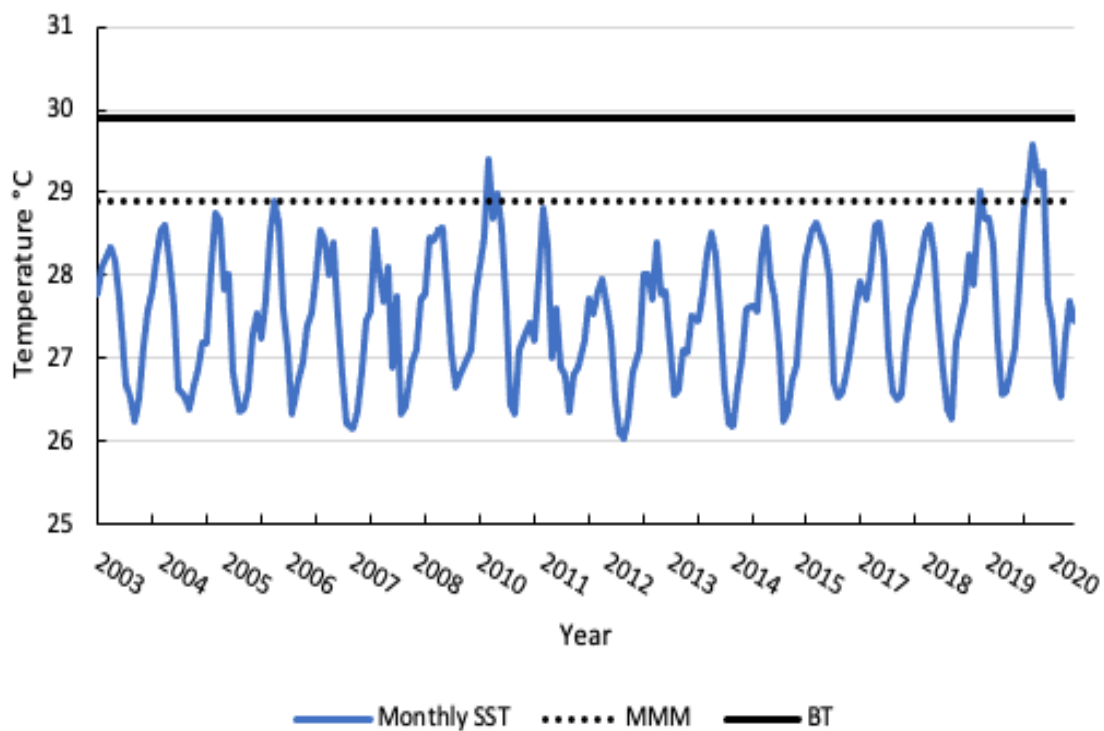
Source: author

The low-latitude marginal reefs were hit by the SSTA, which reached the maximum of 0.7 °C during the initial months of 2020 (Figure 4), and temperatures were above average in the first half-year. After the SST anomalies registered at the beginning of the year, the SSTA increased again in July (0.36; the month of bleaching register) and after in September and October, but to a lesser degree when compared to the first six months of 2020 (Figure 4).

Figure 4 - SST anomalies (SSTA) throughout 2020, showing that the largest anomalies occurred in the year's initial months (Austral summer). Captions: J (January), F (February), M (March), A (April), M (May), J (June), J (July), A (August), O (October), N (November), D (December).
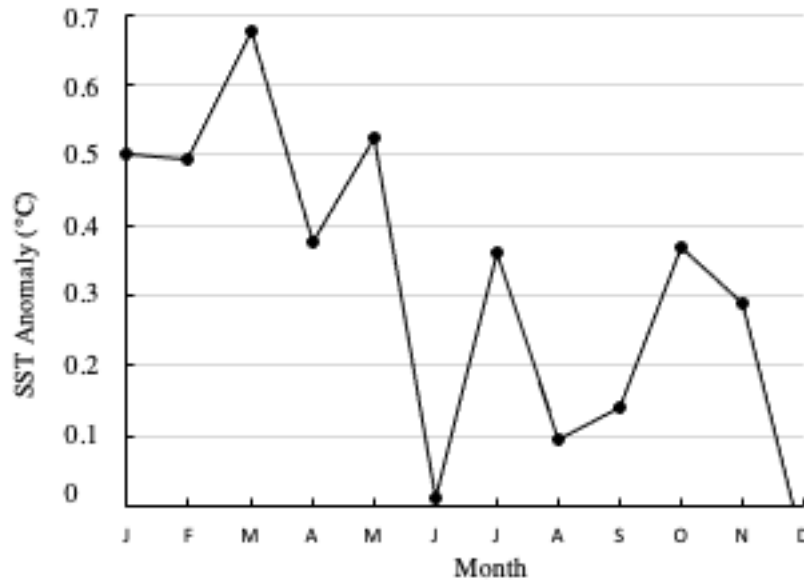
Source: author

An evaluation of the time series was carried out using the DHW and showed that the highest DHW recorded in the last century at the Ceará State coast occurred in May 2020 (17.6 °C/week) (Table 2). The low-latitude marginal reefs suffered increasing thermal stress from January until May but remained until August. The higher values of DHW were observed in April (14.8 °C/week), May (17.6 °C/week), and June (14.5 °C/week). In July, the month of record coral bleaching, DHW reached 7 °C/week (Table 2). The highest DHW records for the equatorial South Atlantic were reported in 2020 (Table 2).

In 2020, while the highest SSTAs were reported in March (0.7 °C) and May (0.5 °C), the highest DHW occurred in May. *Siderastrea stellata* bleaching on shallow-water reefs was reported in July (Figures 4 and 5). In general, the DHW data showed that the accumulation of heat stress in the equatorial region increased during the first six months of the year, reached its maximum in May, and then decreased during the second half-year (Figure 5). April, May, and June presented the highest DHWs (Figure 5).

Figure 5 - Heat map showing monthly Degree Heating Week (DHW) values between 2010 and 2020 in the Equatorial Southwestern Atlantic (Ceará coast, Brazil). Cells without values mean DHW is zero. Color changes with minimum values shown in light yellow and maximum values shown in dark red. Captions: J (January), F (February), M (March), A (April), M (May), J (June), J (July), A (August), O (October), N (November), D (December).
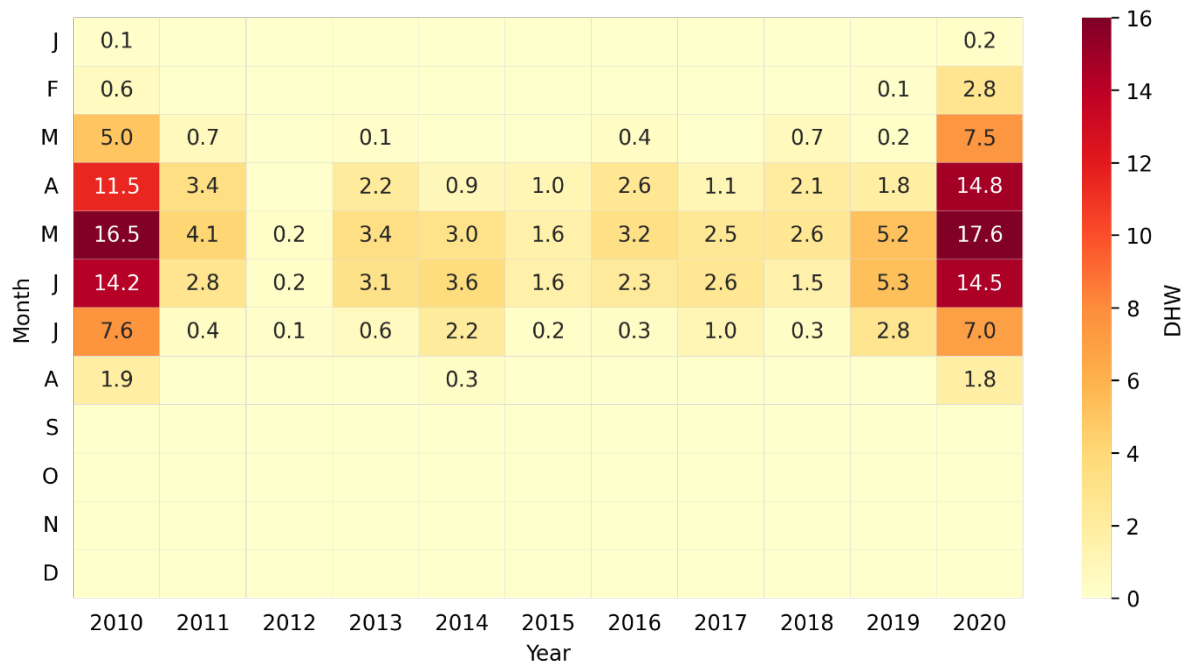
Source: author

We also used MHW, a recent product for marine heatwaves analysis that qualitatively observes periods of thermal anomalies lasting at least 5 days in a given location. During the first six months of 2020, the marginal coral reef region underwent three moments of MHW, totaling 157 days of elevated thermal stress in this region (Figure 6). The longest single period lasted 76 days, from the end of February until the beginning of May (immediately before the diving surveys in which coral bleaching was observed). From May until June (during the diving survey), the marginal reefs experienced another 35-day extreme warming (Figure 6). The final two periods showed maximum intensities of approximately 2 °C and 1.25 °C, respectively, and these represent the maximum temperatures, above average, found during each MHW event (Figure 6). The repeated and intense MHWs in May and June (Figure 6) probably explain the bleaching events observed in this equatorial region (Figure 2).

Figure 6 - Three marine heatwave (MHW) events during the first half-year of 2020 with their beginning and end dates, duration (days), and intensity (°C). Thermal stress MHW event is represented by orange areas. The lightest orange areas represent moderate MHW and the darkest strong events.
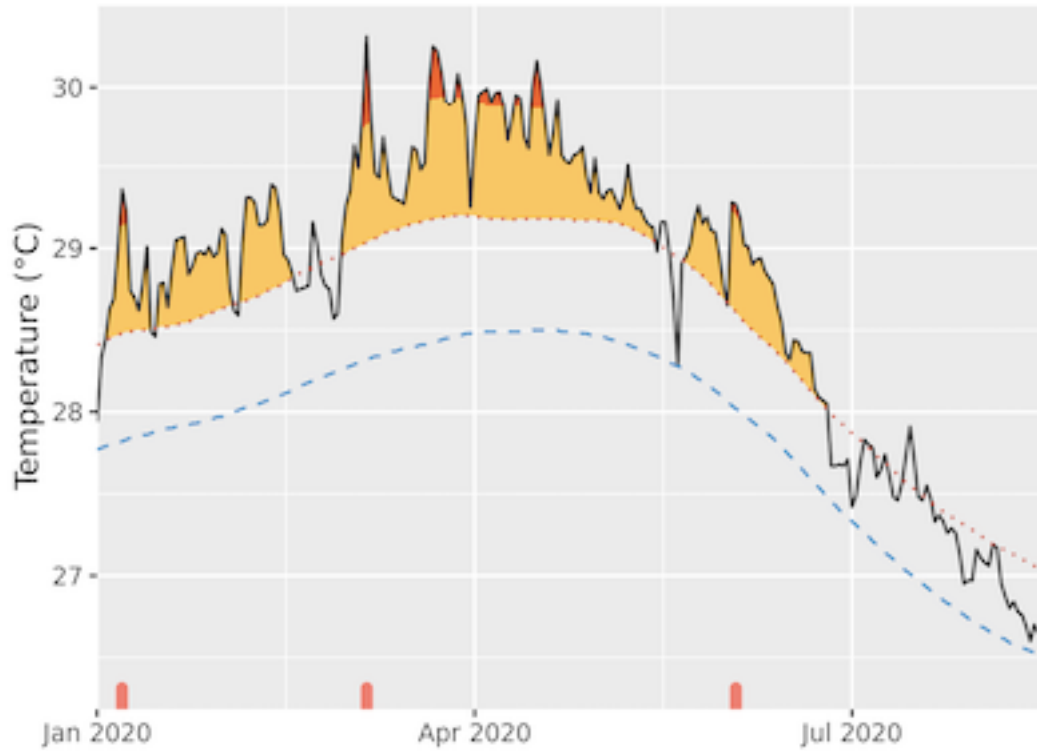
Marine heat wave event	Begin-End	Duration (days)	Maximum Intensity (°C)
1	3/01/2020 - 17/02/2020	46	1.54
2	29/02/2020 - 14/05/2020	76	1.99
3	22/05/2020 - 25/06/2020	35	1.25

Source: author

2.7.3 Changes in turbidity and wind speed

In 2020, the wind speed increased from March (1 m/s) until August (3.4 m/s). Turbidity, conversely, reached its minimum in March (0.041/m, before bleaching detection) and its maximum in November (0.056/m) (Figure 7). Therefore, the lowest average turbidity and wind speed and the most intense heat stress (DHW and MHWs) were observed during the first six months together with bleaching events (Figures 5 and 6).

Figure 7 - Monthly means and standard deviations of the wind speed (A) and light attenuation coefficient (Kd490) (B) on the Equatorial Southwestern Atlantic coast (Ceará coast, Brazil) during the bleaching event in 2020. Captions: J (January), F (February), M (March), A (April), M (May), J (June), J (July), A (August), O (October), N (November), D (December).
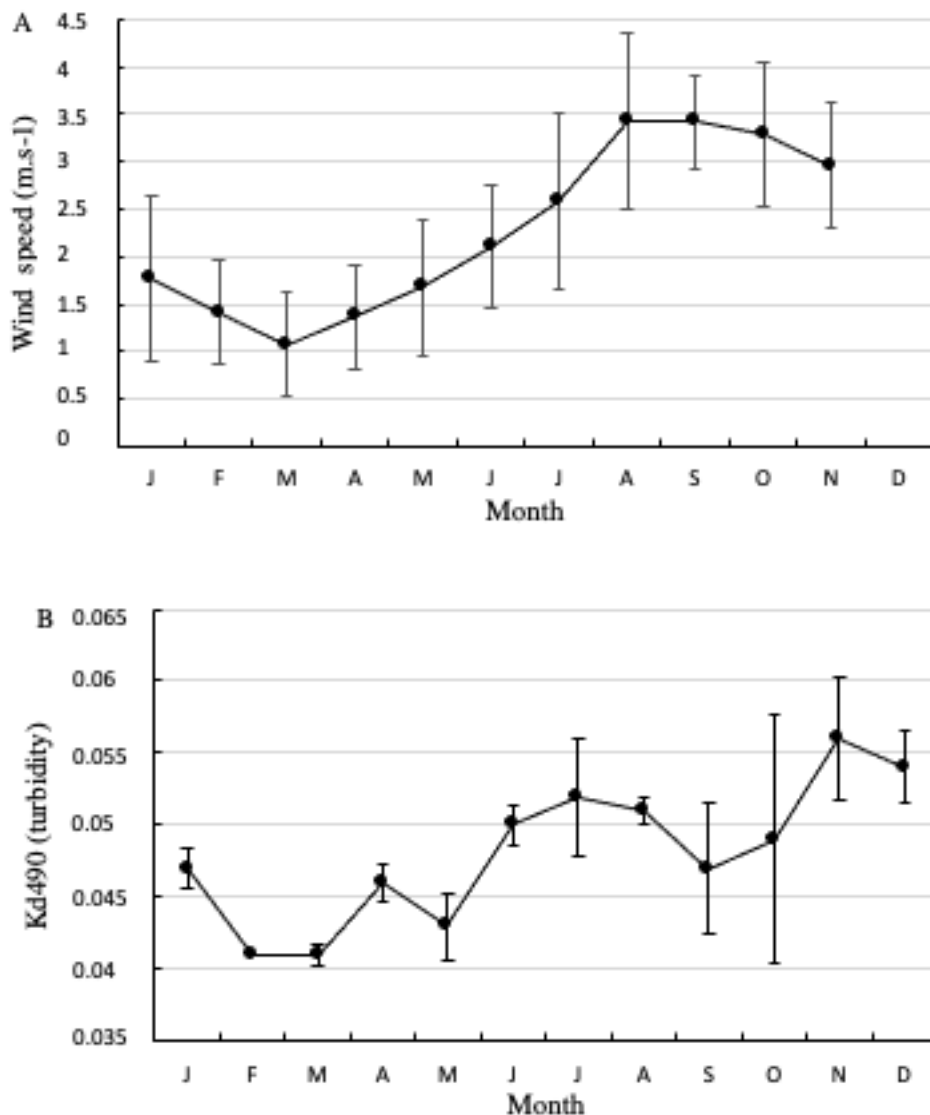
Source: author

2.7.4 Data analysis

From the statistical analysis of covariance and Pearson's correlation for the monthly data for 2020, it was possible to observe that the relationships between SST, turbidity, and wind speed were stronger. Among these, SST and turbidity (r = -0.70), and SST and wind speed (r = -0,95) were inversely proportional, turbidity and wind speed (r = 0.70) were directly proportional. Pearson correlation had a medium value for DHW and wind speed (-0.56) and DHW and SST (0.51). The determination coefficient showed the variation in turbidity may be explained by 91% for SST.

Table 1- Pearson correlation (r) and determination coefficient (r^2) for environmental factors (SST, DHW, turbidity, and wind speed) for the 2020 year.

	Wind speed	Turbidity	SST
DHW	r = -0.56 r^2 = 0.32	r = -0.37 r^2 = 0.13	r = 0.51 r^2 = 0.26
SST	r = -0,95 r^2 = 0.91	r = -0.70 r^2 = 0.49	-
Turbidity	r = 0.70 r^2 = 0.50	-	-

Source: author

2.8 Discussion

2.8.1 Bleaching and heat-light stress

This research highlights a bleaching event that occurred in shallow turbid zone reefs on the Equatorial SWA coast in 2020. This year was marked by intense and prolonged warming of the waters, which, together with decreased protection from heat-light stress due to weak trade winds and moderate turbidity, may have resulted in the bleaching of Equatorial marginal reefs (Table 1). This study is the first record of bleaching in low-latitude marginal reefs during the most intense heat stress event recorded in this century (2020) for this area (Figure 5 and 6).

The lesser vulnerability of South Atlantic massive corals to bleaching relative to Caribbean and Indo-Pacific corals may be due to their deep bathymetric range, tolerance to nutrient discharge and turbidity, diversity of symbionts, and morphological characteristics (MIES et al., 2020). Turbidity may alleviate intense light, especially in shallow areas where scleractinians (especially those that are turbid tolerant) are better adapted to harvest light (ENRÍQUEZ et al., 2017). However, the results of this study suggest that a match between lower turbidity and heat stress (DHW and MHW) could affect the scleractinian coral, *S. stellata* despite their tolerance to heat stress and turbidity (LEÃO et al., 2010; SOARES et al., 2019).

During July 2020 (Figure 2), coral bleaching (>90% bleached corals) was detected. The first months have shown the highest levels of bleaching in previous surveys conducted in this region, particularly during 2010 (SOARES and RABELO 2014; Soares et al., 2019), which has the second-highest DHW recorded in times series used in this study (May of 2010; 14.9 °C/week) (Figure 5). All thermal indicators utilized had high values during the first six months of 2020. The constant and positive SSTA observed during the initial months (Figure 4) must have favored the high DHW that reached the equatorial reef region during the first half-year. The bleaching observed in July, probably happened due to accumulated heat stress.

Some bleaching records for the Equatorial SWA are from 2010. The first bleaching record occurred in 2010 in Ceará, in the species *S. stellata*, *Favia gravida*, and *Z. sociatus*, and these species recovered fully in intertidal reefs (SOARES AND RABELO 2014). In the same study, was reported bleaching of 100 % *S. stellata* colonies coinciding with SSTA (1 to 2 ºC) and SST (30 to 32 ºC) (SOARES and RABELO 2014). On the coast of Paraíba State, still in 2010, the scleractinians *S. stellata*, *Porites astreoides*, *Agaricia agaricites*, and *Mussismilia harttii*, and the hydrocoral *Millepora alcicornis* suffered bleaching associated to high SST (31 °C) and DHW (4 °C/week) (DIAS and GONDIM 2016). In Rocas Atoll, located in the oceanic region, bleaching was related to a thermal anomaly of 1.6 °C (FERREIRA et al., 2013). There is also a register of *S. stellata* bleaching in 2010 in the same study local of our research when temperatures ranged from 28.5 to 29.5 °C (SOARES et al., 2019). The years 2010 and 2020 showed similar data for bleaching and thermal stress indicators in Equatorial Atlantic, indicating that 2020 bleaching also was triggered by thermal factors.

Siderastrea spp. which is common at both shallow and mesophotic depths, is adapted to low-latitude reefs with little temperature variation (SOARES and RABELO, 2014; SOARES et al., 2019). This species also has high specificity with Symbiodininaceae clade C, which is recognized as one of the most bleaching-resistant microorganism groups (COSTA et al., 2008; MONTEIRO et al., 2013). In Brazil, *Siderastrea* spp. samples were identified as

radians/*stellata* and associated with *Symbiodinium* strains B5, C3, C3 + B5, C46, C46 + B5, and C1 (MONTEIRO et al., 2013). In general, Symbiodininaceae clade B also seems to be relatively tolerant of higher light intensities. Therefore, large thermal range events make these corals unable to withstand high temperatures and result in bleaching. Corals begin to show stress when SST is 1 °C above the MMM (within the monitoring period) (GLYNN and D'CROZ 1990). However, it is important to emphasize that marginal reefs that undergo intense bleaching and recovery demonstrate resilience, and represent potential climate-change refugia for surviving of the few stress-tolerant species that inhabit them (TEIXEIRA et al., 2019; DUARTE et al., 2020).

This study observed thermal stress and bleaching of reef-building coral *S. stellata* at the same time on the Equatorial SW Atlantic coast. Heatwaves have become the most significant pressure source on marginal reefs due to their growing impact observed in recent years. DHW and SSTA are used to detect these temperature changes and are therefore good predictors of bleaching phenomena in this low-latitude region. Several studies in Brazil reported a link between DHW and the coral bleaching (SOARES et al., 2019; TEIXEIRA et al., 2019; DUARTE et al., 2020). Three shallow reefs (4–8 m) were analyzed during severe heat stress in 2019, and partial (15.4 to 28 %) and total (13.3 to 32.2 %) bleaching percentages for *S. stellata* were recorded (DUARTE et al., 2020). The same study showed that the DHW reached 19.6 °C/week for the sampled region, and represented one of the most severe events on the Brazilian coast (DUARTE et al., 2020). Another study showed severe bleaching, 90.9 %, in *S. stellata* colonies when DHW ranged from 8 to 9 °C/week in July 2010 (SOARES et al., 2019). In the Abrolhos region in 2014, 2015, and 2016, DHWs reached 8.4, 6.7, and 9.7 °C/week, respectively (TEIXEIRA et al., 2019). The percent cover within the partially bleached category ranged from 2.7 to 57.1 % and the heavily bleached category from 10.8 to 85.1 % during 2016 (TEIXEIRA et al., 2019). The bleaching event in 2016 was one of the most severe on record and affected several species, including *S. stellata* (TEIXEIRA et al., 2019).

Relative to previous studies in this century, our data include the highest DHW for the Equatorial SW Atlantic region (17.6 °C/week) and one of the most significant for the South Atlantic. DHW is an important index calculated through the average of the local temperatures and allows for comparison between different places. The DHW observed in the present study (17.6 °/week) is well above the established threshold for bleaching, even in stress-tolerant corals such as *S. stellata*. A DHW equal to 4 generally results in bleaching of 30%–40%, and a DHW above 8 generally results in bleaching of more than 70% of colonies (LIU et al., 2006; KAYANNE 2017).

MHW is one of the most recently derived tools used to explain bleaching events. In addition to showing non-patterned occurrences, MHWs vary widely in both frequency and magnitude across oceans (OLIVER et al., 2018). The bleaching of *S. stellata* was analyzed and correlated with ENSO and MHW in Rocas Atoll (the same latitude as the region investigated in this study) in 2016, 2017, and 2019 (GASPAR et al., 2021). Among these, 2019 had the most intense and longest MHW events, two events with an average duration of 31.5 days and a cumulative intensity of 31.51 °C. 2019 also had the highest percentage of bleaching, which was likely intensified by MHW (GASPAR et al., 2021). Bleaching percentage were 11.71% in 2016, 1.52% in 2017, and 88% in 2019 (GASPAR et al., 2021). Similar results were found in our research in 2020, as we showed that this region suffered the longest, repeated, and most intense thermal stress. The percentage of bleaching was > 90 % of colonies. Thus, the analysis of MHW over large time scales can help monitor areas that are susceptible to bleaching (DONNER et al., 2005; OLIVER et al., 2021). The number of MHWs has doubled in the last century, and these phenomena have become the main drivers of coral bleaching worldwide, including in marginal reefs (OLIVER et al., 2018). MHW evaluations indicated that longer-lasting events were related to higher SSTA means, and these events also included weak winds and clear waters (SEN GUPTA et al., 2020). The present study included periods of high thermal anomalies and weak trade winds before and during MHWs, suggesting that these calm water conditions may have acted together to provoke the bleaching phenomenon.

2.8.2 Turbidity and wind speed conditions

Intra-seasonal variation in wind speed, rainfall, and temperature in equatorial semiarid Brazil are quite evident in this region, making it one of the most important regions in South America for conducting climate observations (KAYANO and ANDREOLI, 2009). The climatic and oceanographic characteristics observed in this study, including low turbidity, light winds, and thermal stress, may have acted together to trigger bleaching in stress-tolerant corals in 2020 (Table 1). Therefore, the present study corroborated the previous hypothesis that low turbidity, low wind speed, and intense thermal stress acted together during the first half of the year and may have promoted bleaching of massive corals even in turbid and deep reefs. Our results show a positive linear correlation between turbidity and wind speed ($r = 0.70$; $r^2 = 0.50$) and a negative linear correlation with thermal indicators such as DHW x Wind speed ($r = -0.56$; $r^2 = 0.32$) and SST x Wind speed ($r = -0.95$; $r^2 = 0.91$) (Table 1). Massive corals in

equatorial semiarid Brazil are adapted to lower light intensity than are corals in other areas of the world (SOARES et al., 2020a), and this suggests that the adaptation may be constrained if harvested light increases (SCHUBERT et al., 2017). Strong winds promote a mixture of the surface layers and increase the number of suspended particles in water, thus reducing the penetration of UV solar irradiation (BAKER et al., 2008) and operating as anti-bleaching factors in turbid-tolerant species such as *Siderastrea* spp. (MCCLANAHAN et al., 2007).

2.9 Conclusions

Marginal reefs located on the Equatorial Southwestern Atlantic coast are susceptible to bleaching events during the first half-year due to their climatological and oceanographic characteristics. Thermal stress, weak winds, and low turbidity drive these events in marginal reef species. The results of our research suggest that the main heat stress factors driving the 2020 bleaching event were the MHWs and DHWs. Probably, the increase in the frequency and duration of these thermal stress events can damage marginal reef environments. These indicators are related to prolonged and intense periods of thermal stress, indicating that although disturbance-tolerant corals on these low-latitude reefs are adapted to stable high temperatures, bleaching may occur if thermal stress is long-lasting and extreme. This, in turn, can lead to the expulsion of their Symbiodinaceae, and the absence of turbid- and depth-refugia.

Our study observed coral bleaching at shallow-water reefs of the Atlantic equatorial margin, implying the need for monitoring shallow reefs to understand future seascapes in the Anthropocene. Climate projections for Equatorial Southwestern Atlantic indicate weather hotter and drier. These conditions, probably, will affect negatively corals in this region. In addition, future studies should investigate turbidity, wind speed, and thermal stress indicators to better understand the current characteristics of species in the equatorial Atlantic and possible changes that will occur in reef ecosystems due to climate change. Therefore, it is necessary to monitor, investigate, and promote ways to reduce the pressure in these unique marginal reef systems.

3 CHAPTER II

Marginal environmental conditions drive small-sized colonies and chronic coral bleaching

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3.1 Hypothesis

Chapter II deals with the observations of a prolonged bleaching during 2013-2015, and environmental factors that may have caused this lasting bleaching in the Equatorial SW Atlantic. We used the hypothesis that the lack of rain altered the turbidity of the water, reducing the number of particles in the water and protection against light and heat for the stress-tolerant corals. Thus, they became more vulnerable to bleaching.

3.2 Objectives

3.2.1 General objectives

- Understanding population structure of bleached colonies over rainfall anomaly period.

3.2.2 Specific objectives

- Measuring the percentage of bleached colonies of *Siderastrea stellata* per bleaching status and the number of bleached colonies by size category.

- Investigating the climatic and oceanographic factors that may have been responsible for bleaching: rainfall, turbidity, solar irradiance, wind speed, surface sea temperature (SST), sea surface temperature anomaly (SSTA), degree heating weeks (DHW), marine heating waves (MHW).

3.3 Abstract

Suboptimal environmental conditions are expected to increase worldwide due to climate change, highlighting the importance of studying marginal reefs. However, the drivers of coral bleaching in present-day marginal reefs are understudied. We describe the population structure of a major and resilient coral (*Siderastrea stellata*) in a turbid-zone reef and the bleaching effect associated with the different size classes. *S. stellata* is the only reef-building coral to compose this seascape with encrusting and low-relief colonies characterized by short life spans and recruitment. We analyzed the environmental factors (rainfall, wind speed, turbidity, solar irradiance, sea surface temperature, degree heating weeks, and marine

heatwaves) and the link with the bleaching phenomena under the worst recorded drought cycle (2013-2015) in the Tropical South Atlantic. The results indicate that there were large anomalies in sea temperature (temperature range 26.6 °C to 29.3 °C) and marine heatwaves were absent but an extreme rainfall deficit (ranging from 30 to 40% less annual volume precipitation) was detected. We analyzed 2,880 colonies and most of them (~ 93%) fit in the first size group (2 - 10 cm) with a small number (~ 1%) of larger and older colonies (> 20 cm). In general, a high proportion of bleached colonies were found throughout the years (44 to 84% of colonies) when turbidity decreases. The population, even after the bleaching effect, survived and remained stable during this study. During drought periods there are reduced cloudiness, turbidity, wind speed, and increased solar irradiance, driving higher bleaching rates in these turbid-tolerant corals. Our results suggest that precipitation anomalies are an important and neglected driver of coral bleaching.

Keywords: Coral bleaching*,* Turbidity, Global warming, Drought, Turbid-zone reef.

3.4 Highlights

- Small size colonies seem to be persistent in extreme conditions environments

- Rainfall deficit also can be a drive of coral bleaching

- Turbid-zone reef may be a short-term refuge site for *S. stellata*.

3.5 Introduction

Coral reefs are commonly associated with clear, oligotrophic, and warm waters in low latitude areas. These environmental factors are recognized as optimum conditions for coral growth, sustaining older and architecturally complex colonies (PERRY and ALVAREZ-FILIP, 2019). It is widely acknowledged, however, that many tropical reefs are increasingly exposed to turbid waters (e.g., due to deforestation and increased siltation by river runoff) and unusually high temperatures associated with global climate change. Suboptimal (or marginal) conditions are expected to become more prevalent in some tropical areas due to accelerated global environmental change (CAMP et al., 2018). These conditions are expected to reconfigure shallow coral reefs, probably leading to the loss of stress-sensitive species and a decline in ecosystem goods and services (ALVAREZ-FILIP et al., 2009; HUGHES et al., 2017a).

Marginal coral communities are currently common in areas characterized by suboptimal conditions (LYBOLT et al., 2011; SOARES, 2020). These conditions include high sea surface temperatures (SST), frequent marine heatwaves, re-suspension of sediments, extreme variability in rainfall, and low light penetration (RESTREPO et al., 2016). These marginal reefs are generally dominated by stress-tolerant species resistant to at least one of the suboptimal conditions (PERRY and LARCOMBE, 2003; CAMP et al., 2018). The occurrence of these species could confer to these reefs a large resistance and capacity to recover from certain disturbances (GLYNN 1996; RIEGL and PILLER 2003). In addition, coral size structure has been observed as an important factor to understand the persistence and survival of coral communities under repetitive disturbances (FONG and GLYNN, 1998; RIEGL and PURKIS, 2009).

Marginal reefs were placed in the spotlight because some of their species (e.g., *Siderastrea*, *Montastraea*, *Mussismilia*) exhibited record levels of resistance to marine heatwaves such as turbid-tolerant corals (GUEST et al., 2016; FISHER et al., 2019; MIES et al., 2020). These already adapted corals have undergone lower rates of bleaching and/or had a higher resistance capacity with lower mortality rates even after severe heatwaves (SOARES, 2020). This resistance is one of the factors that led to the formulation of the hypothesis that some marginal turbid-zone reefs represent climate-change refugia (CACCIAPAGLIA and WOESIK, 2015). In other words, although these extreme reefs have a lower species richness, their corals are usually more resistant, at least to suboptimal environmental parameters (e.g., turbidity, extreme pH values, or variable temperature). However, a large resistance to all types of human and natural impacts is not expected in marginal reefs and they are also under severe threat (SOARES, 2020).

Turbid-zone reefs are one of the most studied extreme habitats concerning the resilience potential of coral populations in face of global environmental change. Moderate turbidity is one of the factors that can protect stress-tolerant corals by shading from sea surface temperature anomalies and high irradiance (heat-light stress). CACCIAPAGLIA and WOESIK (2016) identified turbid nearshore refuges for corals between latitudes 20–30° N and 15−25° S, where there was a significant coupling between turbid waters and tidal oscillations. Their model also suggests that turbidity will mitigate high thermal stress bleaching for 9% of shallow reef habitats (0–30 m depth). Moreover, SULLY and WOESIK (2020) suggested that approximately 12% of reefs worldwide exist within the "moderating turbidity" range (Kd490, a measurement positively related to turbidity, between 0.080 and 0.127), including some of the Brazilian reefs.

Brazilian nearshore reefs are considered marginal due to the occurrence of significant levels of sedimentation and turbidity (SUGGETT et al., 2012; MIES et al., 2020) yet represent the unique and richest reefs in the Tropical South Atlantic (LEÃO et al., 2016a). Overall, these reefs are dominated by massive stress-tolerant corals (LEÃO et al., 2016a) such as *Siderastrea* spp. (LOIOLA et al., 2019; TUNALA et al., 2019). The Equatorial Southwestern Atlantic (Ceará State) recently suffered a rainfall deficit (2012-2015) considered the most severe drought registered in Brazilian history (MARENGO et al., 2016). This rainfall deficit decreased the water flow from continent to coast, which probably interfered with the discharge of particles to the sea changing the water turbidity. Particles in the water column can shade corals, diminish damage light-heat, and bleaching occurrences over coral (MCCLANAHAN et al., 2007; SULLY and van WOESIK, 2020). These marginal reefs in this recent event thus provide a unique scenario to understand the effects of suboptimal conditions and extreme droughts on the coral bleaching (TEIXEIRA et al., 2019; SOARES et al., 2019). However, long-term research analyzing intra-annual and inter-annual variation in coral bleaching and environmental factors is scarce.

Research on the role of marine heatwaves and prolonged warming as drivers of coral bleaching is increasing particularly for marginal reefs occurring in optimal environmental conditions (HUGHES et al. 2017a, 2018; SULLY et al., 2019). The role of thermal stress as a driver of bleaching in corals currently exposed to turbid-zone conditions and extreme droughts is less well understood. Additionally, the knowledge of causes and consequences, thermal tolerance and coral survival, and spatial extension of bleaching in these suboptimal conditions may provide some useful insights into their refugia potential (CAMP et al., 2018). Studies of coral bleaching in marginal conditions are mainly conducted in subtropical and temperate reefs (Cameron and HARRISON, 2016; NG and ANG, 2016; THOMPSON et al., 2022), which are significantly different from their tropical counterparts (SOARES, 2020). The knowledge about the drivers and effects of coral bleaching in tropical marginal conditions under high and stable temperatures, extreme climate variability (floods and droughts), and turbid waters are still scarce (CAMP et al., 2018; BURT et al., 2020).

Coral bleaching in marginal reefs is less understood due to several drivers (thermal, turbidity, sedimentation) that can trigger this phenomenon (SOARES et al., 2019; MIES et al., 2020). Climate change is predicted to increase the frequency and intensity of extreme events including droughts, large precipitation events and flash floods (HOOVER et al., 2022). While many studies have focused on the bleaching impacts of individual events (e.g., a heatwave),

the effects of drought, temperature and other environmental phenomena on bleaching on marginal reefs are unknown.

The present study analyzed the percent number of colonies bleached and population structure (in size categories) of the weedy coral *S. stellata* during 3 years under the drought cycle of 2013-2015. We also correlate the percent of fully-bleached colonies with key environmental factors (rainfall, occurrence of marine heatwaves, mean sea surface temperature, turbidity, insolation, and wind speed) to understand the main drivers of coral bleaching in marginal conditions. We hypothesized rainfall deficit provoked a decrease in turbidity, reducing the number of particles in water and protection against heat-light stress over coral, which may have produced bleaching (BAKER et al., 2008; MCCLANAHAN et al. 2007; van WOESIK & MCCAFFREY, 2017). However, intense and short precipitation events ("deluges") can provide temporary protection against bleaching.

3.6 Material and Methods

3.6.1 Study area

A quantitative survey was carried out along the Equatorial Southwestern Atlantic coast (Brazil) (Figure 1). The Northern Brazilian nearshore reefs are characterized by marginal and highly dynamic environmental conditions including extreme droughts and floods, high temperatures for prolonged periods (e.g. 1951-1954 and 1979-1983), high insolation rates, turbid waters, and highly variable speed winds (SOARES et al., 2019, DA SILVA et al., 2017). Corals in this low-latitude region do not form biogenic structures, are exposed to turbid waters and siliciclastic-carbonate sediment resuspension (TUNALA et al., 2019), but rather occur as isolated colonies above sandstone or rocky reefs (SOARES et al., 2016). Monotypic marginal coral communities may occur dominated by the stress-tolerant *S. stellata,* a species that thrives under suboptimal conditions (OIGMAN-PSZCZOL and CREED, 2011; SOARES et al., 2019). *S. stellata* is also common in Western Atlantic and is an important reef-building coral along the Brazilian coast (MILOSLAVICH et al., 2010; LEÃO et al., 2016a).

Figure 8 - Study site in the Equatorial Southwestern Atlantic coast (Ceará State coast, Brazil). Black star indicates the reef site.
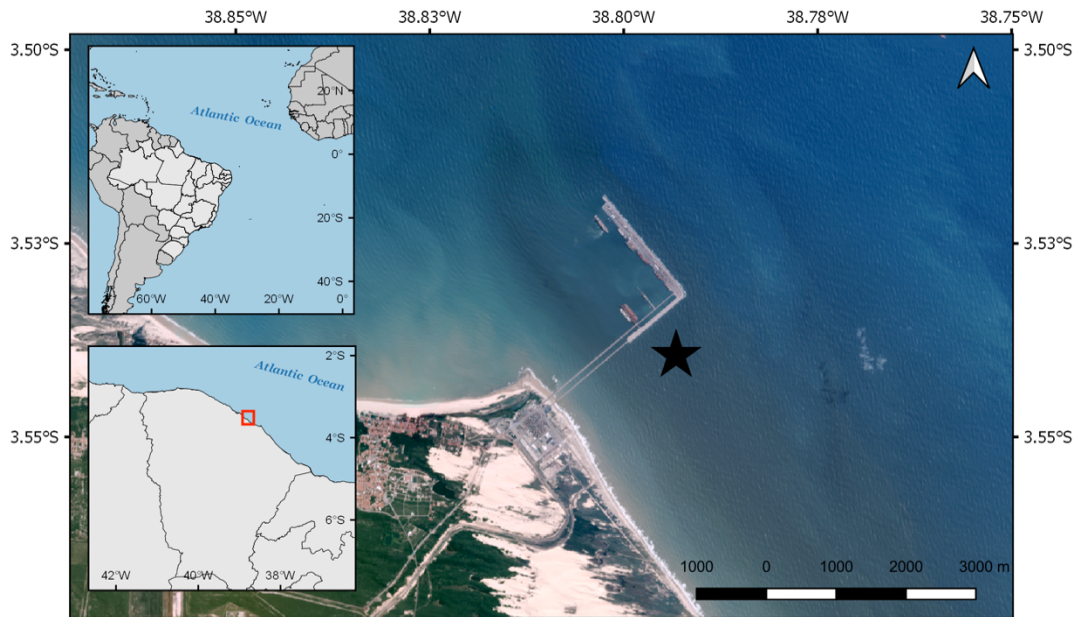
Source: author

The near-equatorial location of the study site (Figure 8) is exposed to low levels of intra and interannual SST variability with values ranging from 26,5 to 29,5 ºC in the last 20 years (TEIXEIRA and MACHADO, 2013; SOARES et al., 2019). The winds, rainfall, and cloudiness pattern in the region are seasonally modulated due to the meridional migration of the ITCZ (Intertropical Convergence Zone) (MARENGO et al., 2016). From January to July, the ITCZ migrates to the southern hemisphere leading to local lower trade wind speeds (1-3 m.s^{-1}), rain, and cloudiness. From July to December, the ITCZ migrates to the northern hemisphere leading to high trade winds speeds (i.e. 5-7 m.s^{-1}) and dry conditions locally (SOARES et al., 2019). The rainy period extends from January to June and concentrates 90-95 % of the total annual rainfall (MARENGO et al., 2016). These two periods usually define the tropical semiarid coast where the present study was conducted (MARENGO et al., 2016; SOARES et al., 2021a). This region in Brazil (Figure 1) is also vulnerable to high interannual rainfall variability, and climate change scenarios indicate that this region will be severely affected by rainfall deficit and increased aridity in the current century (BRITO et al., 2017).

3.6.2 Data collection: population structure, coral bleaching, and environmental factors

Data collection was conducted using SCUBA in different months during low spring tides when reefs were uncovered. The bleaching status and size category of coral colonies were assessed in 2013 (May, June, July, August, October, December), 2014 (March, May, June, August, September, December), and 2015 (March, April, June). Rainfall ranges from 157 to 421.5 mm month[-1] during the rainy season (March-June) and 0 to 88.6 mm month[-1] during the dry season (July-December) (Appendix B, Table S1).

We quantify coral bleaching defined here as the percent number of colonies within different bleaching status and sizes (in diameter) in *S. stellata*. Underwater bleaching surveys were conducted at the depths of 2, 4, and 6 m. Three transects per month and three photo quadrats per transect were surveyed (n= 9 quadrats per month, Figure 9). The photo quadrats were randomly distributed along the transects (Appendix B, Figure S1). Each photo quadrat was analyzed with the software Image J to measure colonies and also classify coral colonies according to their bleaching status indicated by the Coral Health Chart in categories: healthy, with fully pigmented; moderate bleaching, with reduced pigmentation; and strong bleaching, with total white tissue. These criteria are according to the published by SASSI et al. (2015) and SOARES et al. (2019) (Appendix B, Figure S1). Following LEÃO et al. (2016a) colonies were classified into four size categories (i.e. 2-10 cm, 11-20 cm, 21-30 cm, and 31-40 cm) to characterize the size structure of the *S. stellata* population. The analysis of photo quadrats provided monthly data on the percent of colonies in each size category (diameter) and the percent number of bleached colonies in each category of bleaching status (healthy, moderate bleaching, and strong bleaching).

Figure 9 - Encrusting and low-relief coral colonies of *S. stellata* in a tropical marginal reef region (Equatorial SW Atlantic, Brazil). Bleached corals in May 2013 (A) and June 2013 (B). Fully pigmented coral colonies at the same site were photographed in March 2015 (C) and April 2015 (D). Quadrats are 30 x 30 cm in size.
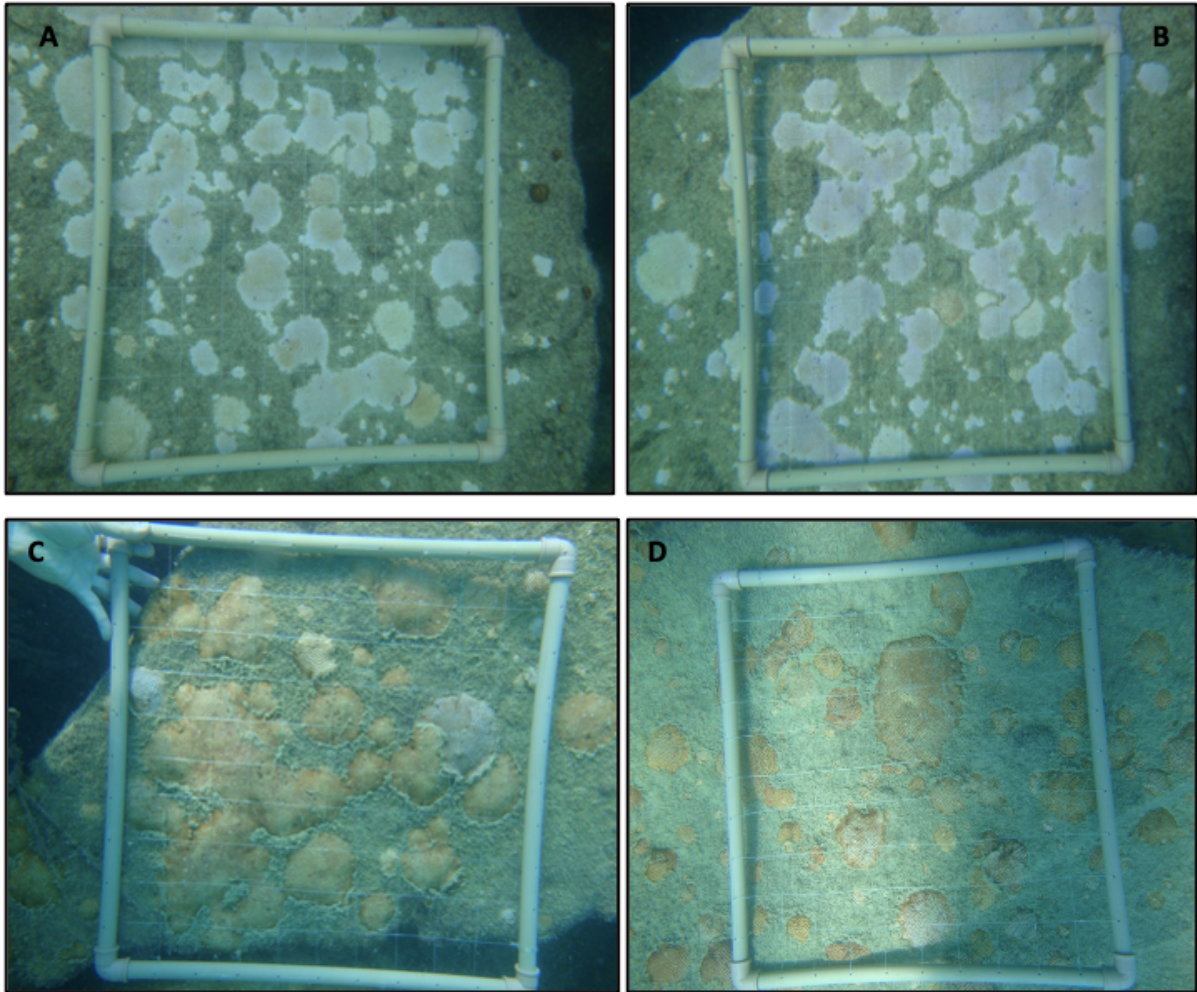
Source: author

We verify the relationships between environmental factors (SST, turbidity, insolation, wind speed, and rainfall) *S. stellata* coral bleaching. SST, SST anomalies (SSTA), and diffuse light attenuation coefficient (related to turbidity) at 490 nm (Kd_{490}) values were obtained from the Giovanni NASA platform (https://giovanni.gsfc.nasa.gov/giovanni/). We used monthly values of SST and Kd_{490} from the MODIS Aqua sensor with a 4-km spatial resolution covering the period from 2013 to 2015 in the study area. The SSTA was calculated using the climatological values from the entire Modis Aqua mission at the analysis date (2013-2015). The Kd_{490} provides a measure of water transparency because it is directly related to particles scattered in the water column. A higher Kd_{490} value means smaller attenuation depth and lower clarity of ocean water. This methodology is similar to that previously used by BANHA et al. (2019), SOARES et al. (2019), and TEIXEIRA et al. (2019) on the Southwestern Atlantic reefs. Monthly wind speeds (m second^{-1}), rainfall (mm month^{-1}), and irradiance (daylight hours month^{-1}) were collected from the BDMET (Brazilian Meteorological Database) and

FUNCEME (Ceará State Foundation for Meteorology and Water resources) using the data from the meteorological station closest (~10km) to the study site.

Lastly, Degree Heating Weeks (DHWs) were also obtained from the NOAA Coral Reef Watch website (https://coralreefwatch.noaa.gov/satellite/index.php) for the period studied. DHW shows the number of weeks of positive SST anomalies and is used to understand the accumulative heat in the last 3 months. Marine heatwaves also were investigated in the study area to find out the frequency, duration, and maximum temperature of marine thermal events; this data is available at http://www.marineheatwaves.org/tracker.html (SCHLEGEL; SMIT, 2018).

3.6.3 Statistical analysis

The data were used to verify the colony's size distribution patterns (histograms) and to find the percentage of bleaching status (healthy, moderate, and strong bleaching) per month using descriptive statistics (percent number of affected colonies by bleaching; percentage of colonies in each size category). Environmental data (SST, wind speed, solar irradiance, rainfall, and Kd_{490}) were analyzed using statistical models. Two multivariate statistical analyses were carried out: 1) Analysis of similarities to group months with similar strong bleaching, and 2) PCA (Principal component analysis) to group the variables according to their variation, informing which variables are most representative for the entire data set. Firstly, we conducted cluster techniques (UPGMA) by employing the dissimilarity index of the Euclidean Distance (quantitative indicator) to analyze temporal patterns of strong bleaching between months. Moreover, SIMPROF was used to analyze significant differences (P< 0,05) between groups of months generated by the cluster technique. Secondly, the environmental factors (SST, wind speed, irradiance, Kd_{490}, and rainfall) and strong coral bleaching were normalized before proceeding to PCA. For those statistical routines, the software Primer 6.0 (*Plymouth Routines in Multivariate Ecology*) and PAST 4.08 were used. Finally, we used a general linear model (GLM) to predict the possibility of strong bleaching. This analysis was made on the R program version 4.1.2 was used. The generalized additive model (GAM) was not used because we did have data enough to conduct this type of statistical model.

3.7 Results

3.7.1 Size class and coral healthy conditions

We analyzed 2,880 *S. stellata* colonies and most of them (93.42%) fit on the first size group (2-10 cm), 5.44% on second group (11-20 cm), 0.77% (21-30 cm) and 0.37% on the last group (31-40 cm) (Figure 10). This pattern is persistent along with the three-year research when the first size group remains abundant which shows the stability of the monotypic population dominated by young coral colonies (Appendix B, Table S2). Moreover, we found a small number (~ 1%) of larger and older colonies (>20 cm). The encrusting and low-relief colonies shape a monotypic flattened coral seascape that persists along the 3 years (Figure 9; Appendix B, Table S2).

Figure 10 - Percentage of colonies per size category (%) of the coral *S. stellata* in a tropical marginal reef (SW Atlantic, Brazil).
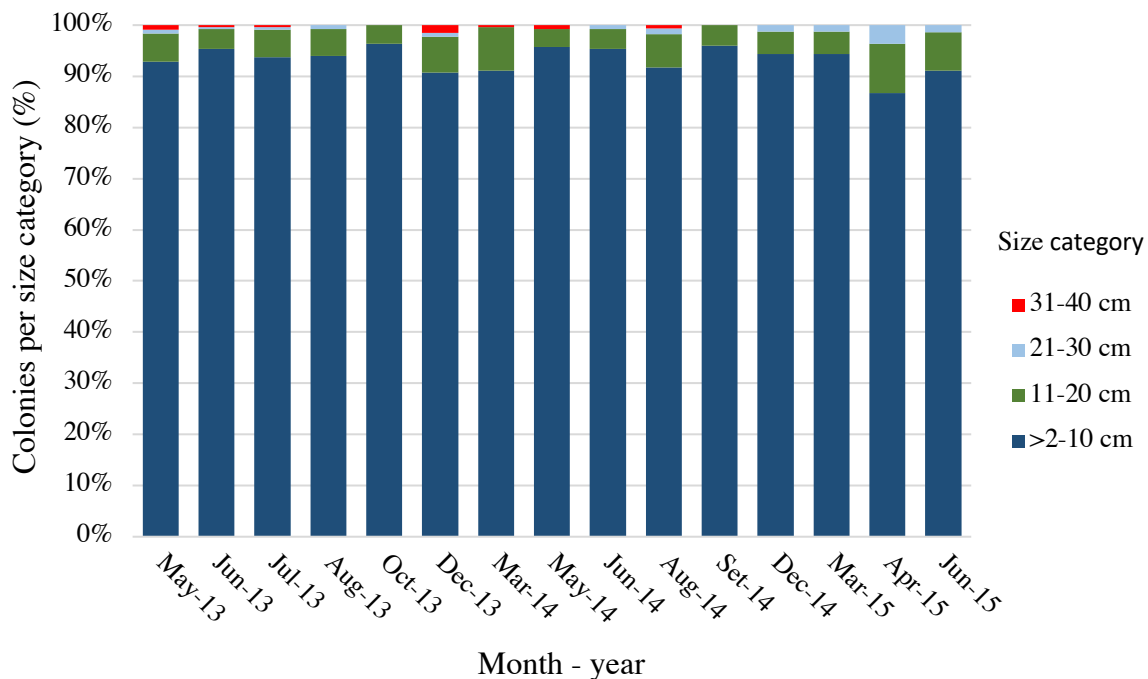
Source: author

The first size group (2-10 cm) also had the most bleached colonies. Overall, over the years, most of these young colonies suffered strong (15%) or moderate (51%) bleaching

(Appendix B, Table S3). The percent of fully bleached colonies (Figure 9A and B) was highest in May and June (2013) and June 2015 (Figure 11). The highest frequency under normal color conditions was in July (2013), March (2014), and December (2014). We found in these months more than 50% of coral colonies were fully pigmented (Figure 11). The results highlight the persistence of chronic bleaching (strong and moderate) throughout the years (2013 to 2015) with variable frequency (44% to 84%) (Figure 11; Appendix B, Tables S1 and S2).

Figure 11 - Coral bleaching of *S. stellata* in a tropical marginal reef region (Equatorial SW Atlantic, Brazil). Figures show the percent (%) of colonies in the category (healthy, moderate bleaching, and strong bleaching) in distinct months and years between May 2013 and June 2015.

	May-13	Jun-13	Jul-13	Aug-13	Oct-13	Dec-13	Mar-14	May-14	Jun-14	Aug-14	Sep-14	Dec-14	Mar-15	Apr-15	Jun-15
☐ Strong bleaching	34%	30%	9%	4%	11%	6%	2%	14%	11%	7%	7%	9%	5%	9%	28%
☐ Moderate bleaching	50%	42%	39%	50%	54%	61%	44%	57%	54%	64%	58%	35%	52%	61%	56%
☐ Healthy	16%	29%	52%	46%	35%	33%	54%	29%	35%	30%	35%	56%	43%	30%	16%
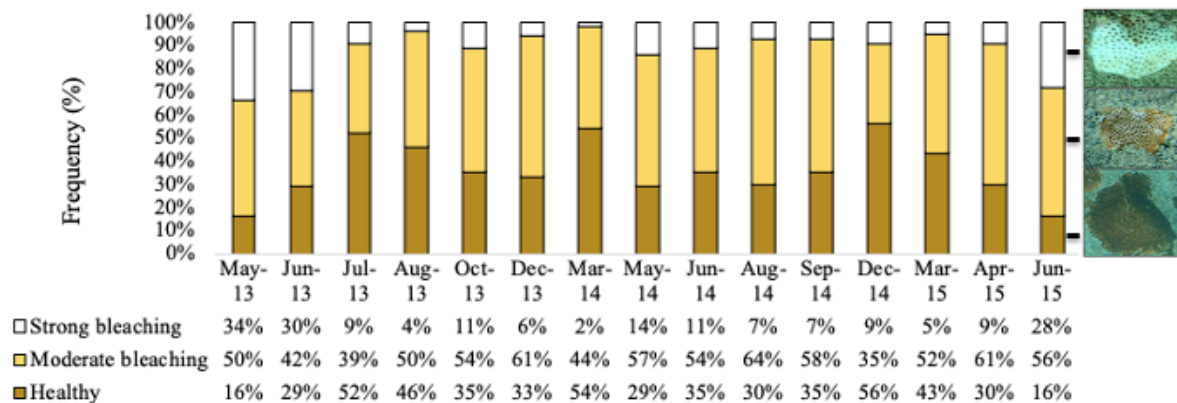
Source: author

3.7.2. Strong bleaching and environmental drivers

The cluster analysis using the variable strong bleaching (fully bleached colonies) showed three main groups (Figure 12). Group A includes the months that have the higher number of fully-bleached colonies and occur only in the rainy period. Group B includes the months with intermediate levels. Finally, group C includes the months with less fully-bleached colonies.

Figure 12 - Representative cluster of months based on variable "strong bleaching" of *S. stellata* colonies in a tropical marginal reef (SW Atlantic, Brazil). A = months with higher fully-

bleached colonies (~ 28 to 34% of colonies are fully bleached). B = months with intermediary levels (~9 to 14% of colonies are fully bleached), and C = months with less fully-bleached colonies (~2 to 7% of colonies are fully bleached).
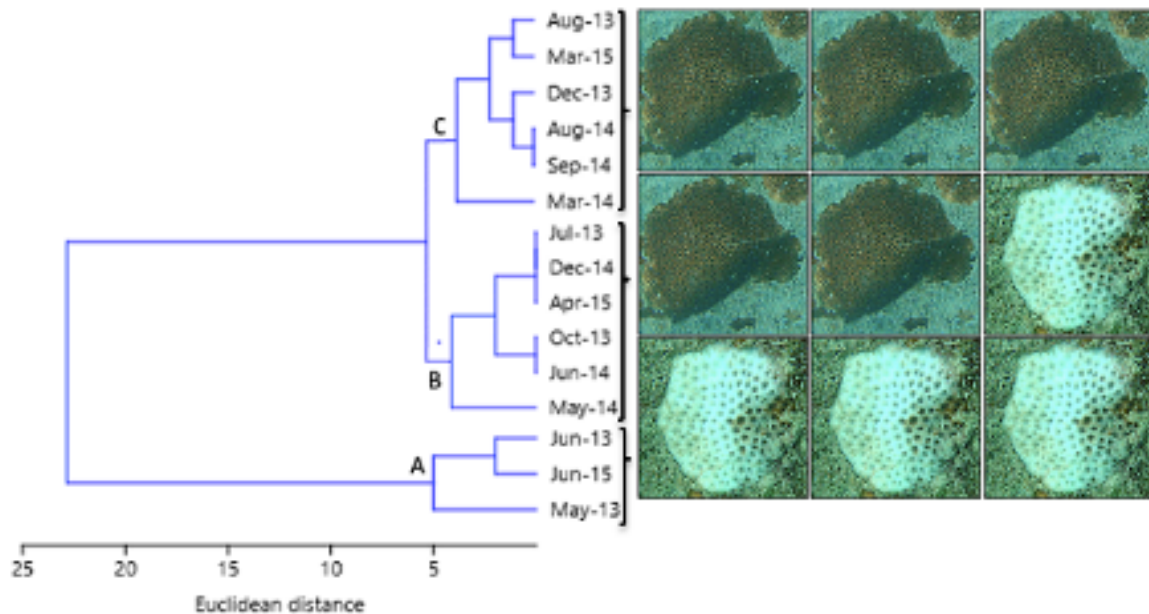
Source: author

Concerning the environmental factors in this marginal reef region, the results indicate that there were no significant anomalies (-0.08 to 0.61) in sea surface temperature (SST). The SST (26.6 °C to 29.3 °C) showed low inter and intra-annual variation (< 3ºC) in this low-latitude region. In the 2013-2015 period, SST displayed a seasonal pattern, with an increase in the first half-year (rainy season) and a slight decrease in the second half-year (Appendix B, Table S1). Other thermal indicators were also assessed, DHW showed low values (< 4), and marine heatwaves were not reported for the turbid-zone reef during the three-year research.

Daylight per month (solar irradiance) varied a minimum of 170.6 hours in March (2015), during the rainy season, to a maximum of 294.4 hours in October (2013) in the dry season (Appendix B, Table S1). Overall, the rainy months had less solar irradiance (170.6 to 242.6 hours/month) and lower wind speed (1.77 to 3.02 m.s^{-1}) than the dry months (solar irradiance = 268.7 to 294.4 hours/month and wind speed = 3.27 to 3.88 m.s^{-1}). (Appendix B, Table S1). Turbidity, represented through Kd_{490}, ranged from 0.06 (May 2013) to 0.16 m^{-1} (April 2015) (Appendix B, Table S1). In general, lower turbidity values are obtained in the first semester under the worst drought cycle and high values are recorded in the dry season (second semester).

In the Principal Component Analysis - PCA (Figure 13), the two first axes explained 83.44 % of the total variation of environmental factors and coral bleaching. Axis 1 (61.22 %) was negatively correlated with wind speed (r = -0.48) and irradiance (r =- 0.49), and positively correlated with rainfall (r = 0.48), SST (r =0.41) and Kd_{490} (r=0.33). Axis 2 (21.84%) was negatively correlated with Kd_{490} (r = -0.54) but positively correlated with severe bleaching (r = 0.82) (Appendix B, Tables S4 and S5).

Based on the differences between environmental variables and bleaching, three distinctive and significant groups (SIMPROF, p < 0.05) were revealed (Figure 13). Regarding how such clusters are distributed on the factorial plane of PCA, it can be observed that Group I is formed by months in the dry period (Figure 13) and is more related to higher solar irradiance and wind speed (Appendix B, Table S1).

Figure 13 - PCA (Principal component analysis) on severe coral bleaching of *S. stellata* and environmental factors (wind speed, irradiance, rainfall, Kd_{490}, and SST – Sea surface temperature) in a tropical marginal turbid-zone reef region (SW Atlantic, Brazil).
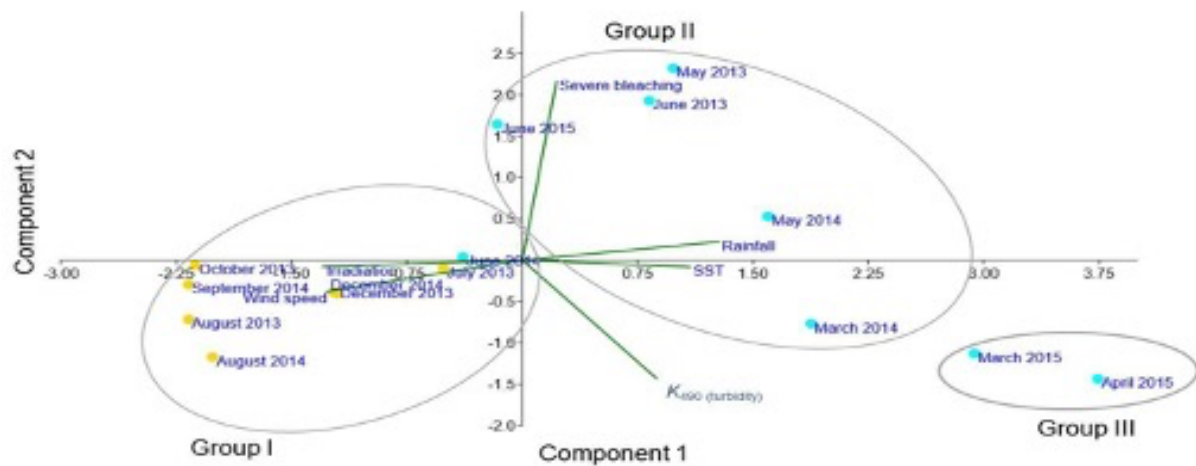
Source: author

Group II is formed by months in the rainy period (Figure 13) and was distinctive from the other groups due to intermediary levels of rainfall, intermediary levels of irradiance, and most of these months (except March 2014) had high levels of severe bleaching (9 to 34% of fully bleached colonies) (Appendix B, Table S1). In this regard, the extreme part of axis 2 shows May 2013, June 2013, and June 2015, which had the highest severe bleaching (28, 30, and 34% of colonies), among the lowest turbidity (0.06, 0.07, and 0.06.), (Appendix B, Table

S1). In the lower part of the axis are shown the months March and May (2014) near the arrows of Rainfall and SST. In these highest rainy months, we found higher sea temperatures (28.86 and 29.29 ºC) but low levels of irradiance due to the cloudiness (Appendix B, Table S1). Also, this part of the PCA showed the month of March 2014 when was found the highest SST (29.29 ºC) but paradoxically the lowest bleaching rate (only 2% of coral colonies are fully bleached) (Figure 13; Appendix B, Table S1).

Finally, the PCA (Figure 13) showed that group III (extreme part of axis 1) encompassed only two rainy months (March and April 2015). This group was related to the most intense rainfall months along the research (352 and 421.5 mm/month), lowest irradiance, highest Kd_{490} (1.2 and 1.6 m^{-1}), and low levels of severe bleaching (5 and 9% of fully bleached colonies). In this way, the highest turbid waters are coincident with the highest precipitation probably due to the concentrated and episodic continental runoff (Appendix B, Table S1).

GLM analysis showed a significant interaction between SST anomalies and turbidity. The statistical model using these factors was able to explain 29% of the strong bleaching phenomenon on colonies studied during the 2013-2015 years. Considering our data, environmental conditions of low turbidity and rise of SST anomalies are linked to strong bleaching suggesting there is a higher probability to occur bleaching when turbidity decrease (Figure 14).

Figure 14 - Generalized linear models (GLM) for the relationship between SST anomaly and diffuse light attenuation coefficient at 490 nm (Kd_{490}; turbidity) over strong bleaching probability.
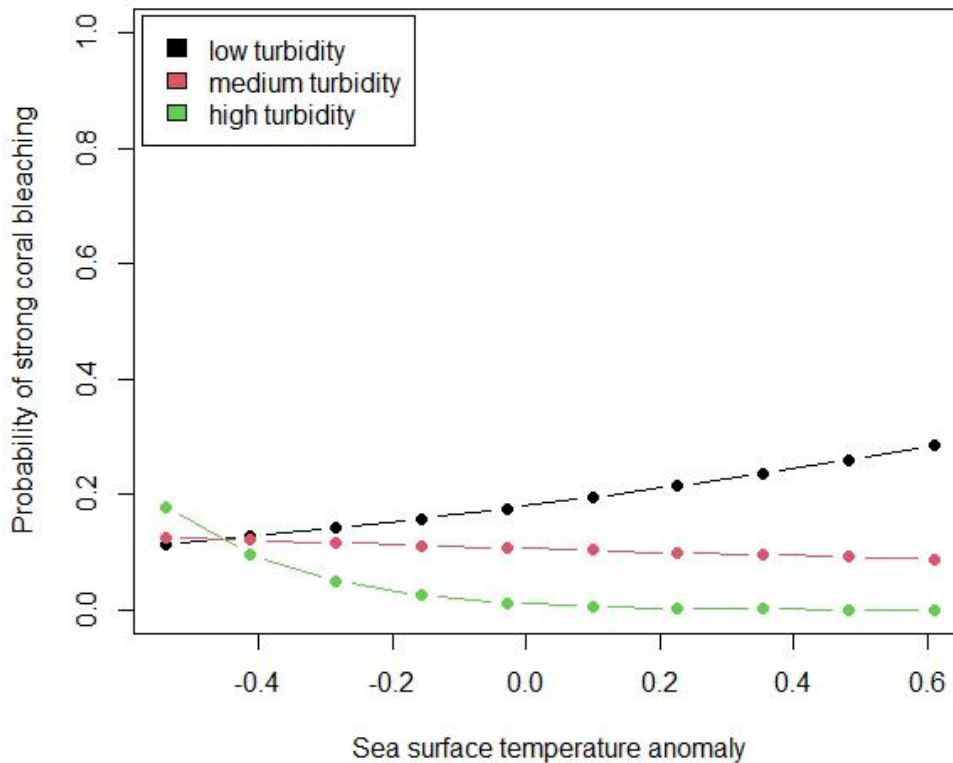
3.8 Discussion

3.8.1 Small-sized colonies and persistence of a unique and resilient coral

We observed a significant number of coral colonies of *S. stellata* fitting in the first size group along the 3 years of monitoring. Moreover, we found a small number of larger and older colonies. This result showed that the population is composed and maintained by young individuals. Size matters in these clonal organisms, being the larger colonies that invest more energy in reproduction and may spawn a larger quantity of potential recruits (COMA et al., 1995; TSOUNIS et al., 2006). Some of the main factors that allow this coral to thrive in marginal environmental conditions analyzed in this study are the gonochoric brooding reproductive strategy, small colony size, high-stress tolerance, and high recruitment rates (LIRMAN; MANZELLO, 2009; OIGMAN-PSZCZOL; CREED, 2011).

The number of oocytes produced per polyp in this weedy coral is highly variable, being always greater in larger colonies, averaging eight oocytes per polyp (LINS-DE BARROS et

al., 2003). Large colonies are the main contributors of the population dynamics not only in local patches but also as exporters of larvae or propagules (BRAMANTI et al., 2016). In *S. stellata*, colonies larger than 5 cm in diameter have at least one oocyte per polyp (LINS-DE BARROS et al., 2003), which means that they can hardly maintain the local patch from which the gonadal output is coming (TSOUNIS et al., 2006). Thereby, the size category distribution of *S. stellata* can be considered to be representative of a non-mature population, with the overall high frequency of colonies with diameters lower than 10 cm (COMA et al., 1995). This result is distinct from more large-sized populations of this coral found in the only ocean atoll in SW Atlantic under clear waters (PINHEIRO et al., 2017), in mesophotic coral ecosystems (SOARES et al., 2018a), and in a subtropical reef in Rio de Janeiro (Brazil) under upwelling conditions (OIGMAN-PSZCZOL; CREED, 2011; TUNALA et al., 2019). All of these examples are representative of more mature and older populations in the tropical South Atlantic.

Oigman-Pszczol and Creed (2011) and Barros et al. (2021) observed a large number of young *S. stellata* colonies in marginal reefs (e.g., intertidal habitats and tide pools) in the SW Atlantic. This species tends to reproduce early and incubate larvae (LINS-DE-BARROS; PIRES, 2006) that are a survival strategy (SOARES et al., 2019). This population is probably characterized by short life spans in this turbid-zone reef. Small colonies are considered advantageous during bleaching events, modeling studies on repeated bleaching episodes suggest that small colony size will be favored (van WOESIK et al., 2012; RIEGL; PURKIS, 2009; RIEGL et al., 2013).

The dominance of young corals may be a response at the population level in face of marginal environmental conditions such as moderate turbidity levels, significant sedimentation inputs, and extreme variability of solar irradiance and rainfall (MARENGO et al., 2016; SOARES et al., 2019). Besides that, we did not observe dead old *S. stellata* colonies in this marginal reef region. The environment seems to have formed recently without time to create huge colonies and with small colonies surviving on stressful suboptimal conditions, including that they do not allow other coral species to thrive besides *S. stellata*.

The genus *Siderastrea* comprises coral species that are abundant, widespread, and major reef-builders in the Atlantic (LEÃO et al., 2016a). The major reef-building and weedy coral *S. stellata*, analyzed here, is resistant to chronic and acute factors (turbid waters, wave action, temperature anomalies, and sediment resuspension), they may recover from the partial burial (TUNALA et al., 2019) and is considered an indicator of stressful conditions (OIGMAN-PSZCZOL; CREED, 2011; PORTUGAL et al., 2016). The reef studied does not have a high

complexity structure and colonies of *S. stellata* are positioned vertically about the main substrate (Figure 2). Structural complexity is a critical factor to support ecological processes such as reproduction (recruitment), predation, and competition (WILSON et al., 2006; GRAHAM; NASH, 2013). Besides that, complex reefs through microhabitats can moderate environmental conditions such as light, water flow, burial, and predators (GALLAGHER; DOROPOULOS, 2017; JOHANSEN; BELLWOOD; FULTON, 2008; DIPERNA et al., 2018).

Frequent bleaching events may minimize the time available for reef-building corals to recover to disturb and can lead to their mortality (HUGHES et al., 2018). According to this hypothesis, Brown (1997) suggested that exposure of corals to frequent stressors can reduce their susceptibility to bleaching. Frequent bleaching events along the years and the presence of regular marginal conditions render the coral host studied here a potential to resist bleaching related stress by shuffling their symbiotic algal partner (BUDDEMEIER et al., 2004), acclimatizing to the environmental stress (OLIVER; PALUMBI, 2011; MANIKANDAN et al., 2016), and compensating energy inputs with heterotrophy (TUNALA et al., 2019). In general, it has been shown that prolonged perturbations reduce the capability of the anthozoans populations to maintain their older and more mature colonies (GÓMEZ-GRAS et al., 2021), being the patches dominated by younger colonies.

Some of the keys to understanding the persistence against repeated bleaching of these mixotrophic stress-tolerant corals analyzed here are the photobiological adaptations and the heterotrophic inputs. Some of the dominant corals (e.g., *S. stellata*) (MIES et al., 2018; ROSA et al., 2018) in SW Atlantic nearshore turbid-zone reefs can incorporate a greater proportion of carbon via heterotrophy when more food is available, and under high turbidity conditions (MIES et al., 2018). In this regard, photosynthesis in the genus *Siderastrea* provides between 75 and 95% of its nutritional needs, and the remaining can be obtained by capturing organic particles such as plankton and detritus with its tentacles (TUNALA et al., 2019) in their small polyps (LEÃO et al., 2016a). This may represent a non-negligible heterotrophic input, as it has been observed in other tropical anthozoans during a seasonal cycle (ROSSI et al., 2020). The diversity and density of zooplankton organisms and detritus in the study site (see plankton data on Soares et al. 2018b) may also be used by this coral to offset reduced photosynthetic rates during the repeated and severe bleaching recorded in our results. Even if densities are low compared to other systems (0.01 to 21.03 individuals/m^3, SOARES et al., 2018b), this may be an important source of carbon and other nutrients for the suspension feeding communities. Because we don't have a clear picture of the seasonal cycles (ROSSI et al., 2020) and the

importance of available organic matter in pulse-like shirt time cycles (ROSSI and RIZZO 2021), is possible that we need a more complete scenario to understand the real importance of autotrophic and heterotrophic inputs in such species to clarify the survivorship of the populations.

3.8.2 Environmental drivers of the sustained and severe bleaching

The analysis of environmental drivers from 2013-2015 indicates that there were no significant anomalies in sea temperatures but an extreme rainfall deficit. The results highlighted that rainfall episodes, cloudiness (which decrease the irradiance), and shading by turbid waters are key factors to mitigate the bleaching (Appendix B, Figures S2 to S5). In this regard, data were collected across 3 years (2013-2015) during a severe rainfall scarcity, with 30 to 40 % less annual volume rainfall concerning the climatological values from 1950 and 2009 (FUNCEME, 2015). The deficit in this equatorial region, which intensified in 2012 and has extended into 2015, is considered the worst drought period registered in Brazilian history in the area (MARENGO et al., 2016). This dryness is accompanied by a lack of clouds when the corals may be more sensible (SCHEUFEN et al., 2017).

The temporal series (2013-2015) of this study occurred during ENSO years and/or Atlantic Meridional (Interhemispheric) mode (MARENGO et al., 2016). In physical terms, changes in sea surface temperature (SST) in the tropical Pacific manifested as the extremes of ENSO influencing precipitation anomalies in turbid-zone nearshore marginal reefs in the SW Atlantic coast. This happens via changes in the zonally oriented Walker circulation and/or induced by changes in the Atlantic Meridional (Interhemispheric) mode (MARENGO et al., 2016). El Nino conditions and the positive phase of the Atlantic Meridional Mode lead to dryer conditions in the region. These atmospheric systems influence the rainfall regime and, consequently, decrease the precipitation. During the high rainfall episodes in summer (such as March and April 2015), the continental runoff may be high and in short pulses. The input of sediments to the coast increases the turbidity (CACCIAPAGLIA; WOESIK, 2015), shading *S. stellate* corals against heat-light stress. Moreover, the time of total insolation is reduced due to the cloudiness, and also, the wind speed is lower. In this scenario, the favorable conditions for coral bleaching (higher temperatures of summer and calm waters) are reduced by the turbid waters and less solar irradiance due to continental runoff and cloud shading associated with the heavy precipitation (Appendix B, Figure S3). This pattern is observed by low rates of severe

bleaching in March 2014, and March and April 2015. One striking example of this scenario was found in March (2014) when the highest SST (29.29 ºC) occurred but the lowest bleaching rate (only 2% of coral colonies are fully bleached) was found.

In May and June (2013 and 2015) the highest rates of severe bleaching were found. Although these months are usually linked to the rainy period (MARENGO et al., 2016), due to the registered drought there was a reduced rainfall and also continental runoff. Rainfall observations for the months of February to May in the study area show that the years 2013, 2014, and 2015 had a decrease of 40.0%, 24.2%, and 30.1%, respectively, about the historical average. The 2013 year is among the ten driest years since 1951 (FUNCEME, 2015). In this way, reduced rainfall, higher solar irradiance, and lower turbidity are linked to severe bleaching even in *S. stellata* (Appendix B, Figure S2). In other words, extensive drought reduces cloudiness and precipitation, consequently decreasing light-heat protection by turbidity, and increases solar irradiance, rising bleaching rates even in stress-tolerant corals. It has been shown that the rainy period is accompanied by a higher chlorophyll concentration per cell (SCHEUFEN et al., 2017a), which is a response to lower light availability. In order to optimize photosynthetic performance, anthozoans may have a specific seasonal response increasing the photosynthetic capacity (SCHEUFEN et al., 2017a, ROSSI et al., 2020), but if an abnormal rainy period demonstrates to be scarcer in cloud presence, this chlorophyll concentration could be counter-productive, producing significant bleaching in the anthozoan colonies (SCHEUFEN et al., 2017b).

Under turbid-zone reefs, corals are more protected from irradiance effects, because suspended particulate matter blocks and disperses solar radiation (Appendix B, Figures S4 and S5). Our results indicate that solar insolation is one of the most important drivers of coral bleaching in this marginal reef. Baker et al. (2008) mentioned that excessive exposure to solar irradiance (UV and in the visible range) increases oxidizing substances which harm the photosynthesis of *Symbiodinium*, resulting in the bleaching process. Moreover, Costa et al. (2008) suggested that the resistance of *S. stellata* is partially shaped by their association with *Cladocopium* (formerly Clade C), which is considered one of the most bleaching-resistant microalgae groups. This association may help the coral's capacity to reverse bleaching across the 3-years monitoring under drought anomalies events, and promote its high resistance to disturbances in the marginal reef. However, those factors are naturally common in the study site (SOARES et al., 2016), which may have caused acclimatization by the *S. stellata* throughout time to promote their stability and persistence despite the frequent bleaching and harsh environmental conditions detected in the study.

Another important aspect is that shallow regions like the study area (between ~ 2-7 meters in depth) may receive higher solar irradiance, however, the suspended amount of particulate matter in the water column is variable in the study site due to turbid waters, wind speed, and resuspension of sediments (SOARES et al., 2016). This pattern is also found in other marginal turbid-zone reefs in the world's oceans (BROWNE et al., 2015; CACCIAPAGLIA; WOESIK, 2015).

We also found that during the dry season (August to November) severe bleaching is overall low in the region despite intense solar irradiance. The stronger winds present during this period increase the turbidity due to sea agitation. Stronger winds end up keeping particulate matter and sediment suspended (KNOPPERS et al., 1999; SAUERMANN et al., 2003) providing shading to corals. This is favorable to coral health because it works as a physical barrier preventing the penetration of UV solar radiation (BAKER et al., 2008) for turbid-tolerant corals such *S. stellata* (SOARES et al., 2019). Therefore, stronger winds are possibly unfavorable to bleaching as noted in PCA and GLM analysis because it protects corals against irradiance.

Coral bleaching associated with the first semester (summer in the Southern Hemisphere) is a phenomenon that has been observed in the South Atlantic (FERREIRA et al., 2013; BANHA et al., 2019; TEIXEIRA et al., 2019). In general, it is commonly reported in February and March (austral summer). Differently, bleaching was reported both in the first and second semester in our study site. The first months of the year are usually linked to bleaching events because have higher average temperatures and occasionally show SST anomalies during strong ENSO events (TEIXEIRA et al., 2019, GASPAR et al., 2021). We did not find significant SST anomalies or MHW events throughout 2013-2015. We found bleaching over the years, especially during months with higher solar irradiance, calm winds, and less turbid waters. Published results (KRUG et al., 2012; SOARES et al., 2019) and also the results exposed in this study indicate these corals are vulnerable to bleaching during periods of clear sky (low cloudiness), rainfall scarcity, weak winds, and less turbid waters, which maximize the negative effects of irradiance.

3.9 Refugia potential and final remarks

Our results suggest that the sea temperature is not always the only important driver of coral bleaching. These results highlight the resistance of *S. stellata* coral and also suggest that this turbid-zone reef may be a refuge site only for this species. Refuge sites are areas that

maintain good conditions previously lost in other places (KAVOUSI; KEPPEL, 2018). The bleached colonies throughout the years indicate that the reef is under recurrent stress. However, this population remains abundant and is the only coral species to compose this monotypic seascape with encrusting (low-relief) colonies.

The resistance and stability of *S. stellata* in the SW Atlantic are also found in tide pools in sandstone reefs (PORTUGAL et al., 2016), nearshore Brazilian turbid-zone reefs (LEÃO et al., 2016a), the only atoll in South Atlantic (PINHEIRO et al., 2017), and even under upwelling waters in high-latitude reefs (TUNALA et al., 2019). This coral is less susceptible to the effect of siltation and resuspension of sediments (MENEZES et al., 2014), and belongs to a genus capable of actively removing sediments (LIRMAN; MANZELLO, 2009), which also explains our results and their persistence and stability in turbid-zone marginal reefs of SW Atlantic (LEÃO et al., 2016a) with the absence of mass mortality even after severe bleaching events along the previous 3 decades (MIES et al., 2020).

The increase of warming and heatwaves (MAGRIS et al., 2015) and more intense droughts (MARENGO et al., 2016) predicted for this region in this century cast doubt about their capacity to act as climate-change refugia. Thus, in warmer and drier weather, the SST anomalies, high insolation, and lower cloudiness (MARVEL et al., 2019) would have severe and cumulative impacts and raises a question about the limits of coral tolerance to cope with this increasing stress in shallow waters and acting as a long-term climate-change refugia (SOARES, 2020). Distribution projections for *S. stellata* show that under relative concentration pathway (RCP) scenarios this species will be its future area altered. Under the critical RCP 8.5 scenario, *S. stellata* will probably lose this currently suitable marginal reef region with the retained area only between 1.5 to 11 ºS limits (PRINCIPE et al., 2021). Moreover, losses of *Siderastrea* are expected along the SW Atlantic coast in all scenarios (RCP 2.6, 4.5, and 8.5), and this loss is critical in the worst greenhouse emission scenario (RCP 8.5) (PRINCIPE et al., 2021). Despite the importance of understanding the spatial and temporal patterns of bleaching (HUGHES et al., 2018), the effects of the higher temperatures combined (or not) with drought anomalies on the health status of corals are overlooked.

Our results highlight the importance to conduct further investigation overseas in optimal and marginal conditions to understand the effects of drought anomalies combined with a warmer ocean and the repercussions on the climate-change refugia sites. Research in scarcely known present-day marginal reefs is important to understand the coral resistance (PERRY; LARCOMBE, 2003; CAMP et al., 2018) to provide resilient-based management of tropical reefs (MCLEOD et al., 2019). An in-depth understanding of the importance of the energy

inputs (autotrophic and heterotrophic) is essential to envisage the future of our seascapes (ROSSI et al., 2019), considering that each location will have its own stressing factors.

4 CHAPTER III

Trophic ecology of dominant zoantharians on Western Atlantic reefs: a review

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4.1 Hypothesis

We will conclude with chapter 3, where a review of the trophic ecology of the zoantharians *Zoanthus sociatus*, *Palythoa caribaeorum,* and *Palythoa variabil*is, common in the Western Atlantic, will be presented. For this chapter we consider the following hypothesis: trophic ecology could help to understand the resistance and vulnerability of these key zoantharians to environmental stress (e.g., coral bleaching).

4.2 Objectives

4.2.1 General objectives

- To address the trophic ecology characteristics of the zoantharians *Z. sociatus*, *P. caribaeorum,* and *P. variabilis* through an integrative review.

4.2.2 Specific objectives

- To gather the research studies involving the trophic ecology of the species *Z. sociatus*, *P. caribaeorum,* and *P. variabilis;*
- To analyze the previous studies on the trophic ecology of these three species and point out future research directions;

4.3 Abstract

Corals and microalgae (Symbiodiniaceae) live in a symbiotic relationship capable of providing shelter and food for microalgae and energetic molecules to the host. Cnidarians also need to obtain energy through external food, balancing autotrophy and heterotrophy as mixotrophic animals. Most of the research about these trophic ecology trends is conducted on reef-building corals with scarce knowledge of other key reef organisms such as zoantharians. An integrative review was carried out on the species *Palythoa caribaeorum*, *Palythoa variabilis,* and *Zoanthus sociatus* (key zoantharians on West Atlantic reefs) to provide up-to-date information on food sources, interaction with environmental factors, and mixotrophic strategies. We identified that these soft corals are at consumer trophic levels. *Z. sociatus*

showed greater uptake of detritus, while *P. caribaeorum* used more phytoplankton and zooplankton as a heterotrophic source of food. In other words, indicate that *Z. sociatus* has a preference for detritus and *P. caribaeorum* has a preference for live prey. We noticed that *Z. sociatus* is essentially autotrophic while *P. caribaeorum* and *P. variabilis* are primarily heterotrophic. There are differences in the trophic plasticity of each species according to their zonation on reef (tidal pools, intertidal and subtidal zone). The availability and quality of food in intertidal and subtidal reefs drive the feeding strategies of *P. caribaeorum* and *Z. sociatus.* *P.variabilis* has the major heterotrophic potential among the zoanthids analyzed in this review, but its information is scarce. We suggest that *Z. sociatus* is most vulnerable to severe and repeated bleaching due their higher autotrophic dependence, being *P caribaeorum* and *P. variabilis* more tolerant to ongoing thermal stress events, explaining their dominance in phase-shifting reefs. We suggest long-term investigations to understand the issues associated with the trophic ecology of these soft corals and its link with resilience and survival considering the ongoing global environmental change.

Keywords: feeding behavior; zoantharians; mixotrophy; environmental factors;

4.4 Highlights

- Zoantharians *Z. sociatus*, *P. caribaeorum,* and *P. variabilis* have different trophic ecology strategies;

- *Z. sociatus* seems to use more autotrophic inputs than heterotrophic;

- *P. caribaeorum* and *P. variabilis* seems to be mainly heterotrophic feeders;

- Climate change may have different consequences for these reef species due to their different ways to obtain energy;

4.5 Introduction

The mutualistic interaction between corals and microalgae plays a crucial role in nutrient-poor waters, influencing the historical process that allowed persistence and carbonate construction of tropical reefs (HIXON and MENGE, 1991; VYTOPIL and WILLIS, 2001; ZHANG et al., 2022). This relationship allows the cnidarians hosts to use energy molecules produced by photosynthetic endosymbionts algae (DAVY, ALLEMAND & WEIS, 2012;

FERRIER-PAGÈS et al., 2021). However, all cnidarians need to acquire food from an external source, in this case, suspended organic particles and plankton through their oral tentacles (DE SANTANA et al., 2015). This mixed trophic strategy (autotrophy and heterotrophy) is called mixotrophy and several cnidarians, especially in shallow tropical nutrient-poor waters, such as scleractinians, hydrocorals, and zoantharians are mixotrophic (HOOGENBOOM, RODOLFO-METALPA and FERRIER-PAGÉS, 2010; TEECE et al., 2011; MIES et al., 2018; ROSSI et al., 2020).

The energy input from autotrophy and heterotrophy for cnidarians are relevant to understanding aspects of survival, changes in benthic cover, and dominant organisms in tropical reefs (SCHUBERT et al., 2017). Drastic changes on benthic cover could occur due global environmental changes (HUGHES et al., 2018; MCCAULEY and GOULET, 2019) and dominance of soft corals (e.g., octocorals and zoantharians) to the detriment of reef-building corals (e.g., scleractinians) are recently observed in South Atlantic (CRUZ et al., 2015ab; LONZETTI, VIEIRA and LONGO, 2022) and Caribbean reefs (RUZICKA et al., 2013; ROSSI et al., 2018; LASKER et al., 2020). Furthermore, the food plasticity presented by cnidarians is a key factor because it can help in the resistance and recovery of these organisms during and after bleaching events (HELMUT et al., 2006; WIEDENMANN et al., 2012). Nutrients and energy are supplied by both the autotrophic and heterotrophic pathways however the autotrophy is impaired during bleaching and the heterotrophy may become the main source of energy at this time, decreasing population mortality (CONTI-JERPE et al., 2020). These fluctuations between the use of autotrophy and heterotrophy can occur due to the phenomenon of bleaching (HIBINO et al., 2013; SANTOS et al., 2021), exposure to air (LEAL et al., 2015; ROSA et al., 2016), nutrient discharge (LEAL et al., 2017), type of endosymbiont (SCHEUFEN, IGLESIAS-PRIETO and ENRÍQUEZ, 2017), turbidity (ANTHONY and FABRICIUS, 2000) and heat-light changes (TITLYANOV et al., 1996; FERRIER-PAGÈS et al., 2011).

Studies on the trophic ecology of cnidarians have been carried out since the year 1910 (SOROKIN, 1993), mainly in scleractinians and hydrocorals (WELLINGTON, 1982; DAVIES, 1984; COMA et al., 1999) with scarce knowledge on other key reef organisms such as octocorals and zoantharians (RAMSBY et al., 2014; ROSSI et al., 2018; MCCAULEY and GOULET, 2019; LEAL et al., 2017; ROSA et al., 2018). Among several methods, visual observations, gastric content dissection, and more recent analysis of stable isotopes of carbon (C: ^{12}C, ^{13}C, ^{14}C) and nitrogen (N: ^{14}N, ^{15}N) and fatty acid composition have been used to improve knowledge on this topic (BENSON et al., 2006; BLESSING et al., 2009; HUNKELER

et al., 2008; AELION et al., 2010; DE SANTANA et al., 2015). These approaches could help to understand trophic ecology aspects such as food identification, feeding behavior, trophic level, mixotrophy, the influence of environmental factors on feeding strategies and the structure tropical reefs food webs including in zoantharians.

Zoantharians belong to the class Anthozoa, the largest class in the phylum Cnidaria. The order Zoanthidae is characterized by soft-bodied individuals with two rows of oral tentacles and clonal polyps (DALY, FAUTIN & CAPPOLA, 2003). Zoantharians are found throughout the equatorial and subtropical range, mainly in intertidal zones, having a high degree of mutualism with symbiotic algae. Furthermore, these have been associated with benthic cover changes in reefs worldwide (REIMER et al., 2021; SOARES et al., 2022). In this regard, their abundance relative to reef-building corals was realized detected especially in Southwestern Atlantic reefs where true phase-shift are detected (CRUZ et al, 2015; REIMER et al., 2021). Due to their occurrence in reefs in the intertidal and subtidal zone, these cnidarians must have developed plastic characteristics relevant to their occupation in these distinct habitats (RABELO et al, 2014; RABELO et al 2015). In these harsh environments, there is the influence of low and high tides, higher salinities, intense solar radiation, temperature variability, and periodic sedimentation events (SOARES et al., 2022). Furthermore, it is considered that the form of energy acquisition is a key factor to understand questions about the resistance and survival of these organisms (FERRIER-PAGÈS et al., 2011; BAUMANN et al., 2014: LEAL et al., 2014a), especially in marginal reef environments (SOARES, 2020b; BURT et al., 2020). However, little is known about autotrophy and heterotrophy in zoantharians.

The South Atlantic reefs have a different benthic composition when compared to the Pacific and Caribbean reefs. They are formed by a few species of reef-building corals such as scleractinians and hydrocorals (23 species) and with a high degree of endemism (FERREIRA and MAIDA, 2006). In addition, they occur in marginal conditions such as high nutrient content, moderately turbid waters, and high sedimentation rates (CASTRO and PIRES, 2001; SOARES et al., 2016). The cover of these reefs is naturally dominated by macroalgae and zoantharians, which may represent more than 50% of the benthic cover (FRANCINI-FILHO et al., 2013; ACOSTA and GONZALEZ, 2007; CRUZ et al., 2015). Among the dominant zoantharians with wide distribution in the South Atlantic Ocean, we have *Palythoa variabilis* (Duerden, 1898), *Palythoa caribaeorum* (Duchassaing & Michelotti, 1860), and *Zoanthus sociatus* (Ellis and Solander, 1786) (Figures 14 and 15) (Soares et al., 2022).

Figure 15 - Distribution of the zoanthids *P. variabilis*, *P. caribaeorum,* and *Z. sociatus* along Western Atlantic Ocean. Sources: Santos et al. (2016, 2019); Soares et al. (2022).
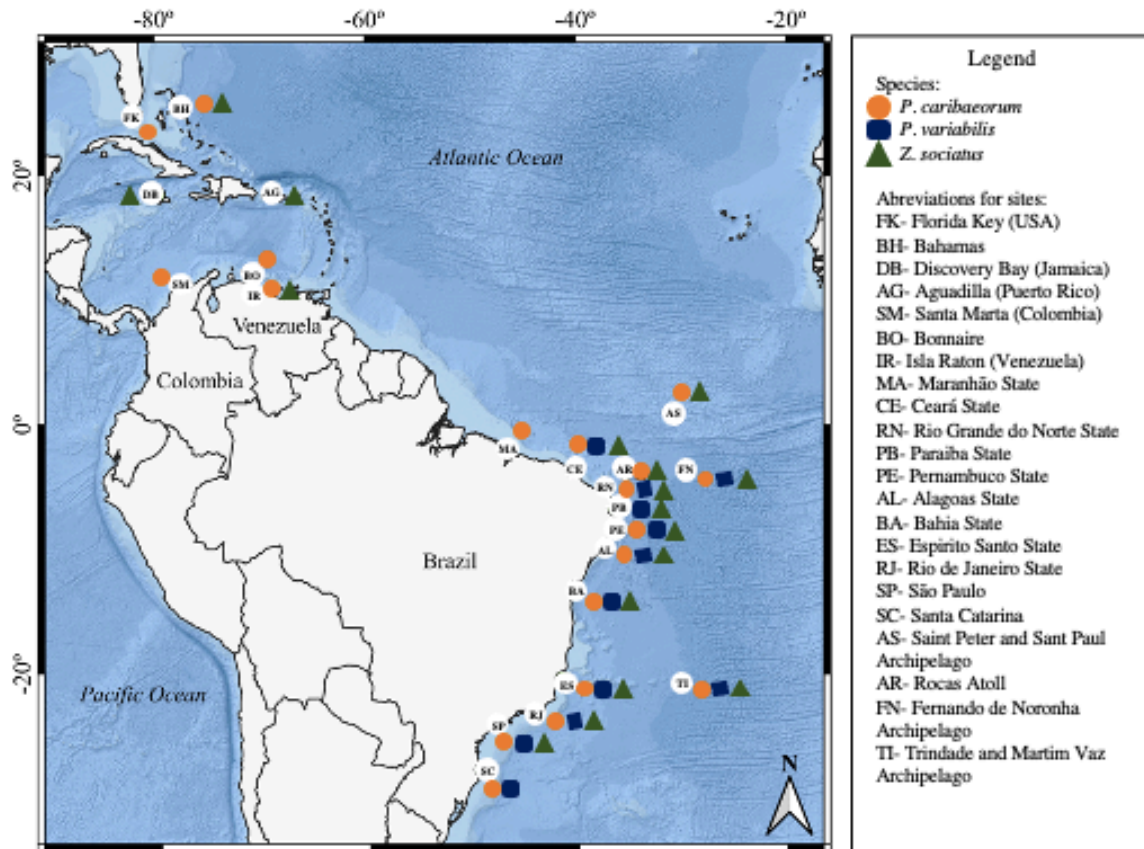
Source: author

These three zoantharians are also common on Caribbean coral reefs, but with less dominance or records (Fig 14). In this context, these zoantharians play a key role in the food webs and associated biodiversity in the Western Atlantic, and their contribution to the reef functioning is underestimated (CRUZ et al., 2015, 2016; REIMER et al., 2021; SANTOS et al., 2021). Thus, up-to-date, information on the trophic ecology of dominant zoantharians has global relevance due to their wide distribution in reef ecosystems. The objective of our perspective article is to review the scientific knowledge on the trophic ecology of the key zoantharians *P. variabilis*, *P. caribaeorum,* and *Z. sociatus* (Figures 14 and 15). This will be done through an integrative review to provide synthetic information that allows the understanding of the current knowledge on the trophic performance and position of these species in the reef food webs. Moreover, this information could help to provide insights on the response of these organisms to environmental changes (e.g., warming waters, associated

bleaching events, nutrient loads, etc.), and identify the gaps in knowledge about their trophic ecology, pointing to future research investigations.

Figure 16 - Dominant zoantharians in South Atlantic. *P. caribaeorum* colonies on the edge of intertidal reefs (A); a colony of *Z. sociatus*, in the upper part with emerged polyps and the lower part with submerged polyps and their tentacle crowns exposed (B); a colony of *P. variabilis* (C). Images from intertidal reefs in northeastern Brazil (Ceará coast).
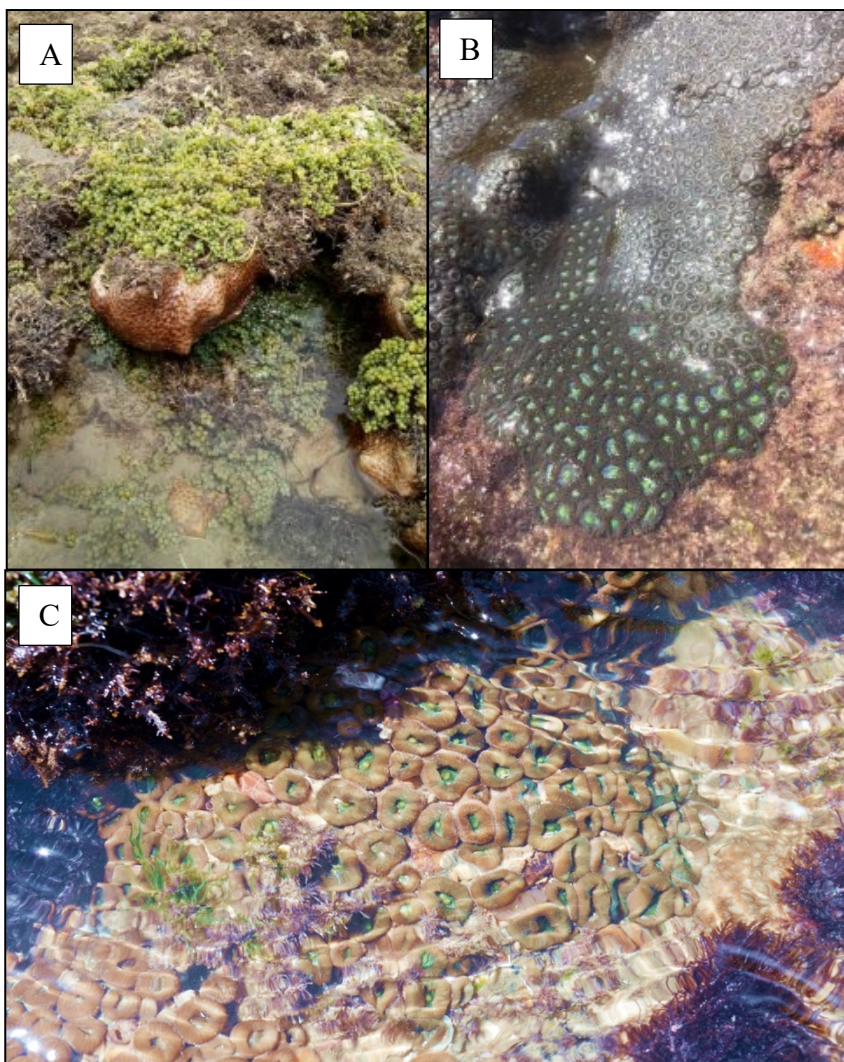
Source: author

4.6 Material and Methods

Our integrative review and perspective article is based on the core question "What are the characteristics of the trophic ecology of the zoantharians *Palythoa variabilis*, *Palythoa caribaeorum,* and *Zoanthus sociatus*?" which guided the analysis of the literature currently published. These three species were chosen due to their abundance and wide distribution (Figure 14) in the West Atlantic reefs (i.e., Southwestern Atlantic and the Caribbean Sea). To answer this main scientific question, we used PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) methodological approach. In this regard, a protocol was developed to improve the reporting of this review (PAGE et al., 2021). The PRISMA method consists of a 27-item checklist and a flowchart prepared for researchers to develop quality systematic reviews and meta-analyses (PAGE et al., 2021). Bibliographic and transversal research was carried out on this topic through publications of scientific articles available in the following databases: Scopus (https://www.elsevier.com/pt-br), Science Direct (https://www.sciencedirect.com/), Web of Science (https://clarivate.com/webofsciencegroup/solutions/webofscience-platform), and Google Scholar (https://scholar.google.com.br).

The search strategy was formulated with the help of the Peer Review of Electronic Search Strategies (PRESS) (Sampson et al., 2009). We used boolean operators (AND, OR) and keywords in the English language in databases such as *Palythoa variabilis*, *Palythoa caribaeorum*, *Zoanthus sociatus*, trophic ecology, autotrophy, heterotrophy, stable isotopes, fatty acids, feeding, and mixotrophy. No time scale is imposed for this literature search. Eligibility criteria (inclusion and exclusion) are used to carry out a review and these are used to identify and define the articles that will be used (Table 2).

Table 2 - Criteria for inclusion and exclusion of scientific works for the literature review used in this article (Based on Lawn & McFarlane, 1991; Goldberg, 2018).

Inclusion	Exclusion
Original scientific studies: articles, master thesis and PhD thesis	Scientific studies: abstracts in congresses
Articles involving the following species: *P. variabilis*, *P. caribaeorum* and *Z. sociatus*	Articles that not analyze the zoantharian species defined here

Source: author

After identifying the eligible studies (Table 2), they were fully read to ensure that they contained the necessary information, and then the data was extracted and the results were synthesized. From the bibliography of selected scientific studies, it was possible to add 2 new studies that were not identified through searching in the databases. These papers were Trench (1974) and Steen and Muscatine (1984). Heterogeneity of the studies was perceived, so we chose to carry out an integrative review. The search found approximately 190 articles however only 16 articles had information about some aspect of the trophic ecology of *P. caribaeorum*, *P. variabilis,* and *Z. sociatus*. The publication of these documents is between the years 1968 and 2021. Information related to eating habits (prey, food selectivity, feeding behavior), trophic level, the influence of abiotic factors on mixotrophy and trophic plasticity were analyzed.

4.7 Results and Discussion

The *Zoanthus sociatus* was the most studied species with nine articles about its trophic ecology. *Palythoa caribaeorum* had eight articles concerning its trophic aspects (Table 2). Only three articles had data on the feeding ecology of *Palythoa variabilis* (the less studied species) (Table 2). Some articles addressed more than one species and technique for studying food habits. Six studies were conducted in the laboratory and ten were performed with *in situ* data.

Table 3 - The number of studies per information category (Eating habits, interaction with environmental factors, trophic level, and mixotrophy) for each zoantharian species: *P. caribaeorum*, *P. variabilis,* and *Z. sociatus*.

	Food habits	Interaction with environmental factors	Trophic level	Mixotrophy	References
P. caribaeorum	8	4	1	1	Lesser et al., 1990; Da Silva, 2021; Junior, 2019; De Santana et al., 2015; Rosa et al., 2016; Vinagre et al., 2018; Santos et al., 2016; Almeida Saá et al., 2020
P. variabilis	-	-	1	1	Reimer, 1975; Steen e Muscatine, 1984; Vinagre et al., 2018

				Junior, 2019; Hadden, 1968; Sorokin, 1991; Leal et al., 2017; Steen e Muscatine, 1984; Rosa et al., 2018; Sorokin, 1993; Trench, 1974; Vinagre et al., 2018
Z. sociatus	7	3	1	3	

Source: author

Food web analysis using stable isotopes in the South Atlantic showed that the species *P. caribaeorum*, *P. variabilis,* and *Z. sociatus* occupy different trophic levels in intertidal reefs. Nitrogen isotope values (δ^{15}N) indicate positions in the food chain structure, a variation from the 2.5 to 4.5‰ increase from prey to predator (OWENS, 1987; POST, 2002). In this regard, *P. caribaeorum* and *Z. sociatus* are at a similar trophic level, with mean values of 7.71 and 7.83 δ^{15}N, whilst *P. variabilis* is placed in a slightly higher trophic level, with a mean value of 9.24 for δ^{15}N. Despite this variation, these species are found at intermediate levels considering the entire trophic chain studied (VINAGRE et al., 2018). They can be considered omnivores, being the heterotrophic food sources a mix between detritus and zooplankton. In this food web, the mean values of nitrogen isotopes for species include it ranged from 3.46 to 12.46 δ^{15}N (VINAGRE et al., 2018). Therefore, the value encountered for *P. variabilis* indicate this species has a more carnivorous behavior respect *P. caribaeroum* and *Z. sociatus*.

4.7.1 Zoanthus sociatus

4.7.1.1 Diet and energy source origins

Z. sociatus is a mixotrophic species and data on its photobiology (abundance of Symbiodinaceae, photosynthesis rate, and respiratory rate) indicate the predominance of the autotrophic pathway (SOROKIN, 1991). The genus *Zoanthus* is characterized by the fact that most of the species do not have a predatory nature (REIMER, 1971b). There are some reports of obtaining food items in the environment for this specie. One of the first studies on the feeding behavior of *Z. sociatus* showed a positive response to sea urchin eggs and a negative response when *Artemia nauplii* and fresh pieces of lobster and crab were offered (TRENCH, 1974). In aquarium experiments, heterotrophic feeding of *Z. sociatus* was measured and food used consisted of fed with *Artemia nauplii*, algae, bacteria, and dissolved organic matter. The assimilation rates of these diets were 176, 372, 370, and 3.750 µg C. g^{-1} dry colony weight. day^{-1} respectively (SOROKIN, 1991). Another study observed the response of *Zoanthus sp.* to

several foods (REIMER, 1971b). Offering and ingestion of live food (i.e., *Artemia nauplii* and adults, polychaetes, nemerteans) and detritus (i.e., fish sticks, artemia adults, and filamentous algae) to *Zoanthus* sp. was observed and the only items ingested were the fish detritus. (REIMER, 1971b).

Polyps of *Z. sociatus* also demonstrated greater uptake of particulate organic matter (POM)/detritus (JUNIOR, 2019). In this regard, individuals had their gastric content analyzed and distinguished between POM, phytoplankton, and zooplankton with abundances of 73.70%, 24.72%, and 1.57% respectively (Table 3) (JUNIOR, 2019), which demonstrates the predominant use of detritus from heterotrophy sources. Biomass of these items were calculated, detritus and phytoplankton had higher importance for carbon contribution to *Z. sociatus*. Moreover, Hadden (1968) also observed the ingestion of non-moving prey and particulate matter by *Z. sociatus*. The behavior to intake of no live prey was suggested because of the few nematocysts content in the tentacles, which are used to capture moving prey (HADDEN, 1968). Besides that, polyps of *Z. sociatus* are smaller when compared to *P. caribaeorum* and *P. variabilis* (SEBENS, 1977; KOEHL, 1977), what can change its capacity to catch food. This can help to understand its little use of external feeding and greater use of autotrophy. Similar to the genus *Palythoa*, excretion occurs approximately 12 hours after food intake (REIMER, 1971b).

Z. sociatus is an essentially autotrophic species, being the species with the highest photosynthesis rate and Symbiodinaceae density among 20 anthozoan species in reefs of Indo-Pacific region (SOROKIN, 1993; LEAL et al., 2017). While the species of genus *Palythoa* sp. are predominantly predators (heterotrophic) (SOROKIN, 1993). Stomachal analysis of 240 polyps of each specie showed lower assimilation of external food items in *Z. sociatus* (625 items) when compared to *P. caribaeorum* (1284 items) (JUNIOR, 2019). This result suggests a different need of detritus, phytoplankton and zooplankton in feeding of *Z. sociatus* and *P. caribaeorum*.

4.7.1.2 Interaction of environmental factors and mixotrophy

The symbiotic algae in *Z. sociatus* can translocate about 95% of the photosynthetic carbon to the soft coral. In this regard, the contribution of these symbionts to energy metabolism is equivalent to 50% of the host (STEEN; MUSCATINE, 1984). In Steen and Muscatine (1984), all colonies were taken from the same environment. However, in other studies, the effect of the habitat has different results to the energetic contribution of the

autotrophic and heterotrophic pathways. In one of these studies, the carbon and nitrogen isotopes were used to understand the trophic ecology in emerged and in tidal pools colonies of *Z. sociatus*. The habitat effect (emerged and in tidal pools) was significant related only to C isotopes with the δ^{13}C signature ranging from 10.68 to 13.96 ‰ (LEAL et al., 2017). Most predominantly autotrophic cnidarians show values of 10 to 16‰ of δ^{13}C. The autotrophic pathway is the main carbon source for *Z. sociatus* both in exposed environments and in tidal pools (LEAL et al., 2017). Possibly, the potential use of autotrophy is associated with the less availability of food for the heterotrophic pathway and factors that favor photosynthesis.

Tidal environments (subtidal, tidal pools and emerged areas) can be related to photobiology changes on photosynthesis rate, symbiotic cells density and quantity of chlorophyll which can disrupt the trophic behavior of corals, and also the composition of food items available for zoantharians (ROSA et al., 2018). *Z. sociatus* in subtidal areas presented lower percentage of the polyunsaturated fatty acids (PUFA) (i.e. 18:4n-3), but a higher percentage of highly unsaturated fatty acids (HUFAs) (i.e. 20:5n-3 and 22:5n-3). In general, the lipids obtained from the autotrophic carbon are mainly composed of SFA and MUFA, the lipids obtained from the heterotrophic carbon are mainly composed of PUFA (YAMASHIRO et al., 1999). In tidal pools and subtidal, the fatty acids considered biomarkers of zooplankton (14:0 C, 16:0 C, 20:1n-9, 20:4n-6 C) were found in higher amounts than in colonies in emerged areas (ROSA et al., 2018). The saturated fatty acids (SFAs) 14:0 and 16:0 together with the monounsaturated fatty acids (MUFA) and 20:1n-9 are biomarkers of copepods (DODDS et al., 2009) while HUFA 20:4n-6 is particulary of cladocerans (KAINZ, BRETT, ARTS, 2009). Fatty acids composed of 18 carbons, characteristic of phytoplankton, were more abundant in *Z. sociatus* emerged colonies during low tide (ROSA et al., 2018). These colonies remained emerged for 3-5 hours in each tidal cycle. Fatty acid 18:4n-3, which is a Simbiodinaceae marker, and composed 16.74, 1.17, and 1.08% of the fatty acids in emerged, tidal pool, and subtidal environments, respectively (IMBS et al., 2010; IMBS; YAKOVLEVA; PHAM, 2010; ROSA et al., 2018). The majority of the FAs characteristics of zooplankton showed a lower percentage in emerged colonies of *Z. sociatus* (ROSA et al., 2018). Thus, tide variations can modify the communities of zooplankton and phytoplankton available for feeding (METAXAS AND SCHEIBLING, 1996), which may change frequency of fatty acids found, and mixotrophy behavior during the day.

Related to trophic level, the information found suggests that *Z. sociatus* is a species positioned at an intermediate level in the food chain. *Z. sociatus* occupies a position above *P.*

caribaeorum and below *P. variabilis*, with an average nitrogen isotope value of 7.83 $\delta^{15}N$ (VINAGRE et al., 2018) (Table 4).

Table 4 - The number of studies for each species *P. caribaeorum*, *P. variabilis*, and *Z. sociatus* and tool used to assess the trophic ecology: stable isotope (C and N) + Carbon content, visual census, fatty acids, stomach analyses, photobiology.

	Stable isotope (C and N) + Carbon content	Visual census	Fatty acids	Stomach analyses	Photobiology	References
P. caribaeorum	1	-	1	2	5	Lesser et al., 1990; Da Silva, 2021; Junior, 2019; De Santana et al., 2015; Rosa et al., 2016; Vinagre et al., 2018; Santos et al., 2016; Almeida Saá et al., 2020
P. variabilis	2	1	-	-	1	Reimer, 1975; Steen e Muscatine, 1984; Vinagre et al., 2018.
Z. sociatus	5	1	1	1	3	Junior, 2019; Sorokin, 1991; Leal et al., 2017; Steen e Muscatine, 1984; Rosa et al., 2018; Sorokin, 1993; Trench, 1974; Vinagre et al., 2018.

Source: author

4.7.2 Palythoa caribaeorum

4.7.2.1 Diet and energy source origins

P. caribaeorum is a mixotrophic species, using both autotrophic and heterotrophic sources. However, the proportion of the use of these energetic ways is still unknown (DE SANTANA et al., 2015). From the analysis of the gut contents in South Atlantic reefs, 13 phytoplankton and five zooplankton taxa were found, in addition to unidentified detritus (DE SANTANA et al., 2015). From those, however, only 8 of these taxa were considered as food items. Among the phytoplankton, the diatoms were the most abundant and frequent. In zooplankton, invertebrate eggs were the most extensive. The size of prey ranged from 6 µm

(cyanobacteria) to 2.18 mm (nematodes). In general, 60% of the food items were smaller than 20 µm. The feeding behavior indicates that, under certain conditions, they use mucus and ciliary apparatus to capture preys that may be ingested with this substance (DE SANTANA et al., 2015).

The genus *Palythoa* is also known for its zooplankton predation rates. The assimilation rates of dissolved organic matter (23 µg C. g^1 dry colony weight. h^{-1}), algae (14.4 µg C. g^1 dry colony weight. h^{-1}), and bacterioplankton (36 µg C. g^1 dry colony weight. h^{-1}) were lower when compared to *Artemia nauplii* (176 µg C. g^1 dry colony weight. h^{-1}) (SOROKIN, 1993). Polyps of *P. caribaeorum* has intermediate height, being taller than *Z. sociatus* and smaller than *P. variabilis* polyps (SEBENS, 1977; KOEHL, 1977). Oral disc of this specie has tentacles less long and distant when compared to *P. variabilis* (KOEHL, 1977). Moreover, food intake starts from chemical stimuli provoked by molecules of proline and glutathione (REIMER, 1971a). These two substances are present in *Artemia nauplii*, suggesting these chemical substances can increase ingestion of certain food items such as *Artemia nauplii* and feeding preference (DE SANTANA et al., 2015). Greater consumption of this item by *P. caribaeorum* was observed in Sorokin (1993). Excretion of metabolites produced by digestion occurs 10 to 12 hours after ingestion (REIMER, 1971b).

Fatty acids, phytoplankton, and zooplankton biomarkers were abundant in *P. caribaeorum*, indicating that heterotrophy is the dominant energy source for this species (ROSA et al., 2016). In tropical reefs, the abundance of plankton is described by a large number of fish larvae and, thus, there is the availability of food for planktivorous coral species, which facilitates heterotrophic feeding (SANTOS et al., 2019). The genus *Palythoa*, when compared to other zoantharian and scleractinian corals, has the lowest assimilation of dissolved organic matter and bacterioplankton among the available food sources (SOROKIN, 1993). The lower use of detrital organic matter was also observed (JUNIOR, 2019). Stomach analysis of *P. caribaeorum* recorded 1284 food items and separated the content into three groups: phytoplankton, zooplankton, and POM. POM was less abundant, representing 16.98% of the content. Phytoplankton had the highest abundance with 65.3%, followed by zooplankton with 17.99% (JUNIOR, 2019). Biomass of detritus, phytoplankton and zooplankton were calculated, and detritus (maximum of 5.5 PgC) was the item with highest contribution for carbon contribution to *P. caribaeorum*. For *Z. sociatus*, detritus (maximum of 4.5 PgC) and phytoplankton were the most important to carbon aport (JUNIOR, 2019).

4.7.2.2 Interaction of environmental factors and mixotrophy

        Environmental factors are known to regulate biotic characteristics in corals (HUGHES; CONNELL, 1999; WILLIAMS et al., 2013). For *P. caribaeorum*, however, no significant differences were found between the types of food consumed in the dry and rainy season on the South Atlantic reefs, with pennate diatoms being the main items consumed (DE SANTANA et al., 2015). However, the analysis of polyps exposed to air and submerged polyps showed different responses in the production of fatty acids by photosynthetic algae. Fatty acids from the autotrophic pathway were produced in smaller amounts in emerged polyps, showing the interference of air exposure on the trophic plasticity of *P. caribaeorum* (ROSA et al., 2016). Lipids are biomolecules used as an energy reserve, for growth, in the reproductive process and are also associated with bleaching tolerance (WARD; HARRISON; HOEGH-GULDBERG, 2000; RODRIGUES; GROTTOLI; PEASE, 2008; ANTHONY et al., 2009; ROSSI et al., 2017b).

        The reef zone (reef flat and back reef) and reef location (coastal and oceanic) showed influence on symbionts density in *P. caribaeorum*. The abundance of symbionts in flat reefs, with an average of 2.99×10^6 cm^{-2}, was significantly higher than in back reefs, with an average of 2.07×10^6 cm^{-2} (SANTOS et al., 2016). Symbiont density was lower in coastal areas (2.07 to 2.99×10^6 cm^{-2}) when compared to oceanic reefs (10.36 to 18.4×10^6 cm^{-2}), probably due to the enhanced light-harvesting capacity to increase chlorophyll amount (SANTOS et al., 2016). Thus, autotrophy may be an energetic pathway of greater relevance in areas far from the coast due to the higher quantity of microalgae found (SANTOS et al., 2016) and lesser availability of organic matter in oligotrophy water areas such as oceans (BRAGA; CHIOZZINI; BERBEL, 2018).

        Changes in symbionts' density and feeding rates were also observed as an effect of temperature in *P. caribaeorum*. In a study using six different temperatures (16, 19, 22, 25, 28, and 31 °C), the density of symbionts was lower at 16 °C with 1.32 ± 0.14 10^5 cm^{-2} (ALMEIDA SAÁ et al., 2020). The highest density was found at 22 °C with 5.72 ± 0.95 10^5 cm^{-2}. Altogether, there was a decrease in photosynthesis/respiration ratio, suggesting that autotrophy is not able to meet the energy demand in this low-temperature conditions. *Artemia nauplii* were used to evaluate feeding rates at 16 °C, the highest rate was observed with an average of 1.10 ± 0.2 nauplii polyp^{-1} h^{-1} (ALMEIDA SAÁ et al., 2020). The density of symbionts increased from 16 to 22 °C and decreased from 25 to 31 °C, implying changes in photosynthetic performance,

energy production and expenditure under the influence of temperature (ALMEIDA SAÁ et al., 2020). The feeding rate (nauplii polyp^{-1} h^{-1}) was measured in laboratory experiments and linked to temperature. The highest average (1.10±0.2) at lower temperatures and the lowest average (0.51±0.1) at higher temperatures (ALMEIDA SAÁ et al., 2020). Therefore, both autotrophy and heterotrophy underwent temperature-mediated changes.

The decrease in the number of symbiotic cells with increasing temperature was also observed in another research. At an average temperature of 26 °C, the concentration of *Symbiodinium* (x10^6) per polyp ranged from 3.46 to 4.59, at an average temperature of 31 °C, from 2.15 to 3.40 (LESSER et al., 1990). The increase in temperature is related to the decrease in Simbiodinaceae and chlorophyll but not necessarily to the decrease in the photosynthesis process (SCHUBERT et al., 2017; ROSSI et al., 2020). Consequently, changes in energy input via autotrophy can occur or not. Therefore, processes such as growth, resistance, and survival may suffer interference from the energy supply by the autotrophic and heterotrophic pathways mediated by thermal changes.

Furthermore, because of its mixotrophy condition, *P. caribaeorum* can be considered polytrophic species. Some studies indicate that *P. caribaeorum* is an intermediate species in the trophic chain, being used as prey for reef fish in Brazil and acting as a link in the food chain (FRANCINI-FILHO; MOURA, 2010; MENDONÇA-NETO et al., 2008). *P. caribaeorum* has the lowest mean value for nitrogen isotope (7.71 δ^{15}N) among the three zoanthids studied in this work (VINAGRE et al., 2018), suggesting its lower predatory capacity.

4.7.3 Palythoa variabilis

4.7.3.1 Diet and energy source origins

In the relationship between *P. variabilis* and symbiotic algae, it was observed that 88.8% of their fixed carbon was translocated to the coral from the microalgae. However, the carbon values used in *P. variabilis* respiratory requirements are high and the carbon contribution from Symbiodinaceae to *P. variabilis* respiration needs represented 13.1%. Therefore, *P. variabilis* may need about 87% carbon from an external source to supply its respiratory process. The authors found a greater need for heterotrophy for *P. variabilis* (STEEN; MUSCATINE, 1984). In some cases, heterotrophy behavior can be influenced by biochemical molecules. Certain oils affect the ability to ingest. The food response triggered in *P. variabilis* can be altered by molecules of the amino acid proline and by some types of crude

oils. These oils can increase the polyps' potential to distinguish between active and inert particles for 3 to 5 days. Polyps exposed to proline have slower ingestion after 3 days of contact with this amino acid (REIMER, 1975).

Related to its contribution to the trophic chain, *P. variabilis* also behaves as an intermediate species in tropical reef food webs. However, when compared to *Z. sociatus* and *P. caribaeorum*, it is in a trophic position above these with an average value of 9.24 for $\delta^{15}N$ (VINAGRE et al., 2018). Morphological studies show that polyps of *P. variabilis* are taller than *Z. sociatus* and *P. caribaeorum* (SEBENS, 1977; KOEHL, 1977). Besides that, individuals are connected by stolon on their bases but separated from each other along with their height and have an oral disc with longer and spaced tentacles (KOEHL, 1977). The distance among polyps increases the contact area with mass water which can improve touching with food items. Suggesting this species has the major predatory behavior and heterotrophic potential among the zoanthids analyzed in this review.

4.7.3.2 Interaction of environmental factors and mixotrophy

No data were encountered about this topic.

4.7.4 Bleaching tolerance and mixotrophy in dominant zoantharians

Bleaching events in corals are one of the major pressures faced by reef environments, and several abiotic factors are associated with these events (SMITH; SUGGETT; BAKER, 2005; SCHEUFEN; IGLESIAS-PRIETO; ENRÍQUEZ, 2017; HUGHES et al., 2018). One of the main factors stems from the warming of the oceans and the increase in heatwaves that rise the frequency of bleaching phenomena (HUGHES et al., 2018). It is known that there is a link between high rates of heterotrophy with greater tolerance and recovery after bleaching events. That occurs because heterotrophic pathway lipids act as energy supplies and guarantee vital processes which are damaged due to the lower photosynthesis rates caused by bleaching (BAUMMAN et al., 2014; HOULBRÈQUE; FERRIER-PAGÈS, 2009). In the zoanthid *Palythoa tuberculosa*, greater use of heterotrophy appears to be related to higher survival rates during bleaching (HIBINO et al., 2013; SANTOS et al., 2021).

The genus *Palythoa* has been used as a previous indicator of bleaching in reef ecosystems (GOLDBERG; WILKINSON, 2004; PARKINSON et al., 2016). *P. caribaeorum* seems to demonstrate a high metabolic capacity to withstand heat stress (ALMEIDA SAÁ et

al., 2020). High survival rates of this species after bleaching events are associated with mixotrophy (DE SANTANA et al., 2015). The greater use of heterotrophy may allow the resistance and recovery of this species (DE SANTANA et al., 2015; ROSA et al., 2016; DURANTE; CRUZ; LOTUFO, 2018). In 2019, colonies of *P. caribaeorum* suffered one of the most intense heat stresses ever recorded on the Brazilian coast. Bleaching caused by marine heatwaves affected between 3.9 to 41.1 % of colonies and provoked mortality of only 2.1% of these (DUARTE et al., 2020). The evaluation of *Palythoa* sp. kept under heat stress (30 ºC) and with external food (microencapsulated diet) showed that this group had better metabolic performance when compared to colonies maintained without external food. Therefore, higher heterotrophy rates may help recover to heat stress and bleaching events (DA SILVA, 2021). In addition, climate models predict that increasing salinity and thermal-stress bleaching projected by end-of-century emission scenarios favor the dominance of the generalist species *P. caribaeorum* in some areas (KEMP et al. 2006; DURANTE; CRUZ; LOTUFO, 2018).

The increase in sea temperature and other factors associated with bleaching events can cause changes in reef cover and occupation. Considering the autotrophic nature of *Z. sociatus*, this species may suffer more damage due to its higher need for symbiotic algae for energy supply and metabolic functioning (SOROKIN, 1991; LEAL et al., 2017). Thus, the abundance of *Z. sociatus* on tropical West Atlantic reefs may decrease after long and intense bleaching events (SANTOS et al., 2021; CONTI-JERPE et al., 2020).

4.8 Conclusions and final considerations

In our article, we conclude that the zoantharians addressed here are little studied and the trophic ecology of *P. caribaeorum*, *P. variabilis,* and *Z. sociatus*, especially that of *P. variabilis*, is poorly known. From the data obtained in this research, *P. caribaeorum* seems to have a preference for live prey and less assimilation of dissolved organic matter. *Z. sociatus* seems to prefer particulate organic material from heterotrophic sources. Although the three species are common in shallow areas, which would indicate light dependence and predominance of autotrophy, we noticed differences in the trophic plasticity of each species to zonation. The availability and quality of food in exposed and intertidal environments influence the feeding pattern of *P. caribaeorum* and *Z. sociatus*. Among the three species, *P. variabilis* is the least addressed with higher hetetrophic rate although *Z. sociatus* has the higher autotrophic rate. Considering the near future of climate changes, these species may face

different situations. *Z. sociatus* is a species more dependent on the autotrophic pathway, indicating that damage to its photobiology may have more serious negatives consequences for this species such as decrease of distribution limits and reef coverage. *P. caribaeorum* and *P. variabilis* are less dependent on autotrophy, suggesting that they may be more resistant and survive in environments with high temperatures and moderate turbidity, which are crescent suboptimal conditions.

Virtually all aspects involving the trophic ecology of P. *variabilis* are unknown. Questions related to feeding characterization, trophic level, fluctuations in mixotrophy, and factors that influence the feeding pattern of this species need to be investigated. It is interesting to note that most of the studies carried out in the laboratory and nature were punctual. From the best of our knowledge, there is no record of research covering long periods and consecutive evaluations. Therefore, we suggest long-term investigations to understand the issues associated with the trophic ecology of these key and important zoantharians.

The study of aspects associated with the trophic ecology of these organisms should support the understanding of how the coral-Symbiodinaceae relationship and coastal areas where there is a high flow of sediments and suspended organic matter can influence the resilience and survival of corals in the face of the effects of changing environment.

Improving the knowledge about the diets, trophic levels and mixotrophy of zoantharians can provide information on the degree of competition, and tolerance of these soft corals to local climatic characteristics and global climate change (HELMUT et al., 2006; VENN et al., 2008; HUGHES and GROTTOLI, 2013). This information is important for understanding their increase or decrease in geographic distribution and their population flourishment or decline depending on the type of reef environment (REIMER et al., 2021). In addition, the trophic structure of an ecosystem can show the functioning of the system due to the presence of species that can keep the environment stable, modifying biodiversity and productivity (PAINE, 1980; WORM and DUFFY, 2003).

5 CONCLUSÕES FINAIS DA TESE

A pesquisa desenvolvida nesta tese se baseia no branqueamento e ecologia trófica de corais e zoantídeos que podem estar associadas a resistência e resiliência em ambientes recifais com condições subótimas. Por meio dos resultados obtidos neste trabalho é possível sugerir que as características ambientais do Atlântico Sudoeste Equatorial possuem singularidades para o crescimento e sobrevivência de espécies que habitam a região. Águas com temperatura

alta e estável, regime de chuvas sazonal e turbidez moderada são peculiaridades dessa região e, possivelmente, proporcionam mudanças nas respostas fisiológicas dos corais expostos a essas condições como no branqueamento.

No capitulo I exploramos o branqueamento de *S. stellata* em um recife raso no ano de 2020 e indicadores climáticos que poderiam ter provocado o fenômeno de branqueamento. Encontramos fatores térmicos (DHW e MHW) intensos e prolongados atuando na região do Atlântico Sudoeste Equatorial durante o período estudado, sugerindo que estes podem ter sido a causa do branqueamento, juntamente com baixa incidencia de ventos e turbidez reduzida. No capitulo II estudamos o evento de branqueamento em *S. stellata* durante os anos de 2013-2015 e sua ligação com o déficit de chuva, além de outras características ambientais ao longo desse período. Foi possível observar variações na pluviometria e turbidez da região, o que pode ter diminuído o sombreamento e a proteção contra forte irradiação solar provocando o branqueamento em determinados momentos. Assim, o regime de chuvas também deve ser considerado para estudos futuros sobre o branqueamento de corais na região do Atlântico Equatorial por sua função moduladora de turbidez, em conjunto com o vento. Além disso, foi possível observar a persistência de colônias de pequeno tamanho de *S. stellata* durante esse branqueamento prolongado.

Por fim, o capitulo III reuniu aspectos da ecologia trófica dos zoantideos *P. caribaeorum*, *P. variabilis* e *Z. sociatus* comuns em recifes do Atlântico Sudoeste. Estes zoantideos apresentam diferentes hábitos alimentares, usos da sua capacidade autotrófica e heterotrófica, e posições na cadeia alimentar, o que pode estar associado a sobrevivência e permanência destas espécies diante das singularidades da costa do Brasil e as respostas ecofisiológicas as mudanças climáticas. *Z. sociatus* é uma espécie mais dependente da via autotrófica, indicando que danos a sua fotobiologia (branqueamento prolongado) podem ter consequências mais sérias para a sua sobrevivência. *P. caribaeorum* e *P. variabilis* são menos dependentes da autotrofia, sugerindo que eles podem ser mais resistentes em ambientes com condições subótimas de temperaturas altas e moderada turbidez, bem como em eventos de branqueamento.

A abordagem por meio de uma revisão integrativa surge como uma alternativa para compreensão da ecologia trófica desses organismos no Atlântico Sudoeste devido a impossibilidade da realização de etapas analíticas por conta da pandemia de SARS-CoV-2 (COVID-19). Os autores deste trabalho possuem material biológico conservado que será analisado em momento oportuno e que complementará o entendimento do uso das vias autotróficas e heterotróficas por esses organismos.

Neste trabalho indicamos que o aquecimento das águas, o déficit pluviométrico e a baixa turbidez podem estar ligados a eventos de branqueamento no Atlântico Sudoeste Equatorial. Em especial a turbidez moderada que pode estar associada tanto ao sombreamento, e assim, proteção dos recifes, quanto a quantidade de microrganismos e matéria orgânica na coluna d`água que podem ser utilizadas como alimentos favorecendo a via heterotrófica em algumas espécies resistentes (como *S. stellata* e *P. caribaeorum*). Portanto, esses fatores devem ser considerados e analisados conjuntamente para a interpretação de causas de eventos de branqueamento. Além disso, um esforço cientifico deve ser aplicado para a compreensão do funcionamento dos ambientes recifais sob essas condições singulares no Atlântico Sul.

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APPENDIX A – CHAPTER I - CABEÇO DO BALANÇO REEF DATA

The number of studies per information category (Eating habits, interaction with environmental factors, trophic level, and mixotrophy) for each species: *P. caribaeorum*, *P. variabilis*, and *Z. sociatus*.

Cabeço do Balanço Reef

INDICATORS	J	F	M	A	M	J	J	A	S	O	N	D
SST (°C)	28,7	29	29,5	29,1	29,2	27,7	27,4	26,7	26,5	27,2	27,7	27,4
SSTA (°C)	0,5	0,49	0,67	0,37	0,52	0,01	0,31	0,09	0,14	0,37	0,29	-0,06
DHW (°C/semana)	0,2	2,8	7,5	14,8	17,6	14,5	7,0	1,8	-	-	-	-
Kd490	0,047	0,041	0,041	0,046	0,043	0,05	0,052	0,051	0,047	0,049	0,056	0,054
Speed Wind (m.s^{-1})	1,77	1,40	1,07	1,37	1,67	2,11	2,58	3,42	3,41	3,29	2,96	-

Marine heating waves (MHW) characteristics for the coast of Ceará State in 2020. Data for the area that includes Cabeço do balance Reef

Geographic coordinates	Event	Date (begin)	Date (peak)	Date (end)	Duration (days)	Mean intensity	Maximum intensity	Accumulated intensity
-38,375 Longitude -3,625 Latitude	1	03/01/2020	07/01/2020	17/02/2020	46	0,99	1,54	45,63
	2	29/02/2020	06/03/2020	14/05/2020	76	1,19	1,99	90,88
	3	22/05/2020	03/06/2020	25/06/2020	35	0,85	1,25	29,94
	4	09/10/2020	14/11/2020	12/12/2020	65	0,82	1,26	53,81

APPENDIX B – CHAPTER II - SUPPLEMENTARY MATERIAL 1

Table S1. Environmental variables and coral bleaching in the tolerant species *Siderastrea stellata* in a marginal turbid-zone reef (SW Atlantic, Brazil). Yellow = Dry months (0-88.6mm/month). Blue = Rainy months (157 to 421.5 mm/month) according to the methodology in the main article. SST = Sea surface temperature. H= no bleaching, MB= partially bleached, SB= fully bleached.

Month/Year	Wind speed (meters/seconds)	Solar irradiation (hours/month)	Rainfall (mm)	H	MB	SB	SST (ºC)	SST anomalies	Diffuse light attenuation coefficient (Kd_{490})
May 2013	2.44	230.6	285.4	16%	50%	34%	28.32	-0.02	0.067
June 2013	2.09	207.8	204.8	29%	42%	30%	27.59	0.03	0.0728
July 2013	2.38	242.6	88.6	52%	39%	9%	27	0.01	0.0833
August 2013	3.63	281	24.8	46%	50%	4%	26.87	0.05	0.0759
October 2013	3.63	297	2	35%	54%	11%	27.5	-0.08	0.0694
December 2013	3.27	294.4	74.6	33%	61%	6%	28.28	-0.16	0,0727*
March 2014	2.06	184.5	179	54%	44%	2%	29.29	-0.03	0.0916
May 2014	1.77	191.8	157.5	29%	57%	14%	28.86	-0.04	0.0767
June 2014	2.95	231	49.4	35%	54%	11%	28.17	0.61	0.0744
August 2014	3.88	284	5	30%	64%	7%	26.89	0.07	0.1073
September 2014	3.70	268.7	12.5	35%	58%	7%	26.94	-0.24	0.0669
December 2014	3.41	278.4	17.4	56%	35%	9%	28.25	-0.19	0.0803
March 2015	1.94	170.6	352	43%	52%	5%	28.78	-0.54	0.1277
April 2015	1.82	176.7	421.5	30%	61%	9%	28.9	-0.21	0.1639
June 2015	3.02	242.5	168.6	16%	56%	28%	27.97	0.41	0.0677

Table S2. Size classes and state of coral colonies of *Siderastrea stellata* in a marginal turbid-zone reef (SW Atlantic,Brazil).

	Size classes/state of colony	> 2 – 10 cm		11 – 20 cm		21 – 30 cm		31 – 40 cm	
		#	%	#	%	#	%	#	%
	Strong bleaching	80	98.77%	1	1.23%	0	0.00%	0	113 0.00%
	Moderate bleaching	107	89.17%	10	8.33%	1	0.83%	2	1.67%
	Healthy colonies	34	91.89%	2	5.41%	1	2.70%	0	0.00%
May-13	Total	221	92.86%	13	5.46%	2	0.84%	2	0.84%
	Size classes/state of colony	> 2 – 10 cm		11 – 20 cm		21 – 30 cm		31 – 40 cm	
		#	%	#	%	#	%	#	%
	Strong bleaching	82	98.80%	1	1.20%	0	0.00%	0	0.00%
	Moderate bleaching	90	90.91%	7	7.07%	1	1.01%	1	1.01%
	Healthy colonies	77	97.47%	2	2.53%	0	0.00%	0	0.00%
Jun-13	Total	249	95.40%	10	3.83%	1	0.38%	1	0.38%
	Size classes/state of colony	> 2 – 10 cm		11 – 20 cm		21 – 30 cm		31 – 40 cm	
		#	%	#	%	#	%	#	%
	Strong bleaching	18	85.71%	2	9.52%	0	0.00%	1	4.76%
	Moderate bleaching	81	94.19%	4	4.65%	1	1.16%	0	0.00%
	Healthy colonies	111	94.87%	6	5.13%	0	0.00%	0	0.00%
Jul-13	Total	210	93.75%	12	5.36%	1	0.45%	1	0.45%
	Size classes/state of colony	> 2 – 10 cm		11 – 20 cm		21 – 30 cm		31 – 40 cm	
		#	%	#	%	#	%	#	%
	Strong bleaching	9	100.00%	0	0.00%	0	0.00%	0	0.00%
	Moderate bleaching	115	93.50%	7	5.69%	1	0.81%	0	0.00%
	Healthy colonies	108	93.91%	6	5.22%	1	0.87%	0	0.00%
Aug-13	Total	232	93.93%	13	5.26%	2	0.81%	0	0.00%
	Size classes/state of colony	> 2 – 10 cm		11 – 20 cm		21 – 30 cm		31 – 40 cm	
		#	%	#	%	#	%	#	%
	Strong bleaching	19	95.00%	1	5.00%	0	0.00%	0	0.00%
	Moderate bleaching	78	97.50%	2	2.50%	0	0.00%	0	0.00%
	Healthy colonies	61	95.31%	3	4.69%	0	0.00%	0	0.00%
Oct-13	Total	158	96.34%	6	3.66%	0	0.00%	0	0.00%
	Size classes/state of colony	> 2 – 10 cm		11 – 20 cm		21 – 30 cm		31 – 40 cm	
		#	%	#	%	#	%	#	%
	Strong bleaching	8	100.00%	0	0.00%	0	0.00%	0	0.00%
	Moderate bleaching	73	92.41%	5	6.33%	0	0.00%	1	1.27%
	Healthy colonies	36	85.71%	4	9.52%	1	2.38%	1	2.38%
Dec-13	Total	117	90.70%	9	6.98%	1	0.78%	2	1.55%
	Size classes/state of colony	> 2 – 10 cm		11 – 20 cm		21 – 30 cm		31 – 40 cm	
		#	%	#	%	#	%	#	%
	Strong bleaching	4	100.00%	0	0.00%	0	0.00%	0	0.00%
	Moderate bleaching	46	90.20%	5	9.80%	0	0.00%	0	0.00%
	Healthy colonies	100	90.91%	9	8.18%	0	0.00%	1	0.91%
Mar-14	Total	150	90.91%	14	8.48%	0	0.00%	1	0.61%
	Size classes/state of colony	> 2 – 10 cm		11 – 20 cm		21 – 30 cm		31 – 40 cm	
		#	%	#	%	#	%	#	%
May-14	Strong bleaching	36	100.00%	0	0.00%	0	0.00%	0	0.00%

	Size classes/state of colony	> 2 – 10 cm		11 – 20 cm		21 – 30 cm		31 – 40 cm	
		#	%	#	%	#	%	#	%
	Moderate bleaching	141	96.58%	4	2.74%	0	0.00%	1	0.68%
	Healthy colonies	69	90.79%	6	7.89%	0	0.00%	1	1.32%
	Total	246	95.35%	10	3.88%	0	0.00%	2	0.78%
	Size classes/state of colony	> 2 – 10 cm		11 – 20 cm		21 – 30 cm		31 – 40 cm	
		#	%	#	%	#	%	#	%
	Strong bleaching	24	100.00%	0	0.00%	0	0.00%	0	0.00%
	Moderate bleaching	80	94.12%	4	4.71%	1	1.18%	0	0.00%
	Healthy colonies	18	94.74%	1	5.26%	0	0.00%	0	0.00%
Jun-14	Total	122	95.31%	5	3.91%	1	0.78%	0	0.00%
	Size classes/state of colony	> 2 – 10 cm		11 – 20 cm		21 – 30 cm		31 – 40 cm	
		#	%	#	%	#	%	#	%
	Strong bleaching	11	100.00%	0	0.00%	0	0.00%	0	0.00%
	Moderate bleaching	96	88.89%	10	9.26%	2	1.85%	0	0.00%
	Healthy colonies	48	96.00%	1	2.00%	0	0.00%	1	2.00%
Aug-14	Total	155	91.72%	11	6.51%	2	1.18%	1	0.59%
	Size classes/state of colony	> 2 – 10 cm		11 – 20 cm		21 – 30 cm		31 – 40 cm	
		#	%	#	%	#	%	#	%
	Strong bleaching	5	100.00%	0	0.00%	0	0.00%	0	0.00%
	Moderate bleaching	41	95.35%	2	4.65%	0	0.00%	0	0.00%
	Healthy colonies	25	96.15%	1	3.85%	0	0.00%	0	0.00%
Sep-14	Total	71	95.95%	3	4.05%	0	0.00%	0	0.00%
	Size classes/state of colony	> 2 – 10 cm		11 – 20 cm		21 – 30 cm		31 – 40 cm	
		#	%	#	%	#	%	#	%
	Strong bleaching	13	92.86%	1	7.14%	0	0.00%	0	0.00%
	Moderate bleaching	53	94.64%	2	3.57%	1	1.79%	0	0.00%
	Healthy colonies	83	94.32%	4	4.55%	1	1.14%	0	0.00%
Dec-14	Total	149	94.30%	7	4.43%	2	1.27%	0	0.00%
	Size classes/state of colony	> 2 – 10 cm		11 – 20 cm		21 – 30 cm		31 – 40 cm	
		#	%	#	%	#	%	#	%
	Strong bleaching	13	92.86%	1	7.14%	0	0.00%	0	0.00%
	Moderate bleaching	53	94.64%	2	3.57%	1	1.79%	0	0.00%
	Healthy colonies	83	94.32%	4	4.55%	1	1.14%	0	0.00%
Mar-15	Total	149	94.30%	7	4.43%	2	1.27%	0	0.00%
	Size classes/state of colony	> 2 – 10 cm		11 – 20 cm		21 – 30 cm		31 – 40 cm	
		#	%	#	%	#	%	#	%
Abr-2015	Strong bleaching	4	100.00%	0	0.00%	0	0.00%	0	0.00%
	Moderate bleaching	38	88.37%	3	6.98%	2	4.65%	0	0.00%
	Healthy colonies	30	83.33%	5	13.89%	1	2.78%	0	0.00%
	Total	72	86.75%	8	9.64%	3	3.61%	0	0.00%
	Size classes/state of colony	> 2 – 10 cm		11 – 20 cm		21 – 30 cm		31 – 40 cm	
		#	%	#	%	#	%	#	%
Jun-15	Strong bleaching	77	97.47%	2	2.53%	0	0.00%	0	0.00%

Moderate bleaching	140	88.61%	15	9.49%	3	1.90%	0	0.00%
Healthy colonies	39	88.64%	4	9.09%	1	2.27%	0	0.00%
Total	256	91.10%	21	7.47%	4	1.42%	0	0.00%

Table S3. Size classes and number of *Siderastrea stellata* colonies by type of bleaching in a marginal turbid-zone reef (SW Atlantic, Brazil)

	Strong Bleaching	**Moderate Bleaching/Pale**	**Healthy Colonies**
> 2 – 10 cm	13.99%	42.77%	32.01%
11 – 20 cm	0.31%	2.81%	2.01%
21 – 30 cm	0	0.38%	0.20%
31 – 40 cm	0.03%	0.29%	0.17%

Table S4. Eigenvalue and % of variance on the PCA analysis using environmental variables and severe bleaching in the coral *Siderastrea stellata* in a marginal turbid-zone reef (SW Atlantic, Brazil). The two first axes are used on the main text and explain most data variation.

PC	Eigenvalue	% Variance
PC 1	3.70	61.22
PC 2	1.31	21.84
PC 3	0.57	9.46
PC 4	0.30	5.09
PC 5	0.06	1.07
PC 6	0.05	0.90

Table S5. Loading plots of PCA analysis between environmental variables and severe bleaching (frequency of fully bleached coral colonies per month) in a marginal turbid-zone reef (SW Atlantic, Brazil).

	PC 1	PC 2
Wind speed	-0.48	-0.14
Irradiation	-0.49	-0.03
Rainfall	0.48	0.08
SST	0.41	-0.03
Severe bleaching	0.08	0.82
Kd 490 (turbidity)	0.33	-0.54

Figure S1. Methodological design showing the transect and photoquadrats system in a homogeneous shallow water column (without thermocline). The classification of the coral bleaching in *Siderastrea stellata* in a tropical marginal turbid-zone reef (SW Atlantic, Brazil) is shown on the left side: Strong bleaching = completely white shade; pale/moderate bleaching = intermediate shade; healthy = dark shade. N.M.M. = Average sea level.
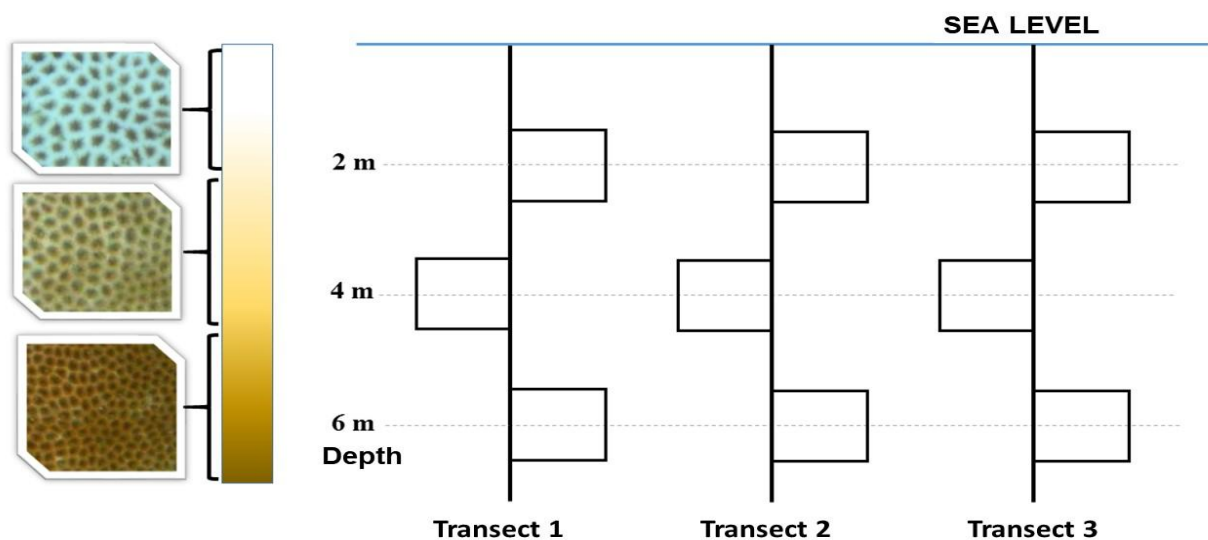
Figure S2. Scenarios of coral bleaching in *Siderastrea stellata* in a marginal tropical reef (SW Atlantic, Brazil), considering changes in the oceanographic and meteorological factors (SST - Sea surface temperature, wind, insolation, rainfall, and turbidity). A: Critical scenario. N.M.M. = Average sea level. Absence of rainfall, clear waters, calm winds, significant sea surface temperature, and solar irradiation for several weeks.
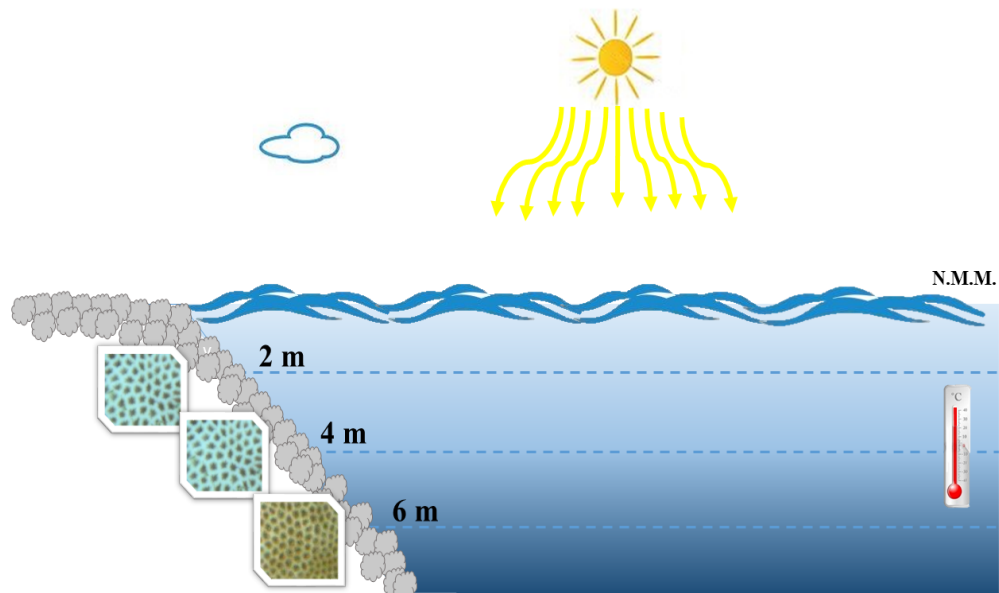

Figure S3. Scenarios of coral bleaching in *S. stellata* in a marginal tropical reef (SW Atlantic, Brazil), considering changes in the oceanographic and meteorological factors (SST – Sea surface temperature, wind, insolation, rainfall, and turbidity). B: First-semester scenario without environmental anomalies (rain, temperature, etc.). N.M.M. = Average sea level. Rainfall, significant cloudiness, moderate turbidity, and low solar irradiation.
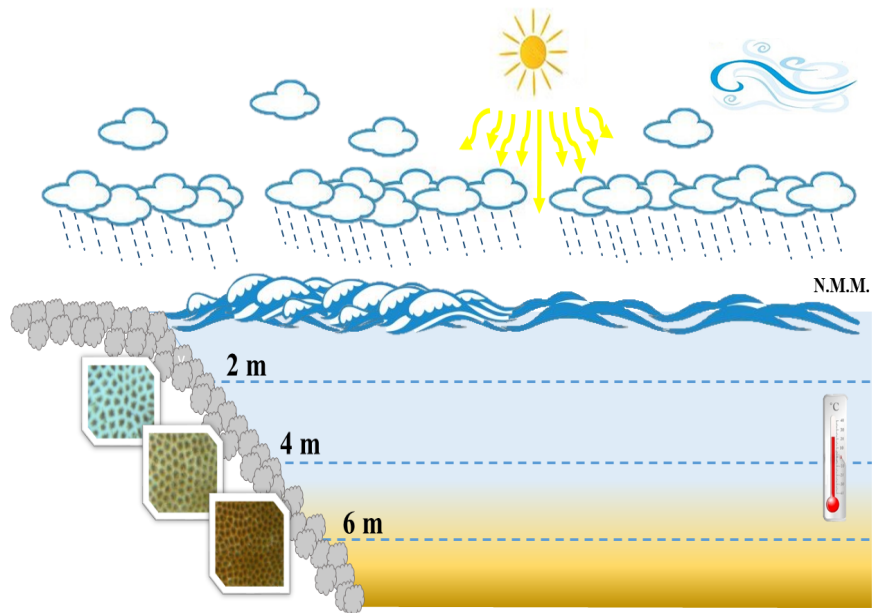
Figure S4. Scenarios of coral bleaching in *Siderastrea stellata* in a marginal tropical reef (SW Atlantic, Brazil), considering changes in the oceanographic and meteorological factors (SST - Sea surface temperature, wind, insolation, rainfall, and turbidity). C: Second-semester scenario with more bleaching. N.M.M. = Average sea level. Intense solar irradiation, trade winds are intermediary levels, turbid waters, and absence of rainfall.
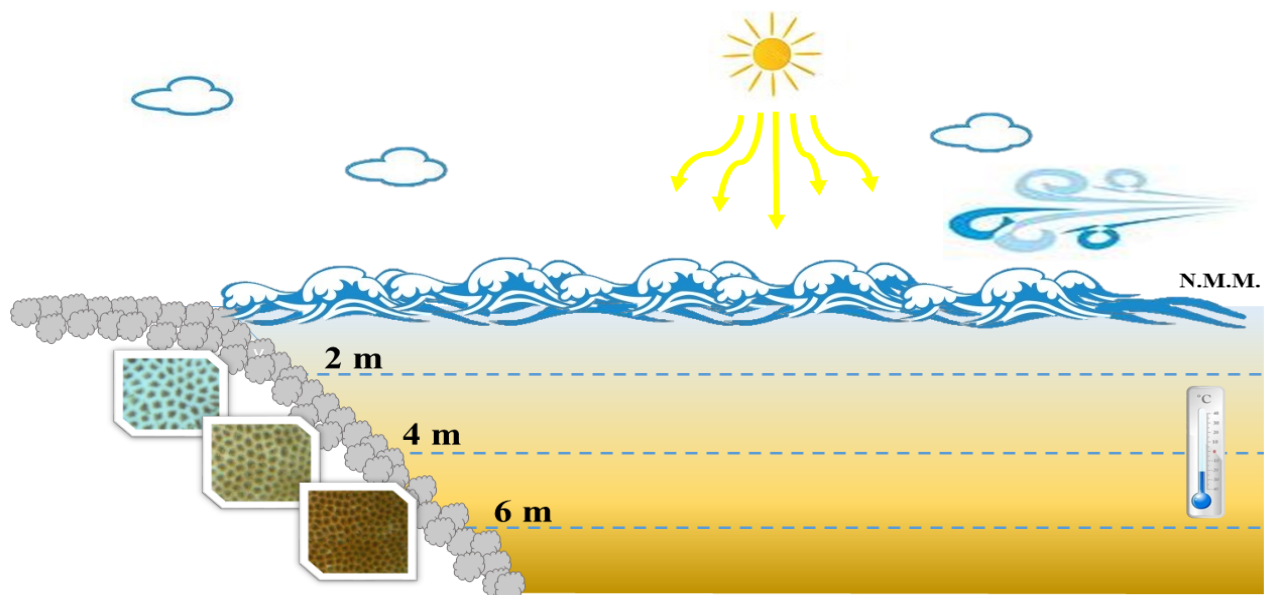
Figure S5. Scenarios of coral bleaching in *Siderastrea stellata* in a marginal tropical reef (SW Atlantic, Brazil), considering shifts in the oceanographic and meteorological factors (SST - Sea surface temperature, wind, insolation, rainfall, and turbidity). D: Second-semester scenario with less bleaching. Low cloudiness and lower temperature. Intense trade winds, severe insolation, and turbid waters. N.M.M. = Average sea level.
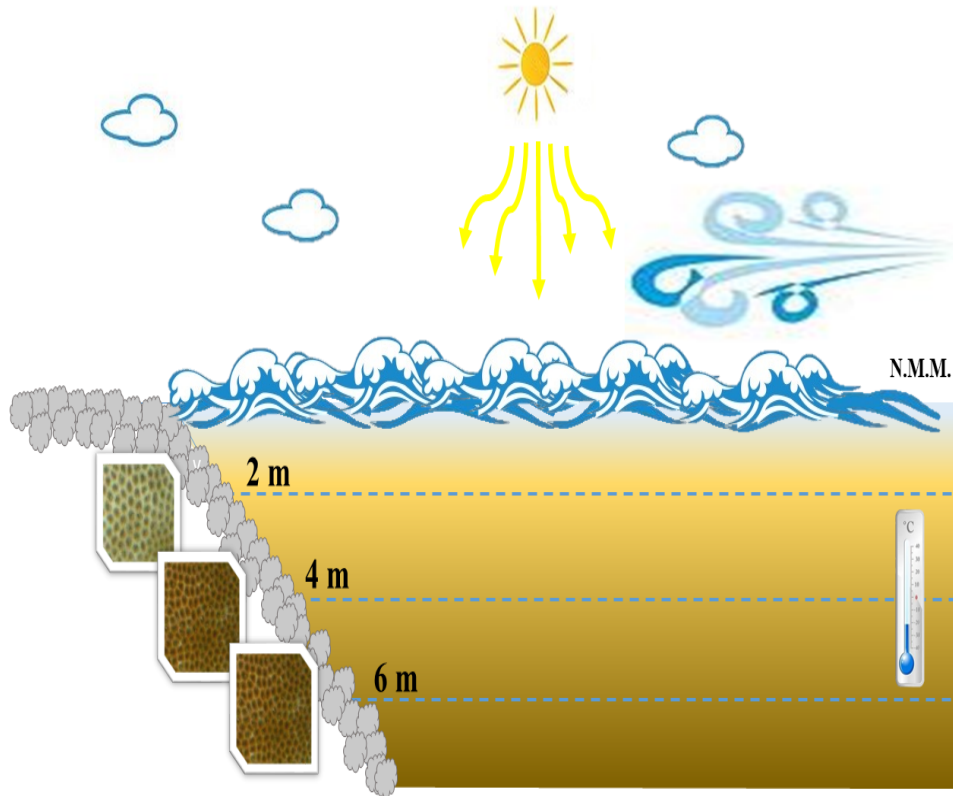

Figure S6. Degree Heating Weeks (DHWs) for May 2013. DHWs indicate the number of weeks of positive SST anomalies observed in May (2013). This month with June (2013) ranked among the highest with severe bleaching.
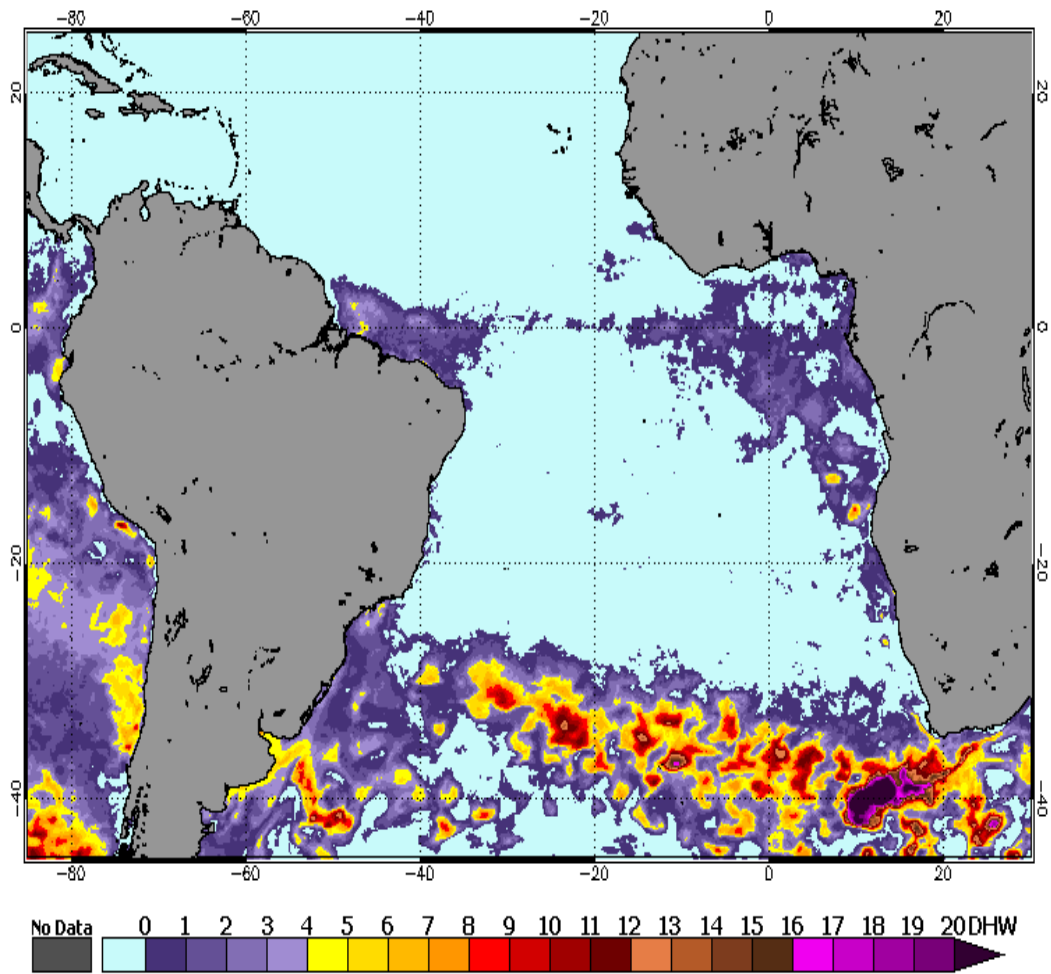
Figure S7. Degree Heating Weeks (DHWs) for June 2013. DHWs indicate the number of weeks of positive SST anomalies observed in June (2013). June with May (2013) ranked among the highest with severe bleaching.

NOAA CRW 5km Degree Heating Week Monthly Maximum (Version 3.1)   Jun 2013