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Da fisiologia ao nicho: presente e futuro dos bancos de rodolitos brasileiros

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Da fisiologia ao nicho: presente e futuro dos bancos de rodolitos brasileiros.

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"Many people seem to think it foolish, even superstitious, to believe that the world could still change for the better. And it is true that in winter it is sometimes so bitingly cold that one is tempted to say, 'What do I care if there is a summer; its warmth is no help to me now.' Yes, evil often seems to surpass good. But then, in spite of us, and without our permission, there comes at last an end to the bitter frosts. One morning the wind turns, and there is a thaw. And so I must still have hope."

Vincent Van Gogh

RESUMO

As mudanças climáticas já exercem efeito sobre as espécies bentônicas marinhas. Associativamente, impactos locais, como a poluição, interagem e intensificam os efeitos das mudanças climáticas. Observam-se efeitos de mortalidade de espécies-chave e estruturadoras sistêmicas, como as algas calcáreas de vida livre (rodolitos). Frente às ameaças atuais e os cenários futuros para a mudança das condições abióticas, os impactos sobre a fisiologia e a distribuição destes organismos podem acarretar em danos sistêmicos. Portanto, compreender e descrever os principais impactos em escalas global e local aos bancos de rodolitos brasileiros, e investigar quais os efeitos destes para a fisiologia e a adequabilidade de habitat no presente e futuro, é de extrema importância para fomentar decisões de manejo e mitigação destas mudanças. Este estudo é focado em uma importante espécie formadora de rodolitos com ampla distribuição nas províncias biogeográficas brasileiras, o *Lithothamnion crispatum* (Hauck, 1878), com ampla distribuição nas províncias biogeográficas. A presente dissertação está estruturada em dois capítulos. No primeiro, realizou-se um levantamento dos principais estudos experimentais realizados com espécies de rodolitos, no mundo e no Brasil, verificando-se as forçantes ambientais mais investigadas. Observou-se ausência de experimentos que considerem a interatividade entre estressores e os efeitos de ondas de calor marinhas para as espécies brasileiras, bem como baixa frequência de trabalhos que analisam os efeitos de eutrofização e acidificação oceânica. Assim, realizou-se um experimento para análise da combinação destas três forçantes: aumento repentino de temperaturas (onda de calor marinha), aumento na concentração de nutrientes (eutrofização) e aumento de $p\text{CO}_2$ (acidificação oceânica). Foi verificada a resposta no rendimento e na produção fotossintética de *L. crispatum* após 5 dias de exposição interativa a essas forçantes, e a sua possível recuperação após a remoção desses fatores e restabelecimento das condições iniciais ótimas. Associativamente, um modelo de nicho ecológico foi desenvolvido para determinar que variáveis ambientais explicam a atual distribuição de *L. crispatum* na costa brasileira, e também para estimar a futura adequabilidade de habitat dessa espécie. *L. crispatum* sofreu uma grande queda em desempenho fotossintético após 5 dias de exposição às forçantes globais e locais, mas apresentou uma resposta de recuperação após retorno a condições iniciais. Esta inferência experimental está de acordo com os resultados obtidos para o modelo de nicho, que demonstrou que a distribuição da espécie na costa brasileira não é explicada pelos fatores ondas de calor marinha ou pH. Além disso, indicou que, no futuro, pode haver a expansão da adequabilidade de habitat da espécie, ao invés de sua contração, o que seria esperado em um cenário de interações entre estressores. Portanto, *L. crispatum* aparenta ter uma certa resistência às condições ambientais futuras, porém uma consideração cuidadosa desses resultados precisa ser feita. Isto porque há limitações próprias do estudo e o isolamento destas variáveis. Com a associação futura destas forçantes às mudanças em outros fatores bióticos, como interação com outras espécies, respostas diferenciadas podem ser obtidas, devendo ser avaliadas através de novas modelagens baseadas em dados fisiológicos da espécie nestes cenários interativos.

Palavras-chave: modelo de nicho ecológico, onda de calor marinha, eutrofização, acidificação oceânica, algas vermelhas, limites de distribuição

ABSTRACT

Climate change has already affected benthic marine species. Local impacts, such as pollution, interact and intensify the effects of climate change. Mortality of key structuring species is already being observed, such as on species of free-living coralline red algae (rhodoliths). In face of the current threats and future scenarios of environmental change, the impacts on the physiology and distribution of these organisms can result in systemic damages. Therefore, comprehending and describing the main anthropogenic impacts, in local and global scales, to Brazilian rhodolith beds is of extreme importance to inform managing and mitigation actions of these environmental changes. This study is focused in one highly important rhodolith-forming species, *Lithothamnion crispatum* (Hauck, 1878), with a wide distribution across biogeographical provinces. The present thesis is structured in two chapters. In the first, a literature survey was done looking for the main experimental studies developed with rhodolith-forming species in Brazil, examining the main environmental drivers investigated. An absence of experiments considering the interaction between these stressors and the effects of marine heatwaves was observed, as well as a low presence of studies analyzing the interaction between eutrophication and ocean acidification. For this reason, in the second chapter, an experiment was run to understand the effects of the combination of three drivers: a sudden increase of temperatures (marine heatwave), increased nutrient concentrations (eutrophication) and increased $p\mathrm{CO}_2$ levels (ocean acidification). The physiological response of *L. crispatum* was evaluated by measurements of photosynthetic production and yield after five days of exposition to the combined drivers, and the possible recovery of individuals after the removal of drivers and return to optimal initial conditions was also measured. Simultaneously, an ecological niche model was developed to determine which environmental variables explain the current distribution of *L. crispatum* in the Brazilian coast, and the future habitat suitability of this species was also estimated. *L. crispatum* experienced a great decrease in photosynthetic yield after 5 days of exposition to global and local drivers, but presented a recovery response after returning to the initial conditions. Experiment results are in accordance with model results, which demonstrated that the species' distribution in the Brazilian coast is not determined by heatwaves and pH. Moreover, the ecological niche model showed that in the future, *L. crispatum* may expand its habitat suitability, instead of losing suitable areas, which was first expected in a scenario of combination of multiple stressors. Therefore, *L. crispatum* appears to hold a certain resistance to future environmental conditions, although a careful consideration of these results needs to be done, as there as limitations in the study and in the isolation of these variables. With the association of these variables and biotic factors, such as interactions with other species, different responses may be obtained, and must be evaluated through new modeling techniques based in both physiological and biotic data for the species.

Keywords: ecological niche model, marine heatwaves, eutrophication, ocean acidification, red algae, range limits.

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CAPÍTULO II

SUMÁRIO

1. INTRODUÇÃO

Nas últimas décadas, as alterações humanas em sistemas naturais têm aumentado em intensidade e formas (ELLIS; BEUSEN; GOLDEWIJK, 2020). A alteração da atmosfera é uma das quais mais atenção é dada, devido aos seus efeitos em cascata que já são e serão ainda mais sentidos por ecossistemas do planeta inteiro (DONEY et al., 2012). O principal foco é o aumento do dióxido de carbono (CO_2), causado pela queima de combustíveis fósseis e atividades industriais (LÜTHI et al., 2008). Maiores concentrações desse gás na atmosfera alteram o clima, e como principal consequência, causam o aumento da temperatura média global (HARTMANN, 2016). Dependendo da trajetória de emissões de gases de efeito estufa (*Representative Concentration Pathway* – RCP) que seguirmos, a temperatura média global pode aumentar até 4.3 graus até 2100 – além do 1 grau que já aumentou desde o século XIX (IPCC, 2019), e que já causou diversos impactos, como branqueamento em massa de corais (EAKIN; SWEATMAN; BRAINARD, 2019) e deslocamento na distribuição de espécies marinhas (PARMESAN, 2006; PECL et al., 2017; POLOCZANSKA et al., 2013). O aumento da concentração de CO_2 também altera o pH dos oceanos, tornando-os mais ácidos e modificando o sistema carbonato, fenômeno chamado de acidificação oceânica (DONEY et al., 2009), com projeção de queda de até 0.4 unidades de pH em 2100 (HARTIN et al., 2016). Além disso, as alterações no clima também terão como consequência o aumento na frequência e intensidade de eventos extremos, como ondas de calor marinhas (LAUFKÖTTER; ZSCHEISCHLER; FRÖLICHER, 2020). Adicionalmente aos impactos globais, também existem alterações antrópicas regionais com diversos impactos em ecossistemas marinhos. A descarga fluvial e pluvial drena para a costa muitas substâncias utilizadas no ambiente terrestre, como agrotóxicos e fertilizantes, assim como aquilo que é despejado em rios, como esgoto. O deságue de esgoto e fertilizantes gera o aumento da concentração de nutrientes em ambientes costeiros, conhecido por promover alteração na comunidade de algas nos locais mais impactados (SCHERNER et al., 2013).

Essas forçantes (do inglês *drivers*) antropogênicas resultam em mudanças generalizadas em ecossistemas marinhos, alterando processos chave na manutenção de populações, consequentemente causando mudanças na estrutura, funcionamento e resiliência de ecossistemas (SCHEFFERS et al., 2016). As consequências das alterações ambientais levam espécies a sofrerem modificações em processos populacionais, como *fitness*, abundância, fenologia e interações biológicas, induzindo mudanças nos seus limites de distribuição geográfica, e nos piores cenários, o colapso de populações e consequente extinção (PECL et al., 2017). Desta forma, determinar a resposta de espécies e populações frente a futuras alterações antropogênicas do meio natural é de extrema importância para informar ações de manejo e minimizar impactos em ecossistemas (BOYD et al., 2018). Entretanto, as mudanças ambientais são naturalmente complexas, sendo uma grande combinação de concomitantes variáveis físicas, químicas e biológicas, cada qual interagindo com outras de diversas formas (BOYD; HUTCHINS, 2012). Estudar os efeitos combinados de diversas forçantes é um dos maiores desafios da biologia de mudanças globais atualmente (GUNDERSON; ARMSTRONG; STILLMAN, 2016).

A biologia da conservação busca estudar como preservar a maior diversidade biológica possível dentro de uma pequena escala de tempo. Para isto, dentre as muitas estratégias propostas, uma alternativa é focar em espécies que são importantes na estruturação de ambientes e que hospedam uma grande biodiversidade (CRAIN; BERTNESS, 2006), como os rodolitos. Rodolitos são algas vermelhas coralinas não articuladas, com grande importância ecológica, sendo considerados bioconstrutores ambientais (HORTA et al., 2016). Diversas espécies dessas algas formam bancos de rodolitos em substratos arenosos, aumentando a heterogeneidade ambiental e fornecendo habitat para diversas espécies, e consequentemente, aumentando a biodiversidade local (FOSTER et al., 2013). Esses sistemas bioconstruídos também funcionam como um “banco de sementes” de diversas espécies de micro e macroalgas, recuperando a diversidade de sistemas que sofreram perturbações recentes (FREDERICQ et al., 2019). Bancos de rodolitos não apresentam somente estas funções, mas esses organismos também têm um papel importante no ciclo global do carbono, contribuindo para o seu sequestro em forma de carbonato de cálcio biogênico (AMADO-FILHO et al., 2012; MARTIN et al., 2007; VAN DER HEIJDEN; KAMENOS, 2015).

Entretanto, essas algas formadoras de rodolitos estão sendo ameaçadas por condições ambientais relacionadas com mudanças climáticas globais e alterações ambientais regionais. A sua distribuição é diretamente influenciada pelas condições físicas do ambiente (CHAPMAN, 1987), e temperaturas extremas são especialmente importantes na determinação da sua distribuição (WILSON et al., 2004) e nas suas taxas metabólicas e de calcificação (MARTIN; HALL-SPENCER, 2017). Além disso, avaliações experimentais têm demonstrado que a produtividade primária e a produção de carbonato de bancos de rodolitos sofrem um declínio em tratamentos com condições acidificadas e de aumento de temperatura (BURDETT et al., 2018; SCHUBERT et al., 2019). Desta forma, as crescentes alterações ambientais irão resultar não somente em impactos diretos na fisiologia de algas calcárias (escala temporal curta), mas também representam uma mudança na distribuição espacial dessas populações (escala temporal longa).

Contudo, a distribuição das espécies e as alterações em seus limites de ocorrência não são somente determinados por fatores climáticos, e os padrões atuais de distribuição são na realidade resultado da interação de diversos fatores dinâmicos, tanto ambientais, quanto antropogênicos e ecológicos (RILOV et al., 2019). Desta forma, definir ações para conservação de espécies, de ecossistemas e das funções e serviços fornecidos por esses se torna uma tarefa desafiadora. Uma abordagem interdisciplinar é a melhor forma de predizer a resposta de espécies-chave frente a essa grande diversidade de estressores que estão atualmente presentes em ambientes marinhos. Portanto, ao buscar a melhor estratégia para a conservação de bancos de rodolitos, é necessário levantar informações sobre i. as forçantes ambientais naturais e antropogênicas predominantes no ambiente marinho e seus principais impactos em algas coralinas formadoras de rodolitos, e ii. os mecanismos fisiológicos e ecológicos de espécies chave frente a forçantes locais e globais. Partindo disso, devemos então integrar essas informações para mapear a adequabilidade de habitat atual e futura de espécies formadoras de rodolitos, identificando mudanças nos seus limites de ocorrência, e ocasional ganho ou perda de habitats adequados.

1.1. FORÇANTES AMBIENTAIS E ANTROPOGÊNICAS EM ESPÉCIES FORMADORAS DE RODOLITOS

Os estudos fisiológicos, nas últimas décadas, têm buscado entender a resposta dos organismos frente a cada variável ambiental independentemente, em experimentos controlados, para avaliar o desempenho de cada indivíduo a variações de cada forçante (MILES, 2009). Já nas últimas duas décadas, muitos estudos tentam compreender a resposta de populações a futuros cenários, testando, por exemplo, cenários do IPCC (Painel Intergovernamental sobre Mudanças Climáticas) com diferentes níveis de CO_2 na atmosfera. Essa abordagem baseada em cenários testa os efeitos individuais e combinados de algumas forçantes. Mas cada uma dessas abordagens tem suas limitações dentro do número de réplicas que é possível ser trabalhada dentro de um experimento (BOYD et al., 2018). Avaliar somente o efeito de uma variável permite testar o gradiente dos efeitos desta, enquanto que testar um cenário requer a existência de uma condição controle e as condições com os cenários para cada variável ambiental, o que retira a chance de se testar um gradiente de variáveis e também testar muitos fatores (BOYD et al., 2018). Esse é o balanço que a ecologia experimental tem lidado nos últimos anos: aumentar a relevância ecológica ao custo de entender os mecanismos individuais.

Entretanto, considerando a natureza multifacetada das mudanças ambientais, cada vez se torna mais necessário entender a resposta de populações a várias forçantes ambientais (MILES, 2009). Mas estimar o destino delas diante desses diversos fatores é um grande desafio, não somente pelo grande número de variáveis que podem atuar sobre os organismos, mas também pelo fato de que cada indivíduo ou comunidade pode ter uma resposta negativa ou positiva a cada forçante (por isso aqui o uso do termo forçantes, e não estressores, conforme proposto por BOYD; HUTCHINS, 2012). Isso faz com que experimentos investigando o efeito de apenas uma variável dificilmente providenciem informações confiáveis sobre as respostas dos organismos frente a um ambiente multifatorial, já que a interação entre esses fatores muito comumente media as respostas dos organismos (BOYD et al., 2018). Isso já é observado em experimentos com mais de um fator feitos com espécies formadoras de rodolitos, onde alguma forçante pode exacerbar, melhorar ou não influenciar no efeito de alguma outra forçante. Como exemplo, a acidificação dos oceanos pode piorar os efeitos do aumento da temperatura na fisiologia de algumas espécies de rodolitos (KROEKER et al., 2013; VÁSQUEZ-ELIZONDO; ENRÍQUEZ, 2016) ou aumentar a fotossíntese e calcificação de outras espécies (SORDO et al., 2019).

E além da combinação de forçantes globais, é também necessário considerar a interação entre essas mudanças ambientais globais e as locais, características da região em que a população se encontra (RUSSELL et al., 2009). Considerando a costa brasileira, a poluição costeira demanda grande atenção, principalmente quando levamos em conta os atuais desastres ambientais que acometeram ambientes marinhos, como o rompimento da barragem em Mariana e em Brumadinho (em 2015 e 2019, respectivamente), e o derramamento de petróleo em 2019. Mas além de perturbações pontuais como estas, perturbações crônicas também se apresentam como uma importante ameaça a bancos de rodolitos. A fertilização das águas costeiras por poluição orgânica e fertilizantes agrícolas se mostra como uma das principais ameaças a ambientes marinhos da costa brasileira, atrás das mudanças climáticas e atividades pesqueiras e náuticas (MAGRIS et al., 2020). E assim como o efeito da interação entre aquecimento e acidificação dos oceanos sobre espécies formadoras de rodolitos precisa ser investigado, o efeito da interação entre essas mudanças globais e o aumento de nutrientes em águas costeiras também merece atenção. Poucos estudos investigaram a interação entre enriquecimento de nutrientes e aquecimento em rodolitos, mas os que o fizeram observaram uma interação positiva para a espécie (JOHNSON; CARPENTER, 2018; QUI-MINET et al., 2019) ou nenhum efeito (SCHUBERT et al., 2019).

Além disso, é necessário considerar a predição de aumento da intensidade e frequência das ondas de calor marinhas nas próximas décadas (FRÖLICHER; FISCHER; GRUBER, 2018). Esses eventos extremos já causaram o deslocamento da distribuição de algas marinhas, e dessa forma, serão provavelmente determinantes do futuro de rodolitos (STRAUB et al., 2019). Diferentemente da tendência de aquecimento lento e gradual da temperatura média dos oceanos, as ondas de calor marinha podem superar as capacidades adaptativas de populações e causar danos sérios em comunidades, produção primária e biogeografia de algas marinhas (STRAUB et al., 2019). Isso mostra que ondas de calor são processos chave em mudanças no nível do ecossistema, e o estudo de seus impactos é de grande urgência, já que estes eventos já estão ocorrendo (SMALE et al., 2019). Entretanto, poucos estudos tem investigado o efeito de ondas de calor marinhas em espécies formadoras de rodolitos (CORNWALL; DIAZ-PULIDO; COMEAU, 2019). Mediante do exposto, se torna importante investigar o efeito das ondas de calor marinhas e acidificação oceânica em combinação com aumento na concentração de nutrientes em ambientes costeiros brasileiros, já que esse desenho experimental, mesmo perdendo a resposta individual a cada variável, tem grande relevância ecológica e é central no entendimento da vulnerabilidade de rodolitos brasileiros frente a mudanças ambientais diversas.

1.2. NICHO ECOLÓGICO

O conceito de nicho foi primeiro introduzido por Joseph Grinnell em 1917, no seu estudo clássico sobre a distribuição da ave “California Thrasher”. Neste trabalho, Grinnell concluiu que a distribuição dessa ave dependia tanto de fatores ambientais quanto fisiológicos (GRINNELL, 1917). Porém, Grinnell apenas descreveu os requisitos ambientais de cada espécie, não incluindo as interações com outras espécies, e consequentemente, seus efeitos na distribuição (LEIBOLD, 1995). Em paralelo, Charles Elton (1927) estava desenvolvendo o seu conceito de nicho, que se baseava nas relações alimentares e de inimigos da espécie, sendo então o nicho a posição da espécie dentro de um ambiente (ELTON, 1927). Além disso, Elton foi o primeiro a introduzir a ideia de que o nicho real de uma espécie pode ser diferente do seu nicho potencial, e incluir os efeitos da espécie no ambiente.

Já em 1957, George E. Hutchinson redefiniu o termo de nicho ao considerar que as variáveis ambientais que cada espécie tolera são dimensões do ambiente, e se um ambiente tem *n* dimensões, o nicho se torna um espaço *n*-dimensional (um “hiper volume”), composto das tolerâncias de cada espécie a uma determinada parte de cada dimensão. Hutchinson (1957) descreveu que esse espaço multidimensional do nicho era composto por variáveis ambientais e bióticas, onde o *fitness* absoluto esperado de uma população é pelo menos zero. Justamente este espaço, onde o crescimento intrínseco da população é positivo, foi chamado por Hutchinson de nicho fundamental. O nicho fundamental considera apenas as variáveis que sofrem poucas alterações ao longo do tempo, ou seja, as condições abióticas, nomeadas por ele variáveis “cenopoéticas” (*scenopoetic*). Já o nicho realizado é um subconjunto do nicho fundamental, e considera as interações com outras espécies que fazem com que a espécie ocorra em condições mais restritas, chamadas variáveis “bionômicas” (*bionomic*). Desta forma, o nicho fundamental de Hutchinson é um conceito abstrato, e a distribuição que observamos das espécies é uma consequência do seu nicho realizado. Desta definição surgem então, três deduções: i. o nicho é um atributo da espécie, não do ambiente; ii. portanto, não existe nicho vazio; iii. e que cada espécie tem seu próprio e único nicho (HERBOLD; MOYLE, 1986). Diante disto, Hutchinson via “oportunidades” ecológicas e evolutivas não em nichos vazios, mas sim em condições ambientais, disponibilidade de recursos e o gradiente de *fitness* de uma espécie (COLWELL; RANGEL, 2009).

Porém, foi somente mais tarde, em um livro publicado em 1978, que Hutchinson descreveu a importante e conhecida “dualidade de Hutchinson”, a dualidade entre o espaço multidimensional do nicho e o espaço físico em que as espécies vivem (biótipo), que permite determinar a distribuição biogeográfica de uma espécie a partir de padrões espaciais de variáveis cenopoéticas (COLWELL; RANGEL, 2009). Assim sendo, a aplicação dessa dualidade em termos biogeográficos é direta: o biótipo é representado por um mapa, com cada ponto tendo sua respectiva coordenada e cada ponto com seus valores de *n* atributos ambientais. É importante notar, entretanto, que assim como uma dualidade matemática, a dualidade de Hutchinson não representa uma equivalência de 1 para 1: cada ponto no hiper volume do nicho pode apresentar vários pontos geográficos, mas também nem todos os pontos no espaço de nicho são representados no biótipo; porém, cada ponto no biótipo corresponde a exatamente um ponto no espaço de nicho (COLWELL; RANGEL, 2009). É a partir dessa regra importante que a reciprocidade entre nicho e distribuição das espécies se encontra, e que se permitiu o desenvolvimento das ferramentas conhecidas como Modelos de Nicho Ecológico (MNE). Os modelos de nicho usam os valores das variáveis ambientais encontradas nas ocorrências atuais das espécies para modelar o seu nicho, e então projetam os pontos do espaço de nicho para pontos geográficos, encontrando, portanto, locais dentro do hiper volume de nicho da espécie (WIENS et al., 2009). É possível, consequentemente, gerar um mapa de conformidade de habitat, que identifica localizações (no passado, presente ou futuro) que possivelmente podem ser habitadas por essas espécies, com base nas características ambientais das localidades de ocorrências conhecidas (ELITH; LEATHWICK, 2009).

A partir do exposto, é possível também explorar essa dualidade dentro da distinção entre nicho realizado e nicho fundamental. À primeira vista, pode parecer que a modelagem de nicho estima o nicho fundamental, já que não inclui as interações com outras espécies, baseando-se somente nas condições ambientais e as suas relações espaciais/geográficas. Todavia, toda observação da espécie no mundo físico é resultado da interação desta com outras espécies, fazendo com que qualquer nicho definido se baseando nessas ocorrências seja, na melhor das hipóteses, o nicho realizado (PETERSON; ANDERSON, 2012). Além disso, é necessário muito conhecimento sobre a fisiologia da espécie, obtido através de experimentos testando os limites fisiológicos desta, para possibilitar a definição do seu nicho fundamental (SOBERON; ARROYO-PEÑA, 2017). Isso porque, como Hutchinson observou, a dimensão total do nicho fundamental pode não ser revelada apenas pelas condições ambientais observadas dentro dos limites de ocorrência, já que podem existir regiões dentro do espaço do nicho que não estão disponíveis para a espécie (HUTCHINSON, 1978). Aqui entra uma distinção importante que é levada no restante deste trabalho: distribuições geográficas são por muitas vezes distintas do espaço de nicho de uma espécie, fazendo com que modelos de nicho, apesar de estimarem e gerarem o hiper volume de nicho de uma espécie baseado nas condições ambientais da conhecida distribuição de uma espécie, não tem como resultado final a potencial distribuição da espécie em si (SOBERON; PETERSON, 2005). Portanto, o resultado dos modelos de nicho é somente uma estimativa de adequabilidade de habitat para aquelas espécies, locais com condições dentro do nicho estimado da espécie (SOBERÓN, 2010; HIRZEL; LE LAY, 2008). Isso reflete também na terminologia da ferramenta: modelos de nicho que utilizam apenas dados de ocorrência e de variáveis ambientais, são, na sua essência, de fato modelos de nicho; não são modelos de distribuição de espécies, outra nomenclatura utilizada comumente como equivalente na literatura. No universo conceitual que esta dissertação trabalha, para um modelo de nicho ser um modelo de distribuição por si, este deve incluir pelo menos alguma característica da capacidade de dispersão da espécie. A habilidade de dispersão de cada espécie pode limitar drasticamente a sua extensão de ocorrência, e podem existir muitos lugares que correspondem a porções do seu nicho fundamental, mas que estão indisponíveis e/ou não ocupados (JACKSON; OVERPECK, 2000). Isso é evidenciado em estudos de espécies invasoras, que mostram que quando esses limites de dispersão são removidos, as espécies podem encontram regiões com habitats adequados que vão além das condições ambientais encontradas em sua distribuição nativa (BROENNIMANN; GUISAN, 2008).

A possibilidade de projetar um modelo de nicho para outros períodos, tanto do passado como do futuro, buscando estimar a adequabilidade de habitat da espécie em outro momento, se baseia no princípio de conservadorismo de nicho (PYRON et al., 2015). A teoria de conservadorismo de nicho tem base teórica e empírica de que nichos tendem a evoluir relativamente devagar nas suas linhagens (SOBERON; NAKAMURA, 2009). Uma das evidências empíricas são estudos capazes de prever eventos de invasão a partir de distribuições geográficas passadas da espécie, e também a tendência de espécies terem nichos mais similares aos nichos de espécies próximas do que de espécies mais distantes filogeneticamente (LOSOS, 2008; MARCELINO; VERBRUGGEN, 2015; PETERSON, 2003; PYRON et al., 2015). Contudo, existem muitas críticas aos MNEs por utilizar essa suposição, já que até mesmo o que o termo compreende ainda é difuso na literatura (SOBERON; NAKAMURA, 2009), e alguns autores argumentam que o nicho pode evoluir relativamente rápido, principalmente quando discutimos mudanças ambientais e invasões biológicas (PEARMAN et al., 2008). Porém, Peterson (2011), através de uma revisão da literatura investigando essas questões conseguiu encontrar um consenso entre estudos: o de que eventos de longa duração, como diferenciações entre filogenias, mostram sinais de quebra do conservantismo de nicho, enquanto que eventos curtos ou recentes (como invasões) têm uma grande tendência à conservação.

Pensando, portanto, nessa escala de tempo, podemos voltar à dualidade de Hutchinson. Quando se estima o espaço de nicho a partir da distribuição geográfica, esse espaço de nicho engloba deslocamentos da espécie, fragmentações da sua distribuição e limites de dispersão das espécies (COLWELL; RANGEL, 2009). Além disso, o espaço de nicho também abrange regiões do biótipo que contêm condições adequadas para a espécie, mas não estão ocupadas (JACKSON et al., 2009). Portanto, a espécie pode sofrer alterações na sua distribuição geográfica se “movendo” dentro do espaço de nicho dela, encontrando por ora regiões em um extremo do seu espaço de nicho, e por ora em outro, sem causar alterações no seu nicho (COLWELL; RANGEL, 2009). Em outras palavras, o espaço de nicho inclui muitos pontos de condições ambientais do mundo físico, já que os próprios deslocamentos da espécie no biótipo incluem mais pontos no hiper volume do nicho; mas a dualidade permite separar o que acontece no mundo físico do espaço de nicho. Mas claro, a ligação entre o biótipo e o nicho não é à toa: o que acontece no mundo físico causa de fato mudanças evolutivas na espécie (DAVIS; SHAW; ETTERSON, 2005), mas aqui retornamos à escala de tempo. Em escalas de tempo relevantes a processos evolutivos, o espaço de nicho de uma espécie pode expandir ou reduzir, de acordo com as mudanças no *fitness* da espécie causadas por mutações, extinção, seleção e deriva genética (HOLT, 2009; PEARMAN et al., 2008). E assim, a distribuição geográfica da espécie pode ser mudada apenas minimamente, ou drasticamente.

Considerando a velocidade das mudanças climáticas (nas centenas de anos), é razoável assumir que haverá uma conservação do nicho das espécies, já que estas não conseguem se adaptar tão rapidamente a novas condições ambientais (BERG et al., 2010). Desta forma, se uma espécie já está nos limites fisiológicos dela, como por exemplo, no extremo do seu nicho térmico, e não conseguir se adaptar às novas condições ambientais, o resultado mais provável é a sua extinção (JUMP; PEÑUELAS, 2005). Entretanto, se esta conseguir se dispersar para novas regiões, a espécie pode rastrear (do inglês *tracking*) o seu nicho, deslocando a sua distribuição para novos locais com condições dentro das necessárias para manter uma população viável (TINGLEY et al., 2009). Porém, a abordagem da modelagem de nicho, por considerar apenas as condições ambientais que estão dentro do nicho da espécie para predizer a sua presença ou ausência em condições climáticas futuras, está fadada a erros, por não considerar diversos outros aspectos que ditarão o verdadeiro impacto das mudanças climáticas na distribuição das espécies. Esses aspectos vão desde possíveis populações que evolutivamente, por estarem sob diferentes pressões evolutivas, podem ser mais resistentes a mudanças, até a interações com outras espécies, que estarão sob as mesmas pressões e sofrerão mudanças também (IKEDA et al., 2017; OCKENDON et al., 2014; VERGÉS et al., 2016). Apesar de todas essas necessárias ressalvas, de áreas da ecologia que ainda estão em construção e evolução, tentar compreender a futura adequabilidade de habitat de uma espécie, baseado em sua atual distribuição, é de grande utilidade tanto para ações de manejo e mitigação das mudanças climáticas, quanto para levantar questões dentro da ecologia daquela espécie.

Agora, considerando o objeto de estudo desse trabalho, poucos estudos têm tentado estimar a distribuição ou adequabilidade de habitat de espécies formadoras de rodolitos. Estudos que geraram modelos de nichos para rodolitos usaram diversas espécies, como o estudo de Martion et al. (2014) que usou ocorrências de todas as espécies formadoras de *mäerl* no Mediterrâneo, o estudo de Carvalho et al. (2020) feito com ocorrências de todas as espécies formadoras de rodolitos do Brasil, e o estudo de Simon-Nutbrown et al. (2020) que utilizou ocorrências de bancos de algas coralinas (registros de *Phymatolithon calcarium, Lithothamnion glaciale* e de *mäerls* no geral) na Escócia. Como comentado anteriormente, uma das pressuposições dos modelos de nicho é de que existe conservação do nicho da espécie, e esta conservação pode ser até expandida para espécies dentro de um mesmo gênero, já que na sua grande maioria, o nicho entre espécies muito próximas é altamente similar. Ao utilizar ocorrências de diversas espécies, principalmente quando falamos de algas formadoras de rodolitos, que compreendem três ordens, esse pressuposto não é respeitado por estes estudos, já que o nicho dessas espécies dificilmente é próximo. Isso também é observado fisiologicamente, já que muito foi se mostrado na literatura de que a resposta de rodolitos a condições ambientais é altamente dependente da espécie e da sua história evolutiva. Dessa forma, é importante também agregar informações sobre a resposta fisiológica das espécies com resultados de modelos de nicho, de forma a testar e validar os resultados dos modelos. Assim sendo, a presente dissertação buscou modelar a adequabilidade de habitat do presente e do futuro de uma espécie formadora de rodolitos da costa brasileira, e investigar sua resposta a combinação de três forçantes ambientais de forma a identificar a vulnerabilidade desta espécie a condições ambientais futuras.

1.3. OBJETIVOS

1.3.1. Objetivo geral

Identificar as principais ameaças de ações antrópicas sobre a distribuição e resistência dos bancos de rodolitos brasileiros, e inferir por modelagem de nicho validada por dados experimentais a vulnerabilidade de uma importante espécie formadora de rodolitos frente às mudanças ambientais em interação.

1.3.2. Objetivos específicos

Capítulo I

1) Identificar na literatura científica as principais ameaças aos bancos de rodolitos brasileiros;

2) Construir um conhecimento base sobre os principais estudos que avaliaram experimentalmente a resposta de rodolitos brasileiros frente a estressores globais e locais.

Capítulo II

1) Avaliar experimentalmente a resposta de *Lithothamnion crispatum* Hauck 1878 a uma exposição de cinco dias à combinação de estressores globais (ondas de calor marinhas e acidificação dos oceanos) e locais (aumento na concentração de nutrientes), e examinar se há recuperação dos indivíduos após a remoção dos estressores;

2) Descrever a adequabilidade de habitat de *Lithothamnion crispatum* através de um modelo de nicho nas condições ambientais atuais, e em dois cenários futuros, determinando

a perda e ganho de regiões com adequabilidade para esta espécie no futuro.

2. CAPÍTULO I: MAJOR THREATS TO RHODOLITH BEDS – OCEAN ACIDIFICATION, GLOBAL WARMING AND LOCAL STRESSORS

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Abstract

Since the industrial revolution the human population has accelerated its magnitude of impact on the world's oceans. The observed consequences of our rising population and globalization have expanded substantially and are expected to affect even the deepest ecosystems. The extensive rhodolith beds along the Brazilian coastline that are present from the shallows down to 133 m are predicted, and already observed to suffer from the consequences of human interference. Rhodolith beds are predicted to experience a daunting diversity of anthropogenic threats, which act at different scales. Global stressors such as ocean acidification and global climate change are shown to affect fundamental metabolic processes, which over time is expected to jeopardize the integrity of these ecosystems. Local stressors such as nutrient runoff, pollution and calcium carbonate mining are expected to interact with global stressors and, in multiple cases, exacerbate already negative prognoses.

Keywords: Anthropogenic impacts, physiological responses, eutrophication, resilience, ecosystem services and functions

2.1. CHANGES IN ATMOSPHERIC CO_2 AND ITS CONSEQUENCES

Earth's climate is greatly defined by the composition of the atmosphere. As radiation enters the atmosphere, it interacts with gases capable of absorbing and emitting the radiant energy. This fraction of gases represents less than 1% of the total atmosphere mass, and is composed, among others, by water vapor, ozone, methane, nitrous oxide, and the now widely known carbon dioxide (CO_2) (Hartmann, 2016). CO_2, among the other gases, is a greenhouse gas, trapping heat radiating from Earth back to space. This phenomenon is responsible for keeping Earth warm enough to sustain life. As such, the concentration of this gas in the atmosphere is directly related to how much heat is retained in the planet. The natural CO_2 concentrations between glacial and interglacial periods ranges between 180-300 ppm (Ruddiman, 2008). As of March of 2019, CO_2 concentration in the atmosphere reached 400 ppm (NOAA, 2019), a value higher than any recorded on Earth in the past 800,000 years (Lüthi et al., 2008). This anthropogenic alteration of the atmosphere has reverberating effects on Earth's climate and biogeochemical cycles, and in important ecosystems, such as rhodolith beds.

2.1.1. Ocean warming

The aforementioned increase in CO_2 concentration in the atmosphere has already resulted in an increase of 1 degree Celsius in the global average temperature since 1880 (NASA, 2018). By the end of the century, the projected global mean surface temperature can reach up to 4.3ºC if emissions stay business-as-usual (IPCC, 2019). Increasing temperatures have cascading effects not only in the climate system, but also in ecosystems and the services provided by them. With a changing climate, species have either to adapt, tolerate, move to a new location or endure extinction, and what will determine the outcome is their physiological, ecological and evolutionary response (Berg et al., 2010). As such, investigating the impacts of ocean warming in coralline algae is of extreme importance to determine the future of rhodolith beds.

The distribution and phenology of marine algae has a strong relationship with temperature (Hoek, 1982). Many metabolic processes in algae are affected by temperature, and rhodoliths are no exception. Enzymatic-regulated processes, such as growth (englobing carbon incorporation, calcification), photosynthesis and respiration are temperature-sensitive in rhodoliths (Steller et al., 2007). In fact, rhodoliths are often used as climate proxies, as their calcification rates vary according to climatic conditions, and their growth bands can be used to obtain paleotemperature information, as less-extensively calcified cells represent fastest growth in warmer temperatures, and more-extensively calcified cells are found in colder temperatures (Kamenos and Law, 2010; Martin et al., 2013). The effects of elevated temperatures in the calcification of coralline algae were recently reviewed by Cornwall et al. (2019). The authors found a general trend across multiple studies that coralline algal calcification is affected when temperatures are ~5ºC above the ambient temperatures of both cool and warm temperate regions, and tropical reefs. However, each species has a specific response to temperature (and other environmental conditions – see Schubert et al., (2019)), and other physiological and reproductive features may be impaired by ocean warming, even when calcification is not (Cornwall et al., 2019). Thus, to understand the general response trends of rhodolith-forming species, we need to look at various indicators of the effects of elevated temperatures in species from different environments (Fig. 1).

The response of coralline algae to elevated temperatures depends on their thermal range of occurrence. Temperatures within the range that the algae species is historically and evolutionary adapted to, present optimal physiological conditions, while temperatures higher or lower to those will represent suboptimal physiological conditions, and above a certain threshold, some temperatures will be detrimental to the algae (Fortes and Lüning, 1980; Lüning, 1990). This relationship with temperature depends on the distribution of the species (temperate species are adapted to a wider range of temperatures than tropical species) and the depth of their occurrence (intertidal species are exposed to a wider range of temperatures than benthic species, for example) (Martin and Hall-Spencer, 2017). A small increase in temperature has positive (Martin et al., 2013) or no effects (Noisette et al., 2013a) in growth, calcification and photosynthesis of rhodoliths. However, temperatures above a certain threshold are damaging for rhodoliths, either from temperate or tropical regions, causing bleaching, and declines in photosynthesis and calcification (Anthony et al., 2008). For example, seasonal fluctuations in seawater temperature cause changes in photosynthetic and respiration rates of *Lithophyllum margaritae* (Hariot) Heydrich, but when temperatures surpassed 30ºC, lower photosynthetic and growth rates were observed (Steller et al., 2007). At 32°C, the rhodolith-forming species *Neogoniolithon* sp. Setchell & L.R.Mason showed losses in photosynthesis and presented photodamage (Vásquez-Elizondo and Enríquez, 2016).

What we can expect by looking at these studies is that the response of rhodoliths to ocean warming will depend on the species, the rate of warming, as well as their life histories and habitat. In addition, populations that are not extinguished by ocean warming will have to adapt to these new conditions, but this does not mean that they will adapt "well": their fitness will likely be affected, resulting in reduced abundance, and their interaction with other species will be altered, reflecting in a reduced competitive ability and defense against predation (Harley et al., 2012). Species which will neither adapt nor became extinct in the future, will have to migrate to new locations. This is a trend already being observed and that is expected to become more frequent in the future, where species experience a range shift to locations with environmental conditions more similar to what they are adapted to (Poloczanska et al., 2013). The bigger expression of this trend is the tropicalization of temperate marine ecosystems, which will also represent changed ecological interactions, as grazers and other organisms will also be under the same shift (Vergés et al., 2014)

2.1.1.1. Marine heatwaves – punctual events but lingering threats

As the ocean absorbs heat from the atmosphere, marine heat waves (periods of extreme warming of the sea surface, lasting from days to months) have increased in frequency, intensity and extension over the last decades, and this trend is set to persist in the remainder of the century (Frölicher et al., 2018). Extreme events are now being regarded as important drivers of species distributions and in biodiversity patterns, and thus the increase in their intensity and frequency will lead to changes in communities composition and cause range shifts of species (Wethey et al., 2011; Wernberg et al., 2013; Rilov et al., 2019). In a long-term monitoring of kelp forests and coral reefs in Western Australia, researchers were able to document how an extreme heat wave caused the loss of approximately 2300 km^2 of kelp forests, leading to a community shift to species of subtropical and tropical waters (Wernberg et al., 2016). The loss of benthic cover by kelp and encrusting coralline algae, and their replacement by turf-forming algae was also observed after a heat wave in 2011 in Australia (Wernberg et al., 2013).

For coralline algae, there are very few studies investigating the impacts of marine heat waves. Short et al. (2015) measured growth, calcification and mortality rates of a crustose coralline algae (CCA) subfamily *Hydrolithoideae* A. Kato & M. Baba in response to a heat wave in Western Australia. During summer, higher calcification raters are expected, but in a summer with registered temperature anomalies, increased mortality was observed, and no changes in calcification rates were detectable between seasons (Short et al., 2015). Sordo et al., (2019), in an experiment testing the effects of marine heatwaves in *Phymatolithon lusitanicum* V.Peña from Portugal, described positive effects of increasing temperatures on photosynthesis, calcification and respiration rates. However, more studies encompassing the responses of rhodolith-forming species to events of anomalous warming are necessary, as this information is virtually non-existent, and species adapted to different environmental conditions will respond distinctively to heat waves (Cornwall et al., 2019). Schubert et al. (2019) investigated the effects of marine heat waves in rhodoliths from a marine reserve in Southern Brazil (27°S, 48ºW). *Melyvonnea erubescens* (Foslie) Athanasiadis & D.L.Ballantine, 2014 and *Lithothamnion crispatum* Hauck, 1878 were exposed to a sudden increase of 5 degrees Celsius (from 23ºC of the field to 28ºC). *M. erubescens* presented a decrease in net photosynthesis and calcification rates in response to the increase in temperature, while *L. crispatum* up-regulated its net photosynthesis, but at the same time, experienced decreased calcification rates. These results indicate that the impacts of heat waves will affect different species composing rhodolith beds distinctively, but the overall losses in primary production and carbonate storage will likely affect the dynamic of these ecosystems. Moreover, the species studied by Schubert et al. (2019) have a wide occurrence in the Brazilian coast, and assessing the response of distinct populations is also important to understand if populations locally adapted to different conditions will be affected differently (Sgrò et al., 2011). Further studies of the impacts of extreme events in the primary and carbonate production by different Brazilian rhodolith populations are necessary to allow the full comprehension of ecosystem's goods and services losses in the future, as well as the response of different populations of the same species.

2.1.2. Ocean Acidification

Not only the ocean absorbs heat, but it is also the main agent in the absorption of atmospheric CO_2, storing approximately 30% of the anthropogenic carbon emitted to the atmosphere (IPCC, 2019). Surely, this exchange comes at a price. The higher uptake of CO_2 by oceans impacts directly water's pH, making it more acid and lowering calcium carbonate ($CaCO_3$) saturation in surface waters. The decrease in pH and alteration in fundamental chemical balances in oceans is called ocean acidification (Doney et al., 2009). According to the last report of the Intergovernmental Panel on Climate Change (IPCC) of 2014, there is high confidence that if CO_2 emissions continue, ocean acidification will persist and highly affect marine ecosystems.

Before the industrial revolution, average ocean surface water pH was of approximately 8.17, but has now decreased to 8.11 and it can decrease even further depending on the rate of emissions (IPCC, 2014). The ocean carbonate system is governed by a series of chemical reactions:

$$CO_{2(atm)} \leftrightarrow CO_{2(aq)} + H_2O \leftrightarrow H_2CO_3 \leftrightarrow H^+ + HCO_3^- \leftrightarrow 2H^+ + CO_3^{2-}$$

When CO_2 is dissolved in seawater, it generates carbonic acid (H_2CO_3), which then forms bicarbonate (HCO_3^-) and carbonate (CO_3^{2-}) by the loss of hydrogen ions (H^+). By adding CO_2 to seawater, the concentrations of bicarbonate and hydrogen ions also increase. More hydrogen ions result in lower pH because:

$$pH = -\log_{10}[H^+]$$

Which, at the same time, decreases carbonate ion concentration.

The ability of global oceans to absorb and store CO_2 depends on the extent of calcium carbonate ($CaCO_3$) dissolution in seawater, which in turn, depends on the concentration of CO_3^{2-} and Ca. $CaCO_3$ has a biogenic origin, found in shells and skeletons of marine organisms, and in the focus of this book, coralline red algae. The saturation state (Ω) of $CaCO_3$ is, therefore:

$$\Omega = \frac{[Ca^{2+}][CO_3^{2-}]}{K'_{sp}}$$

Where K'_{sp} is the apparent solubility product, which depends on seawater's salinity, temperature, pressure and the particular mineral phase. $CaCO_3$ has six polymorphs, two which are important components in the formation of shell and skeleton of marine organisms: aragonite and calcite. Aragonite is approximately 50% more soluble than calcite, which makes its saturation state's value lower. Formation of $CaCO_3$ happens where $\Omega>1.0$ and dissolution occurs where $\Omega<1.0$. Therefore, the increasing input of CO_2 is shallowing the saturation horizons of both aragonite and calcite, as saturation states are directly related to pressure. Coralline red algae deposit $CaCO_3$ in the polymorph of high magnesium calcite (Mg-calcite, or dolomite), more soluble than calcite and aragonite (50% and 20%, respectively), which makes them especially vulnerable to changes in the saturation state (Ragazzola et al., 2013).

Rhodolith beds are, therefore, important in the global carbon cycle, by the storage of carbon in the form of $CaCO_3$. Only in the Abrolhos Shelf in Brazil, the estimative is that $CaCO_3$ production is of 0.025 Gt yr^{-1}, comparable to the production of coral reefs in the Caribbean (Amado-Filho et al., 2012). Considering that rhodolith beds occur from Amazon's mouth to southern Brazil, with 230,000 km^2 of niche suitability only in the Brazilian coast (Carvalho et al., 2019), their global contribution to carbon storage is immense. However, the solubility of their Mg-calcite rich skeletons makes them highly susceptible to dissolution under future scenarios of ocean acidification, and their role in the global carbon cycle will be impaired.

The vulnerability of rhodoliths to ocean acidification has been assessed in many experimental studies. While some studies have found negative effects of decreasing pH in coralline species, such as decreasing photosynthetic (Anthony et al., 2008) and calcification rates (Büdenbender et al., 2011; Kato et al., 2014), and loss of structural integrity (Ragazzola et al., 2012), others have found either no effects or positive effects on such physiological rates (Noisette et al., 2013b, 2013a; Sordo et al., 2016). Nonetheless, it is necessary to consider that these responses are species-specific, and also depend on the proportion of dolomite found in their skeletons (Mccoy and Kamenos, 2015; Nash et al., 2019). In an investigation of the short-term effects of decreased pH (7.4) in the physiology of *Lithothamnion crispatum* from Southern Brazil, decalcification and reduced photosynthetic yield were observed (Muñoz et al., 2018). CCA from north-eastern Brazil also demonstrated a decline in photosynthetic yield after exposure for 23 days to a decrease of 0.9 in pH (Scherner et al., 2016).

Other important factor to be considered is the time of exposition. Sordo et al. (2018) observed that after 11 months of exposure to high CO_2 concentrations, the calcification and photosynthesis rates of the mäerl *Phymatolithon lusitanicum* increased. However, after 20 months of exposure, this pattern was reversed, indicating that although coralline algae can maintain high production rates for some time at low pH, they do not present resistance to it in the long term (Sordo et al., 2018). This lower resistance will facilitate bleaching, diseases, herbivory and reduce the ability of coralline algae to compete with fleshy algae (Short et al., 2014; Sordo et al., 2018). In this regard, Burdett et al. (2018) described the sensitivity of a community formed by coralline algae to CO_2 enrichment, where a short-term exposure to higher concentrations of CO_2 led a shift to net community dissolution of a local coralline algal bed, composed primarily by *Lithothamnion glaciale* Kjellman. This supports the understanding that in a higher-CO_2 world, rhodolith beds will experience a transition in community composition, with species more tolerant to these conditions becoming the foundation of the community (Celis-Plá et al., 2015; Burdett et al., 2018).

2.2. BAD THINGS COME IN MORE THAN THREES

As we alter global climate and biogeochemical systems, we also are changing environments at a local scale. Everything we add in our water ends up draining to the ocean, from chloride to nutrients derived from agricultural lands, even reaching ecosystems far from the coast. The major contributions of agricultural activities to water pollution are nutrients, pesticides, metals, organic matter and sediments, among others (FAO, 2017). Economic activities such as mining and petroleum extraction also pose threats to marine ecosystems, considering the history of accidents related to these activities and the impact caused by offshore exploration. But rhodolith beds have their own economic value due to their $CaCO_3$-rich skeletons. They have been proposed for agronomic applications as fertilizes and for correction of acidic soils (Foster, 2001; Horta et al., 2016). This demonstrates that rhodoliths beds are in a conflict zone – between activities with economic value in these ecosystems, and human use of the functions and services provided by them, their conservation seems like a complicated puzzle. Herein we discuss the major local threats to Brazilian rhodolith beds.

2.2.1. Increased nutrient runoff

The explosive increase in eutrophication of coastal waters globally is related to the human-controlled creation of reactive nitrogen (Howarth, 2008) and phosphorus, especially for the production of fertilizers (Ngatia et al., 2019). As human populations continue to grow, thus increasing the demand for food and the discharge of wastewater - another important source of nutrients to marine waters -, eutrophication in coastal zones related to human activities will continue to increase. Nutrients are important to the growth of macroalgae, but calcareous algae may be sensitive to coastal pollution (Bjork et al., 1995). Brazil has a historical problem with coastal pollution. Half of the population (~ 100 million people) still does not have access to adequate treatment and disposal of sewage (De Sousa and Barrocas, 2017), and where wastewater treatment is available, it does not remove emerging contaminants, such as hormones, pesticides and illicit drugs (Campestrini and Jardim, 2017) Moreover, the use of fertilizers in Brazil reached a historical record in 2018, when 35.506.299 tons were delivered in the country, according to the National Association for the use of Fertilizers (ANDA, 2019). It is difficult to estimate the quantity of nutrients from point and non-point sources transported by rainfall, runoff and leaching that reach the coastal zone, but the effects are already being observed. The increased presence of sewage-derived nutrients in coastal areas of Brazil led to decreasing species richness and resilience of benthic communities (Martins et al., 2012). Scherner et al. (2013) investigated the changes in coastal assemblages in the Brazilian coast caused by increased sewage discharge and demonstrated declines in calcareous algae in regions with high urban pressure.

Primary production is limited by nutrient availability, and it is no different in the marine environment. Moderate nutrient enrichment can be beneficial to algae, increasing growth rates and maybe even helping them cope with climate change (Celis-Plá et al., 2015). However, in high concentrations, nutrients can be detrimental and affect important metabolic processes. For example, phosphorus has been regarded as a “poison” for calcification processes, as it inhibits calcite crystal growth (Simkiss, 1964; Bjork et al., 1995). Moreover, fleshy epiphytes will obtain advantage in a scenario with higher availability of nutrients, as they are fast-growing and can thus rapidly cover calcareous algae, which have much lower growth rates and will likely be affected by eutrophic conditions (Russell et al., 2009). Furthermore, the runoff from coastal zones is accompanied by sediments, increasing the turbidity of the water and reducing light availability for photosynthesis. The congregation of these conditions may lead to a reduced fitness of coralline algae, and consequently, a shift to a different steady-state of the local community.

Some experimental studies have explored the effects of nutrient enrichment in coralline algae. In an investigation of the impacts of increased nitrate (40 µmol/L) and phosphate (1 µmol/L) concentrations on three species of temperate mäerl, Qui-Minet et al., (2019) found no negative effect in calcification in any of the species. Similarly, positive effects of nitrogen enrichment on the calcification rates and photosynthetic pigments of the reef-building CCA, *Porolithon onkodes* (Heydrich) Foslie (Johnson and Carpenter, 2018). Conversely, nutrient enrichment led to lower CCA (*Lithophyllum* Philippi sp.) dry mass, although no impacts in the photosynthetic yield were observed (Russell et al., 2009). In a study of the impacts of nutrient increase in two species of rhodoliths from Arvoredo's Island (Santa Catarina, Brazil), *Melyvonnea erubescens* presented a reduction in net photosynthesis under increased nutrient conditions, while *Lithothamnion crispatum* did not respond to such conditions (Schubert et al., 2019). The results from these studies show that responses to nutrient enrichment are species-specific, and as rhodolith communities are composed of many algae species, community composition will be changed by local nutrient conditions. Therefore, the productivity and carbon storage of rhodolith beds in coastal areas impacted by nutrient runoff will differ according to the species composing the community (Schubert et al., 2019). However, many more studies of the increasing nutrient overload in coastal areas are necessary for the assessment of the precise impacts and possible changes in rhodolith communities' structure, composition and functioning.

2.2.1.1. Experimental evaluation of the impacts of increased nutrient concentrations

Coastal and oceanic populations are exposed to different environmental conditions, and as such, their response to the same stressor may be different. Oceanic islands are considered as "model systems" for ecological studies, being less impacted by human activities than the coastal zone (Vitousek, 2002; Williams et al., 2015). Island populations are adapted to less variation in nutrient conditions, differently than coastal populations, which are exposed to high variation in nutrient concentrations due to continental runoff (Scherner et al., 2012). Therefore, island populations may be less resistant to increased nutrient and reduced light conditions and understanding their response to these condition gives insights about the sensibility of rhodoliths to them. Hence, in order to assess the impact of nutrient increase and reduction of light penetration in the water column in populations of oceanic islands, two field experiments were made, one in Fernando de Noronha (7 days) and one in Trindade Island (15 days). For each experiment, three species were chosen based on their abundance in the island, and each species represented one of the major groups of algae – red, brown and green. As such, in Trindade Island, *Halimeda* sp., *Dictyota* sp. and *Lithothamnion* sp. were used in the experiment. As for Fernando de Noronha, the species chosen were *Sargassum* sp., *Dictyopteris* sp., and a rhodolith-forming species. The depth of sampling of rhodoliths was 6m in Trindade and 1-2m in Fernando de Noronha.

Before the beginning of each experiment, algae were collected, cleaned from epiphytes and weighted to 5 grams of fresh biomass. They were then placed in cylinders (1L of volume) made of a plastic net with holes of 1 cm. Each experiment was composed of four treatments: control (environment irradiance and oligotrophic conditions), low irradiance and oligotrophic conditions, environment irradiance and eutrophic conditions, and low irradiance and eutrophic conditions. To simulate light reduction, a shading screen was placed on top of the cylinders, and the eutrophic condition was replicated by adding NPK nutrients of low and fast dilution. Each treatment had 3 replicas, and cylinders were randomly placed 1m apart in a longline at open sea. To evaluate the physiological conditions of each species, measurements of effective quantum yield (Fv/Fm’) were taken with a pulse-amplitude modulated chlorophyll *a* fluorometer (Diving PAM – Walz Germany). Data was tested for normality with Shapiro-Wilk test (p<0.05) and homogeneity of variances was tested with Levene’s test of the median (p<0.05). An Analysis of Variance (ANOVA) of two factors was then made for each experiment. Post-hoc test of Tukey separated statistically different groups (p<0.05). All data analyses were made in R (version 3.6.0).

The ANOVA analysis showed a significant interaction (p<0.05) between irradiance and nutrient concentrations in different species in the Trindade experiment (Fig. 2), but for the Fernando de Noronha experiment, only different concentrations of nutrients and species presented a significant interaction (Fig. 3). Although the rhodolith-forming species were the group with lower Fv/Fm’ in both experiments, when compared to other species, no significant difference was observed between either different light or nutrient conditions in either experiment (Fig. 2 and 3). The concentration of nutrients used in the experiments was not detrimental to the photosynthetic efficiency of these rhodoliths, similar to what Qui-Minet et al. (2019) observed in a long-term experiment with three *mäerl* species. Moreover, neither condition of light (shaded or unshaded treatments) caused changes in the photosynthetic efficiency of rhodoliths from Trindade. This could be explained by the depth in which the rhodoliths used in the experiments were collected (6m), meaning that they were already adapted to lower light conditions.

2.2.2. Economic activities

Rhodolith beds are spread throughout the Brazilian coast, and as such, they can be found very close to regions with economic interest (Fig. 4). That is the case of the deep-water rhodolith bed in the Peregrino oil field, one of the ten biggest oil fields in Brazil, according to the National Agency of Petroleum, Natural Gas and Biofuels (ANP). The Peregrino oil field is part of the Campos Basin, a region that has been intensively explored not only by activities of oil exploration, but also by calcareous mining and fish dredging, which promote substantial sediment dislodgment (Villas-Bôas et al., 2014). The Peregrino oil field is one example of a conflict area, and another one is the most extensive rhodolith bed in the world, the Abrolhos bank (Amado-Filho et al., 2012). The auctioning of blocks close to the bank (as depicted in Fig. 4), and the oil production fields about 50 km from the reserve, are of great concern for the health of the rhodolith beds (Moura et al., 2013). And more concern about petroleum activities has been raised recently due to the oil spill that affected almost the entire Brazilian coast (Soares et al., 2020). As brought to attention by Sissini et al. (2020), the impacts of this environmental disaster over rhodolith beds are still unknown. The Deepwater Horizon oil spill, which happened in 2010 in the Gulf of Mexico, caused a decrease of the biodiversity associated with rhodolith beds in this region (Felder et al., 2014), and also induced bleaching of rhodoliths (Fredericq et al., 2014). Therefore, it is reasonable to expect that rhodolith beds and associated fauna in regions affected by the oil spill in Brazil will endure impacts.

Rhodoliths are of economic interest as they can be used as a source of calcium carbonate and micronutrients, thus being used as fertilizers and correction of organic soils, and also in the construction sector, as raw material for cement production (Dias, 2000). Their extraction is done by dredging, and this is a practice that has been done in Europe since the 1970s (Grall and Hall-Spencer, 2003). Although rhodoliths are considered as a non-renewable resource, as their growth rate is in average 1 mm yr^{-1}, their extraction in many countries, such as Ireland (5,000 t yr^{-1}) and France (500,000 t $year^{-1}$), is a common practice (Coletti et al., 2017). In Brazil, extraction can be up to 18 t yr^{-1} per company, and Brazilian law refers to rhodoliths as a non-living resource (Santos et al., 2016). While Great Britain have ceased the licensing of rhodolith extraction, and in Spain and the Mediterranean environmental laws regulate economic activities in some rhodolith beds (Salomidi et al., 2012), Brazil still does not have clear regulations regarding these ecosystems.

One of the many byproducts shared by activities of petroleum extraction, mining and rhodolith extraction is the plume of sediments created, which can settle upon benthic assemblages. This load of sediments has been demonstrated to impair the photosynthetic activity of coralline algae (Wilson et al., 2004; Harrington et al., 2005), both shallow (Riul et al., 2008; Reynier et al., 2015) and deep-water species (Villas-Bôas et al., 2014; Reynier et al., 2015). The coverage of specimens *Lithothamnion* Heydrich sp. from a shallow-water coastal reef from Paraíba, Brazil, by a thin sediment layer reduced net production by 70% (Riul et al., 2008). Photosynthetic efficiency is also affected by sediment coverage, as demonstrated by Figueiredo et al. (2015). In this study, the two most dominant species of the deep-water (100 meters depth) rhodolith bed in the Peregrino oil field, *Mesophyllum engelhartii* (Foslie) W.H.Adey and *Lithothamnion* sp., presented a reduction in photosynthetic efficiency of 50% at 70% of sediment coverage, establishing a negative correlation between the added amount of sediment and photosynthetic rates. The reduction in photosynthesis efficiency is mostly due to the sediment coverage of the organisms, which affects not only light availability, but also gas exchanges, important in the primary metabolism of these algae (Riul et al., 2008; Figueiredo et al., 2015). As a matter of fact, it is not only thin sediments that have been proven to affect rhodoliths. Natural coarse sediments from the Peregrino oil field and complete burial of rhodoliths also caused reductions in photosynthetic efficiency, changes in coloration and, in the case of burial, death (Villas-Bôas et al., 2014; Reynier et al., 2015).

Consequently, dredging and extraction activities close or in rhodolith beds must be correctly regulated by environmental agencies. The Environmental Agency of the Brazilian Government (IBAMA) has, in the past, adopted the Precautionary Principle (Cooney, 2004), denying requests of oil or gas drilling near rhodolith beds (Santos et al., 2016). However, considering the position of the new Brazilian federal government regarding the environment, this is not a guarantee anymore. Brazil has historically focused in short-term targets to increase economic growth that often collide with sustainability needs and goals (Pereira, 2019), and new practices, such as the unrestrained release of new pesticides [474 only in 2019 - Oliveira &

Tooge (2019)], or new legislations, like the proposition allowing mining in indigenous protected areas (Souza, 2020), are worsening this tradition. River runoff delivers these contaminants in the coastal zone, and the current mining and agricultural use of pesticides already implicate in polluted coastal zones in Brazil (Liebezeit et al., 2011; de Mahiques et al., 2013). Hydrocarbons from oil and gas exploration can also be found in coastal waters and species of economic interest (Santiago et al., 2016). To incentive the uncontrolled expansion of these activities, especially without a strong environmental agency monitoring and licensing them – IBAMA, the administrative arm of Brazil's Environmental Ministry, has been dismantled in all fronts (Tufanni, 2019) –, is an allowance for the further devastation of marine ecosystems. The impacts of these hydrocarbons, metals from mining, and pesticides in rhodoliths are mostly still unassessed, but have been demonstrated to impact other macroalgae (see Petsas and Vagi, 2017 for a review). For these reasons, there is an urgent need of clear and coherent regulations of these activities, both in land and ocean, to prevent the further degradation of rhodolith beds.

2.3. COMBINATION OF GLOBAL AND LOCAL STRESSORS

While investigating the effects of each of these stressors separately is important to understand individual mechanisms and is a cornerstone in studies of organismal physiology, assessing the impacts of multiple stressors is also important, considering that in the future they will happen simultaneously (Boyd et al., 2018). The interaction between stressors (or drivers) can have either an additive (the sum of their individual effects is either double-positive, double-negative or opposing), antagonistic (less positive or negative than predicted additively) or synergistic effect (when the result is greater, positively or negatively, than the additive effect of individual drivers) (for further explanation of terms, see Piggott et al., 2015). As a result, assessing the combined effects of global and local stressors in rhodoliths is necessary to play out the possible scenarios of species and communities' responses to future environmental conditions.

Many studies have investigated the combined effects of two or three stressors in the physiology of coralline algae, some testing the hypothesis that one stressor may help them cope with another stressor (Hofmann et al., 2014; Qui-Minet et al., 2019). One of the most investigated interactions of stressors under this perspective is of ocean acidification and warming. A few studies have demonstrated that ocean acidification exacerbates the negative effects of ocean warming in rhodoliths (Kroeker et al., 2013; Vásquez-Elizondo and Enríquez, 2016), increasing mortality, bleaching and decreasing calcification and photosynthesis (Anthony et al., 2008; Diaz-Pulido et al., 2012). Conversely, the interaction of increased $p\mathrm{CO}_2$ and temperatures in the physiology of *Phymatolithon lusitanicum* led to higher rates of photosynthesis, respiration and calcification than when only temperatures were increased, indicating an intensification of the effects of temperatures under higher CO_2 concentrations (Sordo et al., 2019). The combination of global and local stressors, specifically nutrient enrichment, have also been investigated under this angle. Higher nitrogen concentration partially ameliorated the effects of higher $p\mathrm{CO}_2$ by increasing calcification rates and photophysiology of *Porolithon onkodes* (Johnson and Carpenter, 2018). Qui-Minet et al. (2019) observed an antagonistic interaction between ocean warming, acidification and nutrient enrichment in the physiology of three mäerl species, with nutrient enrichment partially alleviating the effects of climate change. In contrast, Schubert et al. (2019), when testing increasement of nutrients and temperature, found no effect (negative or positive) of nutrients in calcification in treatments with elevated temperature. Other aspects of coralline algae's life histories will also be affected, and their competition ability may also be impaired. For example, recruitment of CCA under higher nutrient conditions and CO_2 is highly disrupted, while turf increase their recruitment and coverage in the same conditions (Russell et al., 2009). As discussed previously, the individual effects of these stressors are species-specific, and their interaction appears to follow the same trend.

However, other factors also play an important role in mediating the response of coralline algae to changing environmental conditions. Seasonal fluctuations in temperature and irradiance (length and intensity) mediate and partially explain the meliorated effects of ocean warming in rhodoliths, and the effects of warming will also be different between seasons (Qui-Minet et al., 2019). Moreover, coralline algae are exposed to substantial daily changes in pH and temperature, and thus, they may adapt to near future conditions of ocean acidification (Qui-Minet et al., 2018). However, their response to long-term (> 12 months) increasement of temperature and CO_2 concentrations is likely different than their response to short-term exposure, as a result of these daily and seasonal fluctuations (Sordo et al., 2018), which implies that the mitigation of effects of one stressor by the other may also be a short-lived response. For this reason, longer studies exploring the effects of multiple stressors on rhodoliths are necessary to understand this complex dynamic.

Another important aspect that needs to be investigated regarding the impacts of multiple stressors are the effects of these on communities. Changes in community composition, which we can expect based on numerous studies demonstrating lower resistant of some species to altered environmental conditions, while others seem to cope with it, will also reflect in changed interactions. Other taxa, from other algae to fish, for example, will also be under the influence of these conditions, and experience shifts in their assemblages (Vergés et al., 2016). The expression of climate change in the interactions within the community may have greater impact in populations than the effects of abiotic conditions, and thus, have larger effects in the resilience of ecosystems (Ockendon et al., 2014; Strona and Bradshaw, 2018). Therefore, future studies of rhodoliths will need to address the effects of changed community composition and interactions in order to more accurately predict the future of these ecosystems.

In this “perfect storm” of ecological chaos, we cannot forget the underlying driver of change: human society. And human society is going to be heavily impacted by the collapse of ecosystems, as we depend greatly in services and functions provided by them (Worm et al., 2006). Rhodolith beds provide services of production through the provision of important fish habitats, of regulation by their importance in climate regulation, and of support by promoting a high biodiversity and complex ecological interactions, among others (Basso et al., 2016). The loss and/or diminishment of Brazilian rhodolith beds will result in loss of these ecosystem services, and the impacts on Brazil’s economy and society are still to be assessed. To avoid – or to at least attenuate – the loss of these important ecosystems, Brazil and other governments need to make a transformative change in their practices and processes across diverse sectors, especially the economic, business and political ones (IPCC, 2019). Under the future climatic and environmental projections, the underlying socioeconomic and political scenario of Brazil appears to make the achievement of these transformative changes difficult. But still, initiatives around the world can give hope that these changes are achievable. Many countries are implementing plans to completely decarbonise their economies by 2030 or 2050 (Victor, 2020), 1840 local authorities in 32 countries have declared and acknowledged the climate emergency that we are in (CED, 2020), and investors initiatives, such as Climate Action 100+, are looking to ensure that the largest corporate greenhouse gas emitters take action in face of climate change (Climate Action 100+, 2020). We have the technology and the means to change the path we are in, as many other countries have realized. Brazil just needs to pick up the pace.

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3. CAPÍTULO II: PHYSIOLOGY, NICHE AND EXTREME EVENTS: AN INVESTIGATION OF CURRENT AND FUTURE HABITAT SUITABILITY OF A RHODOLITH-FORMING SPECIES IN THE SOUTH WESTERN ATLANTIC

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Abstract

Global climate change and local stressors are the main threats to reef-building organisms and rhodolith beds. Rhodolith beds harbor a great variety of faunal and floral species, and are important in the global carbon cycle by storing organic carbon in their carbonate-rich skeletons. Therefore, it is necessary to investigate how future environmental conditions will affect these organisms and their habitat suitability. Ecological niche models allow the understanding of which environmental factors influence most the current distribution of a species, and can be used to predict the future habitat suitability of species in different climate scenarios. Herein, we investigate the impacts of increased nutrient concentration, $p\text{CO}_2$ and marine heatwaves in a short-term experiment with the rhodolith-forming species *Lithothamnion crispatum* Hauck 1878, also studying the recovery of individuals after the removal of stressors. Furthermore, we developed an ecological niche model to determine which environmental conditions determine the current distribution of this species, also testing if past marine heatwaves have influenced their distribution, and project the model to future climate scenarios (Representative Concentrations Pathways 2.6 and 8.5, IPCC). Although *L. crispatum* suffered a reduction in photosynthetic yield and rates after 5 days of exposure to stressors, after the return of individuals to control conditions, their photosynthetic yield returned to pre-experiment values. The model showed that the most important variables to explain the current distribution of *L. crispatum* in the Brazilian coast are maximum nitrate and temperature, while heatwave intensity was not important. In future ocean conditions, there is a predicted range expansion of habitat suitability of this species, with few areas of lost suitable habitats. Our results raise the possibility of some rhodolith-forming species to be resilient to future environmental change, a perspective that will need to be further explored by future studies. With this information, we can contribute to inform public policies for the conservation of priority areas, aiding the preservation of the marine biodiversity in the South Atlantic.

Keywords: ecological niche model, resilience, ecophysiological experiment, recovery, climate change, local stressors.

3.1. INTRODUCTION

The rate of change of global climate conditions in the last decades has been unprecedent in the last millennium, and further expressive changes are expected in the remainder of this century (Lüthi et al., 2008; IPCC, 2019). Under fast environmental change, besides the defying problem of having a baseline of current biodiversity, understanding the response of species is another challenge, as many biotic and abiotic factors come into play to determine their fate. One of the most important factors is the set of physiological tolerances of a species to each, and the combination of, different environmental conditions (in the absence of biotic interactions), also known as the Hutchinsonian fundamental niche (Hutchinson, 1957; Soberon and Arroyo-Peña, 2017). Depending on the fundamental niche of the species, the magnitude and speed of environmental change can have a great impact on its response. Environmental conditions outside of the range that species are adapted to can lead to range shifts (i.e. species tracking environmental conditions within their physiological limits), extinction or adaptation to the new conditions (Berg et al., 2010). Therefore, one of the first steps in understanding the distribution of species in the future is determining what drivers may be responsible for their current distribution. The patterns of distribution we observe now are the combination of the response of species to complex interactions between multiple environmental and, in the past centuries, human-derived conditions (Wethey et al., 2011), besides historical processes (Wiens and Donoghue, 2004). Great focus has been given to studying the effects of changes in average conditions, based on the assumption that long-term exposure to a certain range of conditions determines the adaptation of species (Wethey et al., 2011; Kroeker et al., 2019). However, the frequency and intensity of extreme environmental conditions can also affect, or even determine the current distribution of species, and represent an important perspective to be explored (Helmuth et al., 2014).

One of the most expressive extreme events with many impacts in marine ecosystems are marine heatwaves, defined as periods of anomalous warming of the water above the 90th percentile of the historical baseline, and lasting more than 5 days (Hobday et al., 2016). Marine heat waves can have important impacts on the distribution of species, being reported as responsible for range shifts and local extinctions of marine foundation species (Wernberg et al., 2016; Smale et al., 2019). Anomalous warming has also been shown to drive significant change in genetic diversity and structure in populations of marine forests, leading to a "genetic tropicalization" (Coleman et al., 2020; Gurgel et al., 2020). The frequency and intensity of marine heatwaves has been increasing in the past decades, driven by human activities, and they are projected to become even more frequent and intense in the near future (IPCC, 2019; Laufkötter et al., 2020), raising concern about the fate of important foundation species. However, marine macroalgae are and will be exposed to other stressors in combination with marine heatwaves. Together with ocean warming driven by greenhouse gas emissions, the increase of atmospheric CO_2 is leading to a decrease in the ocean pH, phenomenon called ocean acidification (Doney et al., 2009). The decrease in pH and changes in carbonate system will have impacts specially in species with carbonate skeletons, such as coralline red algae (CRA) (Martin and Hall-Spencer, 2017). On the local scale, the change in upwelling regimes and continental runoff not only has a high concentration of CO_2 and low pH, causing local events of acidification (Kelly et al., 2011; Rose et al., 2020), but it also carries into the ocean substantial loads of nutrients related to many human activities (e. g. sewage disposal, fertilizers), generating physiological damage in key species, with consequent losses of richness and resilience of macroalgae assemblages (Martins et al., 2012; Scherner et al., 2013).

Of particular importance in the South Western Atlantic coast are the ecosystems built by free-living CRA, rhodolith beds. Rhodoliths harbor a great variety of living organisms, from invertebrates to important life stages of fishes, and are regarded as seed banks for many representatives of fauna, flora and microbiota (Simon et al., 2016; Fredericq et al., 2019; Carvalho et al., 2020b). Not only they increase the local biodiversity (Foster et al., 2013), but they are also important in the carbon global cycle, storing carbon in their calcium carbonate skeletons and in sediments (Martin et al., 2007; Mao et al., 2020). However, global climate change and local stressors are expected to greatly impact and threaten these organisms, reducing their primary productivity and calcification, and consequently, affect the functions and services provided by these ecosystems (Anthony et al., 2008; Diaz-Pulido et al., 2012; Vásquez-Elizondo and Enríquez, 2016; Schubert et al., 2019). Rhodolith beds are formed by many different species of CRA, and the effects of global and local drivers on rhodoliths have been increasingly demonstrated to be species-specific (Cornwall et al., 2019). This has to do with the fact that the group is genetically highly diverse, with around 600 species of non-geniculate algae distributed in three different orders (Corallinales, Hapalidiales and Sporolithales), with different evolutionary origins, histories and ecophysiological affinities (Bailey and Chapman, 1998; Bittner et al., 2011; Peña et al., 2020). Studies linking environmental drivers to the distribution patterns of calcareous algae are revealing, contrary to first assumptions, a wide range of niche breadth, from very specific to more general niches, with many cases of species with very restricted distributions (Twist et al., 2019). Consequently, these differences lead to different physiological responses to global and local drivers, as well as different distributions and ecological niches (King et al., 2018; Straub et al., 2019). Therefore, understanding the physiological response, and consequent possible alterations in the geographical distribution of key rhodolith-forming species, is an important step in the conservation of these organisms and ecosystems.

Considering the necessity to investigate the impacts of combined global and local drivers in the physiology of rhodolith-forming species, herein we tested the combined effects of marine heatwaves (MHW), increased nutrient concentration and $p\text{CO}_2$ on an important and widely distributed coralline alga, *Lithothamnion crispatum* Hauck 1878, and observed the changes in photosynthetic yield and photosynthesis after 5 days of exposure, and the recovery of individuals after the removal of stressors. Moreover, to assess the most important environmental conditions in determining the distribution of *L. crispatum* in the Brazilian coast and predict its habitat suitability in the present and the future, we developed an Ecological Niche Model and projected it to 2100 in two emissions scenarios, one of reduced emissions (Representative Concentration Pathway, RCP 2.6) and the worst-case scenario (RCP 8.5) (IPCC, 2014). We tested three hypotheses: i. *L. crispatum* will be negatively impacted by the exposure for five days to the combination of global (heatwave and acidification) and local drivers (nutrient increasement), not being able to recover its photosynthetic yield to pre-exposure levels; ii. The current distribution of *L. crispatum* in the Brazilian coast is influenced by past intensity of marine heatwaves, nitrate concentration and pH; and lastly, iii. Future climate conditions will reduce *L. crispatum* habitat suitability in the Brazilian coast.

3.2. MATERIAL AND METHODS

3.2.1. Study area and sample collection

Samples of *Lithothamnion crispatum* were collected in the winter of August 2019, from the rhodolith bed at Rancho Norte, within the Arvoredo Marine Biological Reserve (−27°16′25.8″, −48°22′0.99″), a marine protected area off the coast of Santa Catarina state, Brazil. Rhodoliths were sampled at ~8 m depth, kept in coolers with seawater and transported to the Phycology Laboratory at the Federal University of Santa Catarina. Samples were transferred to tanks (V = 2L), with circulating seawater (salinity of 35). Afterwards, rhodolith were cleaned from epiphytes and associated fauna, and acclimated for 3 months under 18 ºC, the temperature in the field during sample collection, and light of 34 μmol photons m^{-2} s^{-1} was provided by fluorescent lamps in a 12-hour light/dark photoperiod. Water was exchanged every

2 weeks. In December 2019, samples were transferred to 20 plastic containers of 1L of volume, each with 4 rhodoliths of similar size. While light conditions and salinity were maintained, half of the replicas (10) were gradually (~1.5 ºC per week) warmed up to 24 ºC, to simulate the summer temperature of the rhodolith bed. Samples were then kept at these acclimation conditions for two weeks, when the experiment started. Rhodoliths are known for its difficult identification based only in morphological traits, as many species are morphologically similar and the group presents many cryptic species (Sissini et al., 2014). To avoid misidentification and help future comparisons between studies using the same taxa, we genetically identified the specimens used in the experiment, and methods followed and results can be found in the Supplementary Material 1.

3.2.2. Experimental conditions and setup

Our experimental design follows a scenario-based approach, or a “collapsed design”, testing the effects of multiple-drives (here, ocean acidification and increased nutrient runoff) as one factor, without loss of statistical power (Boyd et al., 2018). The experiment contained two control temperatures, simulating both mean winter (18 ºC) and summer (24 ºC) temperatures found in the studied rhodolith bed, at the samples collection depth (~ 8 m) (Sarti and Segal, 2018). These control temperatures were accompanied by natural nutrient conditions (i.e. no addition of nutrients in the seawater) and current $p\mathrm{CO}_2$ concentrations (~415 ppm). These treatments simulated the current ocean conditions (COC) to which this population is naturally exposed to. Each treatment (winter/summer) was composed by 5 aquaria (n = 5) with 4 rhodoliths of similar size and shape. The experiment lasted for 5 days. The future ocean conditions (FOC) were then simulated by the addition of nutrients, sudden rising water temperatures and increasing $p\mathrm{CO}_2$ concentration in the water. Nutrient concentrations were simulated by the addition of 70 µM of ammonium ($(NH_4)_2SO_4$), 10 µM of sodium phosphate ($Na_2H_2PO_4.12H_2O$), and 14 µM of sodium nitrate ($NaNO_3$) in the seawater. Concentrations used in the experiment were based in values found by (Pagliosa et al., 2006) in highly urbanized and eutrophic areas in Florianópolis, Santa Catarina. Water was exchange daily in all treatments to ensure constant levels of nutrients. To test for recovery, after 5 days of elevated temperatures, nutrients and $p\mathrm{CO}_2$, conditions of the FOC treatments were ceased and replicas (n = 5) returned to the initial (COC) conditions, and kept for 5 more days in tanks (Fig. 1).

To reproduce marine heatwaves, temperatures were increased by 6 ºC in both winter and summer treatments, reaching 24 and 30 ºC respectively. These temperatures are based in heatwaves recently registered in the Arvoredo's Island, which increased temperatures by 4 ºC (Gouvêa et al., 2017), and the prediction of increasing intensity of marine heatwaves in 2100 (Frölicher et al., 2018) To avoid pseudo-replication, as recommended by Cornwall et al., (2019), temperatures were maintained by individual heaters (Master, Brazil) in the aquaria and controlled automatically by sensors placed in the seawater inside each replica. Temperature in all treatments was also recorded by data loggers (HOBO Pendant Temperature Data Loggers, Onset, Bourne, USA) placed randomly inside aquaria.

Concentration of $p\mathrm{CO_2}$ chosen to simulate future ocean acidification was based on the climate model of IPCC, considering the RCP 8.5, where emissions of CO_2 stay business-as-usual and reach up to 1000 ppm in 2100 (IPCC, 2014). Aeration was provided individually in tanks by a cylinder air stone, to create air bubbles and allow faster water-air equilibration. An example of aquaria used in experiments is shown in figure S2 in Supplementary Material 1. In treatments of FOC, air was pumped to each aquarium from a chamber where CO_2 was mixed with air to reach up the value of 1000 ppm, while in treatments of COC, air was pumped without any injection of CO_2. Concentration of $p\mathrm{CO_2}$ in air in the chamber was controlled by a Proportional-Integral-Derivative (PID) controller, which receives CO_2 readings from a built-in infrared gas analyzer (IRGA) and controls CO_2 injections by opening and closing an in-line solenoid valve. The controller calculates the difference between the measured CO_2 in the chamber and the programmed set point, and adjusts the injection of CO_2 accordingly. Our CO_2 control system was based in Sordo et al. (2016). Measurements of pH in each aquarium were made daily using edge® Dedicated pH/ORP Meter (Hanna Technologies - HI2002) to monitor $p\mathrm{CO_2}$ injection.

3.2.3. Photosynthesis, respiration and photosynthetic yield measurements

Physiological responses to the proposed future scenario were assessed by measurements of photosynthesis and respiration, and photosynthetic yield. In the beginning and in the end of the experiment, photosynthesis and respiration rates were determined by laboratory incubations done in 150 mL sealed acrylic chambers, with circulation provided by a magnetic stirrer. First, respiration measurements were taken before the beginning of the photoperiod. Two rhodoliths were taken from each aquarium and incubated in darkness for 30 min with seawater from the respective aquarium and at the respective temperature of the treatment. Oxygen concentration was measured at the beginning, during and at the end of the incubations with the Optical Oxygen & Temp Meter FireStingO2 (Pyro Science - FSO2-4). Afterwards, incubations to determine primary production were made with the same rhodoliths at an irradiance of 1500 µmol photons m^{-2} s^{-1} for 30 min. This irradiance was chosen because it was demonstrated to be the irradiance of higher photosynthetic activity for this species, in both 18 and 24 ºC, temperatures of the controls. Control incubations without rhodoliths were also carried out to determine fluxes from biological activity in the seawater. Dark respiration (R), net primary production (NPP) and gross primary production were estimated following the equations (1) and (2), and corrected from control incubations.

$$NPP\ and\ R = \Delta O_2 * V/\Delta t * FW$$

$$GPP = NPP + R$$

Where V is the volume of the incubation chamber (L), FW is the fresh weight of the algae (g), Δt is the incubation time (hr) and ΔO_2 is the final minus initial concentrations of O_2 (µmol O_2 L^{-1}).

Photosynthetic yield was measured in the first, third, fifth (days with FOC conditions), seventh, nineth and eleventh (recovery) days of the experiment. Measurements of effective quantum yield (Fv/Fm), estimated by the *in vivo* chlorophyll a fluorescence of photosystem II, were made before the beginning of the photoperiod. Three measurements were taken from each replica, of different parts of the thallus, with a pulse-amplitude modulated chlorophyll a fluorometer (Junior PAM – Walz Germany). The measurement of fluorescence in the dark allows the estimation of the basal fluorescence (Fo), and after the application of a saturating pulse, maximum fluorescence (F) is estimated (Schreiber et al., 1986).

3.2.4. Environmental data

Environmental predictors of the bottom of the ocean were downloaded from Bio-ORACLE v2.0 (Assis et al., 2018) and from the R packages “SCC26” and “SCC85” (Chih-Lin, 2020a, 2020b), which has historical bottom data and climate change projections (RCP 2.6 and 8.5) from the CMIP5 - Coupled Model Intercomparison Project Phase 5, the most recent multimodel dataset underlying the Fifth Assessment Report by the Intergovernmental Panel on Climate Change (IPCC). To test whether events of extreme temperatures contribute to determine the distribution of *L. crispatum*, a layer of the MHW median intensity (the sea surface temperature anomaly associated with an event of heatwave) from 1982 to 2019 was developed in MATLAB R2015a following the methodology and data used by Jacox et al. (2020), which calculates MHW from monthly SST anomalies. We defined MHWs as periods with anomalous warming of the surface of the ocean above a seasonally varying 90th-percentile threshold, in accordance to the definition of Hobday et al. (2016). For further explanation regarding methodology and analysis, refer to Jacox et al. (2020). To match the resolution of the Bio-ORACLE layers, CIMP5 and heatwave layers were interpolated bilinearly using the function *disaggregate* of the R package "raster". Environmental predictors used in the final model were selected based on biological relevance and in combination with experimental settings (temperature, nutrients and pH), and are descripted in Table 1. Multicollinearity between predictors was tested via Variance Inflation Factor (VIF), and all variables had VIF values < 10.

Table 1 - Predictors used in the model, their units and sources. "Future prediction" lists variables which have been predicted to the future scenarios RCP 2.6 and 8.5, and used in the future projections in this study.

Predictor	*Unit*	*Source*	*Future prediction*
Long-term max. nitrate at min. depth	µmol/L	Assis et al. (2018)	*No*
Long-term max. salinity at min. depth	PSS	Assis et al. (2018)	*Yes*
Long-term max. temperature at min. depth	Celsius	Assis et al. (2018)	*Yes*
Minimum depth of the seafloor (bathymetry)	Meters	Assis et al. (2018)	*No*
Calcite saturation state	-	(Chih-Lin, 2020a, 2020b)	*Yes*
Mean pH at seafloor	-	(Chih-Lin, 2020a, 2020b)	*Yes*
Median heatwave intensity	Celsius	Jacox et al. (2020)	*No*

3.2.5. Ecological Niche Models

To build the Ecological Niche Models (ENMs), occurrence data of *L. crispatum* was downloaded from the Global Biodiversity Information Facility (GBIF, 2020) and literature data (Supplementary Material 2). Occurrence data was cleaned of duplicates, and locations were corrected manually in QGIS 3.6 when description of sampling sites did not match the coordinates depicted. The correction of coordinates was curated by the specialist in Brazilian rhodoliths, M.N. Sissini. To reduce sampling bias, occurrences were filtered using the R function envSamp (https://github.com/SaraVarela/envSample). While geographically cleaned occurrences can have similar environmental information, by cleaning occurrences in the environmental space, close occurrences with very different and important environmental information are kept (Varela et al., 2014). The filters for this selection were Maximum Temperature and Maximum Nitrate, described by Carvalho et al. (2019) as the variables most important to explain, respectively, the distribution and abundance of Brazilian rhodolith beds. This step removed 7 occurrences out of the 27 raw occurrences for *L. crispatum,* maintaining 20 occurrences to be used in the model.

Pseudo-absence selection has a great influence in models performance and accuracy, and as such, we followed the recommendations of Barbet-Massin et al. (2012) for the generation of pseudo-absences. The recommended number of pseudo-absences varies with the modelling technique, and accordingly, we chose to focus in three machine learning (ML) algorithms: Gradient Boosting Machines (GBM, also known as Boosted Regression Trees – BRT), Artificial Neural Networks (ANN) and Random Forests (RF). For ML algorithms, a number of pseudo-absences equal to the number of presence yields better predictive accuracy, and when the number of pseudo-absences is different from the number of presences, model predictive quality is better when giving an equal weight for presences and absences (Barbet-Massin et al., 2012). For this reason, we generated 60 pseudo-absences (three times the number of presences, 20), and weighted absences equally to the presences. Considering the low number of pseudo-absences, 10 datasets of pseudo-absences were generated and used for 10 different runs of each model, to reduce the influence of pseudo-absence selection. Barbet-Massin et al. (2012) also recommend selecting pseudo-absences with a geographical exclusion (2º far) when there are few presences, yielding significantly better models. As our model has very few presences, we generated the pseudo-absences within 20 and 25 km around the presences, roughly 2º of distance in the Equator.

To project the current and future habitat suitability for *L. crispatum* in the Brazilian coast, an ensemble modeling approach was applied. All models and pseudo-absences were generated using the "biomod2" R package, as well as model evaluations (Thuiller et al., 2020). Individual runs of each presence-absence algorithm (ANN, GBM and RF) were made with 10 iterations in each one of the 10 pseudo-absence datasets, resulting in 300 models. For each run, the data was split between a calibration and a validation set (70%/30%, respectively). Model parameters were selected according to the recommendations of Elith et al. (2008) for GBM, of Breimen (2002) for RF, and for ANN, default parameters were used. Models' performance was accessed via the receiver operating characteristic (ROC) curve (AUC Fielding and Bell, 1997), and true skill statistics (TSS, Allouche et al., 2006). The ensemble model was composed only by models which obtained TSS values above the 0.8 threshold. Three ensemble algorithms were run: committee averaging (CA, average of binary predictions), weighted mean of probabilities (WMean, the weighted sum by the selected evaluation method scores) and coefficient of variation of probabilities (CV, coefficient of variation of the probabilities over selected models, a measure of uncertainty of the prediction). For further information regarding ensemble algorithms, please refer to Thuiller et al. (2020). The final model was then projected to current and future conditions, in two scenarios of emissions: RCP 2.6 and RCP 8.5. For variables that did not have projections for the future (Table 1), their layers from the present were used.

Variable importance and their respective curves were calculated using Biomod2 functions (Thuiller et al., 2020). The variable importance technique in Biomod2 is similar to the principle of variable importance calculation in RF, and varies between 0 and 1, where highest values represent highest influence of the variable in the model (Thuiller et al., 2020). However, this technique does not account for interactions between variables, and therefore, does not sum to one. Three iterations were run to determine variables' importance, and this result is presented in percentage (variable studied * 100 / sum of all variables' importance) to facilitate interpretation. Response curves generated are based in the Evaluation Strip method (Elith et al., 2005), where n-1 variables are set to a fixed value (in our case, the mean), and only the studied variable varies across the whole data range, where variations calculated show the sensibility of the model to the studied variable (Thuiller et al., 2020).

3.2.6. Statistical analyses

We tested the data (GPP and Fv/Fm) for homogeneity of variances by the Bartlett test, and the absence of this condition led us to run non-parametric analyses. To test if variations observed in GGP and Fv/Fm values are explained by experimental conditions, a Canonical Redundancy Analysis (RDA) was run. The matrix of explanatory variables (y) was composed by the different temperatures among treatments (18, 24 and 30ºC), time (beginning and end of the experiment), and the collapsed conditions of nutrients (addition/no addition of nutrients) and $p\mathrm{CO}_2$ (addition/no addition of $p\mathrm{CO}_2$), named as Nutrients+$p\mathrm{CO}_2$. Physiological data of GPP and Fv/Fm were grouped in the matrix of response variables (x). GPP data, which contained negative values, was transformed to positive values by summing all values to a common constant, the lowest value of the dataset. Data was then transformed by the method of chi-squared, and the collinearity of explanatory variables was verified by VIF < 3. The significance of each RDA axis was determined by permutations and their comparison by Analysis of Variance (ANOVA). To test if there was recovery of the photosynthetic apparatus (Fv/Fm) after treatments were ceased and conditions returned to initial values, a Permutational Analysis of Variance (PERMANOVA) was run with the explanatory variables: temperature, nutrients+$p\mathrm{CO}_2$ and time (days 1, 3, 5, 7, 9, and 11). All analyses were run on R 4.0.2 using the R package "vegan" (Oksanen et al., 2019).

3.3. RESULTS

3.3.1. Experiment

The total variance of the dataset was largely due to constrained (91.57%) rather than to unconstrained variance (8.42%), demonstrating that much of the variance of GPP and Fv/Fm is explained by experiment conditions. The first and second RDA axis explained 76.93% and 13.66%, respectively, of the variance in the response variables (Fig. 3). With 999 permutations, ANOVA results showed that the overall RDA solution is significant ($p < 0.001$, $R^2 = 0.916$, R^2-adjusted = 0.906), as well as both RDA1 and RDA2 axis ($p < 0.001$).

PERMANOVA showed no significant interaction ($p = 0.251$) between the effects of temperature, time and nutrients+pCO$_2$ on the photosynthetic yield of *L. crispatum* in the 10 days of experiment (FOC conditions plus recovery, Fig. 4), and only the effects of temperature and nutrients+pCO$_2$ individually had significant effects ($p < 0.05$, Table S1 in Supplementary Material 1).

3.3.2. Ecological niche model

The ensemble models presented high validation scores, with TSS = 0.987 and ROC = 0.998 for the CA ensemble model, and TSS = 0.968 and ROC = 0.996 for the WMean model (evaluations based on the testing data). The coefficient of variance is small in coastal areas, demonstrating that model projections in the coast have low uncertainty (Fig. S3 in Supplementary Material 1). To facilitate interpretation, we chose to show here only the results of the CA ensemble model, which reached better evaluation metrics, which reached better evaluation metrics, and Kappa, TSS and ROC statistics of each individual model run are available in the Supplementary Material 1 (Fig. S4).

The binary map of current habitat suitability for *L. crispatum* matches the occurrences found for this species (Fig. 5), and shows suitability in the southeastern and northeastern regions of Brazil, with a few other locations in the south and north. The variable with the highest relative importance was maximum nitrate (0.202), followed by maximum temperature (0.048), maximum salinity (0.025), bathymetry (0.021), and calcite saturation (0.010). Median heatwave intensity and pH had low importance for the ensemble model (Fig. 6, values in percentage). Highest probabilities of occurrence for maximum nitrate are from 0 to 5 µmol/L, for maximum temperature from 20 to 28.5ºC, for maximum salinity for 35 to 37, and for calcite saturation, from 1 to 4 (Fig. 7). Response curves for all predictors are in Fig. S5 in the Supplementary Material 1. Under future climate scenarios, there are predicted shifts in the distribution of *L. crispatum* in both RCP 2.6 and RCP 8.5, mostly to the southern and northern coasts of Brazil (Fig. 8). Under RCP 2.6, the predicted loss of suitable habitats is of 1.242%, while the gain is of 43.116%. As for RCP 8.5, the predicted loss is of 4.762%, with 58.489% of gain of suitable habitats.

3.4. DISCUSSION

By the use of an experimental evaluation and the development of an ENM, the present study showed the interesting ability of *L. crispatum* to survive to an extreme event, and that accordingly, such events of extreme warming are not drivers of the distribution of this species in the South Western Atlantic Ocean. Although the combination of heatwave, nutrient and CO_2 enrichment reduced the photosynthetic yield and photosynthesis of *L. crispatum* in both winter and summer, it was not enough to preclude the recovery of individuals after the removal of stressors. This result goes in accordance with model results, which showed no significance of heatwaves and pH in determining the current habitat suitability of this species in the Brazilian coast. Moreover, future climate conditions in both emission scenarios demonstrate that *L. crispatum* may not be strongly affected by changed environmental conditions. This is the first study that we are aware of that models current and future habitat suitability of one rhodolith-forming species. Previous studies have focused in creating models of many rhodolith-forming species of Brazil (Carvalho et al., 2020a), of *mäerl* species in the Mediterranean (Martin et al., 2014), and of multiple species forming coralline algal beds in Scottish waters (Simon-Nutbrown et al., 2020). By looking at one species, we are able to make better inferences about the factors influencing the current and future distribution of these organisms, and raise key points regarding the ecology and resilience of rhodoliths that need to be addressed in future studies.

As our results show, in the past, marine heatwaves have not defined the distribution of *L. crispatum*, and although we have not used a layer with heatwave intensity projection for the future, as it had very little contribution to the overall model, it is unlikely that this would have an impact in the future habitat suitability of *L. crispatum.* However, as these events are predicted to get more severe, long-lasting and frequent (IPCC, 2019), this trend may drastically change, and indeed affect the distribution of this species to some scale. We have tested the effects of extreme events for five days, and the survival of rhodoliths to longer events is likely smaller than what we observed in our experiment, and needs to be assessed. The recovery of some individuals after extreme events will also lead to genetic change, facilitated by the mortality of less tolerant rhodoliths, a trend already observed in other groups of algae (Coleman et al., 2020; Gurgel et al., 2020).

Our observations of *L. crispatum* recovery after the removal of stressors, in both summer and winter simulations, can be due to this species phenotypic plasticity to changes in environmental conditions (Fox et al., 2019), which goes in accordance with its current distribution in the Brazilian coast. This species is found from shallow waters to mesophotic zones, and its latitudinal range stretches from the Amazon's mouth to southern Brazil, being one of the most abundant species in the Brazilian coast (Amado-Filho et al., 2017). Thus, this species is adapted to a wide range of temperatures, leading to the tolerance to 30ºC observed in our study. Moreover, the natural fluctuations in ocean's pH, which are very common during the day, in events of heavy rain and runoff from coastal areas, and according to depth (Hofmann et al., 2011), also can assist to explain the plasticity of *L. crispatum* in more acid conditions. It is also necessary to acknowledge that the pH layer used in our model is from the bottom of the ocean, presenting different values of pH than a surface layer would (see, for example, differences in surface pH in southern Brazil in Carvalho-Borges et al., (2018), where pH in depths < 200m is approximately 8.1), but as *L. crispatum* occurs mostly in the bottom, this goes in accordance with the biology of the species. Besides these natural variations in ocean's pH, CRA have been demonstrated to somewhat control the pH in their boundary layer to sustain calcification, even in simulated scenarios of ocean acidification (Hofmann et al., 2016; McNicholl et al., 2019, 2020), a strategy that likely comes from exposition of this group of organisms to past ocean acidification and warming (Bergstrom et al., 2020). Future research focusing in *L. crispatum* should direct efforts in investigating the different strategies used by this species to cope with decreased pH and elevated temperatures.

One of the assumptions in ENMs is niche conservatism, observed in species phylogenetically close. Phylogenetic niche conservatism is the "tendency of lineages to retain their niche-related traits through speciation events" (Crisp and Cook, 2012, p.1), and therefore, determines which environmental conditions the clade can tolerate (Wiens and Donoghue, 2004). Whether this is a reasonable assumption to be made in ENMs, especially when dealing with fast environmental changes and the projection of species distributions to novel environmental conditions, is a topic of discussion (Peterson, 2011). Interestingly, our experiment results corroborate model predictions of higher habitat suitability of *L. crispatum* in the future, which can be better understood by looking at the evolutionary history of this species and its order. CRA have a great presence in the geological record, which shows that this group likely thrived under a wide range of temperatures, light and nutrient levels, and even are theorized to have peaked in mid Miocene substituting coral reefs due to enhanced trophic resources (Halfar and Mutti, 2005). But more specifically, Hapalidiales, the order in which the genus *Lithothamnion* is inserted, diverged *ca.* 65-117 My ago (Aguirre et al., 2010; Peña et al., 2020), when $p\mathrm{CO_2}$ values (Hönisch et al., 2012) and temperature (Hansen et al., 2013) were higher than those found today [< 600 ppm and < 8ºC warmer than present day, Royer et al. (2004)]. This likely resulted in a resilient adaptation of calcification strategies that allowed CRA to succeed in past ocean acidification and warming oscillations, and may thus allow the survival of some taxa in the future ocean (Bergstrom et al., 2020), supporting our model projections for the future. Our experiment results corroborate the ability of *L. crispatum* to survive to such conditions, and may indicate conservatism of these traits that allowed the group to cope with past ocean conditions, but further phylogenetic and physiological studies need to be done in order to corroborate this hypothesis.

Previous experimental studies have also shown the ability of some CRA species to cope with climate change and local drivers. During the 5-day exposure of *L. crispatum* to the combined drivers, individuals demonstrated a considerable drop in photosynthetic yield and a decrease in GPP, explained by the experiment conditions, in accordance with previous studies, that demonstrated decreasing photosynthesis in CRA when exposed to increased $p\mathrm{CO_2}$ and temperatures (Anthony et al., 2008; Diaz-Pulido et al., 2012; Vásquez-Elizondo and Enríquez, 2016). However, after the removal of stressors, *L. crispatum* restored its photosynthetic yield to control values, similar to the response of other CRA species, that were not negatively affected by higher $p\mathrm{CO_2}$ and temperatures (Sordo et al., 2019; Cornwall et al., 2020) or higher nutrient concentration and $p\mathrm{CO_2}$ (Johnson and Carpenter, 2018). Using the same *L. crispatum* population from southern Brazil, in a longer experiment (30 days) exposing the species to warming and increased nutrient concentration, Schubert et al. (2019) observed no response to increased nutrient concentrations (+21 µmol/L), and higher photosynthetic rates in treatments with +5 ºC, but with decrease in calcification rates. In our model, nitrate was the variable with the highest importance to determine the habitat suitability of *L. crispatum* in the Western Atlantic, with a considerable drop in probability of occurrence in locations with nitrate values higher than 5 µmol/L. This discrepancy between model results and experimental observations can be hypothesized to be a consequence of: i. *L. crispatum* tolerates higher nutrient conditions, but its distribution is limited by another factor, such as another limiting nutrient (e.g. iron); ii. our experiment is very time-limited, and there is a possibility that longer (> 30 days) and more complex experiments, accounting for biological interactions (e.g. in mesocosms), would show a different response; iii. *L. crispatum* may be adapted to cope with acute events of nutrient discharge, but not chronic exposition.

Looking at the future projections of habitat suitability, our model predicts higher suitability in 2100, in both RCP 2.6 and 8.5 scenarios, than in the present. Assessing the accuracy of ENMs projections in the future is tricky, as climate change brings non-analog environmental conditions, i.e., conditions that do not exist in the present, and predicting how species will respond to these conditions is complex (Fitzpatrick and Hargrove, 2009; Refsgaard et al., 2014). One of the variables that can change our prediction in nitrate, as it was the variable that most contributed to our model. We did not find a prediction layer for this variable in the future, and we can expect many changes in concentrations and the spatial distribution of nitrate. Changes in land use in Brazil are already one of the main threats to marine ecosystems (Magris et al., 2020), and with increasing use of fertilizers and sewage discharge, nutrient levels will likely increase in coastal zones worldwide (Galloway et al., 2004; Van Der Struijk and Kroeze, 2010). Therefore, the impacts of changes in nutrient dynamics on *L. crispatum*'s future distribution is still to be investigated, and estimating how much of our prediction is accurate is not possible at this moment, as predicted losses of habitat suitability of this species can be different than what we estimated. However, higher nutrient levels in the past (11-16 My ago) favored the expansion of rhodalgal facies to the detriment of other reef-building organisms, indicating that CRA may still be resistant to a greater availability of nutrients and have advantage in such scenarios (Halfar and Mutti, 2005). As for the second most important variable to explain the distribution of *L. crispatum,* maximum temperature helps explain the range expansion to southern areas of Brazil, as warming is expected in this region in the future, and tropicalization of marine ecosystems in middle latitudes is predicted and already being observed (Vergés et al., 2014).

The model here developed is regarded as an Ecological Niche Model and its results read as habitat suitability because we lack important information about *L. crispatum* (and CRA in general) which would allow the characterization of its true distribution. First, there are very few occurrences for CRA species in Brazil, and even with a species more widely studied as *L. crispatum*, we were able to find only 27 trustworthy occurrences. Thus, it is unlikely that we have described the full climatic niche of the species here (Barbet-Massin et al., 2012), although our model was able to correctly predict habitat suitability for the existing occurrences. Secondly, CRA identification is flawed and in the past was based only in morphological traits, which have been shown with the evolution of molecular tools to not be enough to characterize differences between species, as there are many cryptic species in the group (Sissini et al., 2014;

Richards et al., 2016; Torrano-Silva et al., 2018; Twist et al., 2019). Hence, occurrences available may not be very reliable, especially if identification of the species was done based only in morphological traits and the species is not very well studied and/or described. Here, we used only occurrences which are within the current knowledge of the distribution of this species in the Brazilian coast, and many of the occurrences were registered by people who worked in this study, trying to minimize as much as possible the use of inaccurate occurrences. Thirdly, information about CRA's dispersal capability is still largely undescribed. Although CRA, as all other rhodophytes, disperses mostly by non-motile spores and thus is believed to not reach long distances, some species likely disperse by colonizing a range of surfaces, and can easily raft to new localities (Norton, 1992; Bryan et al., 2012; Fraser et al., 2018; Cornwall et al., 2019; Rindi et al., 2019). However, information about dispersal in specific species is rare, and most of these theoretical predictions still need to be corroborated by populational genetic data (Rindi et al., 2019). Dispersal is highly important in shaping species' geographical distribution, as limited dispersal can restrict the occupation of suitable habitats by the species (Peterson and Anderson, 2012).

Another important factor shaping species distributions and their niche is their interactions with other species, and changes in interactions caused by environmental changes will also play an important part in determining the fate of a species (Ockendon et al., 2014; Vergés et al., 2016; Strona and Bradshaw, 2018). Marine heatwaves have already resulted in increased turf cover in calcification accretion units placed in shallow coralgal reefs at Abrolhos in Brazil (Reis et al., 2016), and increased nutrient conditions and ocean acidification also favor the growth of fleshy algae (Scherner, 2013; Legrand et al., 2017). Trophic interactions will also suffer changes under climate change, such as herbivorous fish interactions that are predicted to decrease in the tropics and expand poleward, exercising more pressure in algal communities in middle latitudes (Inagaki et al., 2020). Grazers control CRA cover by epiphytes and the competition with other groups of algae, but in conditions of increased $p\mathrm{CO}_2$ levels, increased grazing activity by sea urchins and gastropods was shown to weaken the structural integrity of the thalli, making CRA more susceptible to ocean acidification (Rich et al., 2018; Legrand et al., 2019). Not only these interactions will suffer alterations in the future, but also interactions within the rhodolith microbiome, changing the microbial community around the rhodolith and affecting the settlement of invertebrate larvae (Huggett et al., 2018). Therefore, many other factors need to be considered to create more precise predictions of the future of rhodolith-forming species.

Having raised some of the caveats in our model, future predictions, and experiment, it is also necessary to consider the importance of studies investigating the future habitat suitability of key species. Although there is a certain level of uncertainty of predictions, mostly because of data not available about either the species or environmental conditions, conservation actions need information fast to try to mitigate some of the impacts of climate change, and studies like these are important to, at least, bring this discussion to the table of decision makers (Rilov et al., 2019). The importance of rhodolith beds in the past and in the present is colossal, and there is no indication that in the future they will lose their importance to life stages of many species. In fact, if some rhodolith-forming species indeed survive to extreme events and the global environmental change, they may be of utmost importance in creating new habitats for diverse species that will need to dislocate to new locations, tracking their niche. If our study is any indication, *L. crispatum* may be one of those species, and its higher habitat suitability in the future in matching regions where important fishes are predicted to shift their biotic interactions and distributions (Inagaki et al., 2020) can perhaps create the opportunity of these species to survive to novel environmental conditions. Of course, many other studies need to be done to confirm this hypothesis, investigating how the presence of rhodoliths beds influence the distribution of important fauna, and if *L. crispatum* has the dispersal ability necessary to colonize new regions. But considering the higher sensitivity of reef-building coral species to climate change (Anthony et al., 2011; Roth et al., 2020), rhodolith beds formed by tolerant species may be the only option in the future ocean.

3.5. ETHICAL DECLARATIONS

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4. DISCUSSÃO GERAL

No presente trabalho, foi possível observar que os bancos de rodolitos brasileiros estão ameaçados por diversas forçantes ambientais e antropogênicas, e o seu futuro é incerto (Capítulo 1). Ao mesmo tempo, algumas espécies podem ter maior resistência frente a essas forçantes, e talvez representem como o futuro de bancos de rodolitos será (Capítulo 2). Enquanto que existe muita preocupação em entender os efeitos das mudanças climáticas em ecossistemas, pouco se dá atenção as condições locais, climáticas e não climáticas, que podem impactar igualmente ou mais esses ecossistemas (RILOV et al., 2019). E é justamente na escala local que ações de manejo e conservação são feitas, o que torna, portanto, a conservação desses ecossistemas mais complexa, já que são necessárias informações interdisciplinares em diversas escalas. Desta forma, o presente trabalho se encontra exatamente nessa problemática, buscando entender os principais desafios para a conservação de bancos de rodolitos brasileiros, e investigando os impactos de mudanças globais e locais na resiliência e adequabilidade de habitat de uma importante espécie formadora de rodolitos.

As respostas de rodolitos frente a mudanças ambientais têm se mostrado cada vez mais específicas de cada espécie (CORNWALL; DIAZ-PULIDO; COMEAU, 2019). Portanto, as mudanças nas distribuições de rodolitos também serão dependentes da resposta de cada espécie, e variarão muito entre diferentes taxas e regiões (CHEN et al., 2011), reforçando a necessidade de um estudo que investigue os impactos das alterações ambientais em uma espécie, como este. Ao fazermos isso, pudemos observar que *L. crispatum* apresentou uma tendência de resistência a certas condições ambientais, indo contra a tendência da maioria dos organismos calcificantes e construtores de recifes biogênicos (ANTHONY et al., 2011; EAKIN; SWEATMAN; BRAINARD, 2019). Além disso, flutuações nas condições ambientais que exponham os indivíduos a extremos (por exemplo, extremos de temperatura) podem ser mais importantes na distribuição das espécies do que mudanças nas condições médias, principalmente se forem letais ou até mesmo sub letais (WETHEY et al., 2011). Para *L. crispatum*, as ondas de calor marinhas não se mostraram letais e não explicaram a atual distribuição da espécie na costa brasileira. Porém, eventos como este ainda podem ser sub letais para esta espécie no futuro, se considerarmos a variabilidade intraespecífica, que pode selecionar fenótipos mais resistentes e levar a processos evolucionários rápidos (GURGEL et al., 2020).

Porém, para serem criadas predições cada vez mais precisas sobre o destino de espécies formadoras de rodolitos frente a mudanças globais, é necessário o levantamento de muitas outras informações sobre a fisiologia, ecologia e história evolutiva desses organismos. Pouco se sabe sobre o papel do microbioma na resposta de rodolitos as mudanças ambientais, e muito menos sobre como essa aparentemente importante interação será afetada no futuro (CAVALCANTI et al., 2018). Se de fato o microbioma afeta a fisiologia e atua como um "amortecedor" entre o ambiente e o rodolito, as alterações dessa interação irão causar mudanças na resposta dos organismos e consequentemente na distribuição de rodolitos no futuro (CAVALCANTI et al., 2014; LAGE; GRAÇA, 2016). Além disso, ainda existe muita incerteza sobre a diversidade total de espécies de algas coralinas no mundo, com muitas espécies ainda a serem identificadas e muitas dúvidas sobre as atuais descrições de espécies, já que a morfologia variada e a dificuldade de analisar a anatomia de algas calcárias já levou a descrição de espécies crípticas como uma espécie (PEÑA et al., 2020; SISSINI et al., 2014). Isso reflete em poucos estudos genéticos populacionais, e então informações sobre a variabilidade intraespecífica de espécies de rodolitos e possíveis genótipos mais resistentes a mudanças ambientais são praticamente inexistentes (HERNÁNDEZ-KANTÚN et al., 2014; PARDO et al., 2019).Também existem poucos estudos experimentais sobre a resposta de rodolitos a variações ambientais de diversas variáveis, principalmente quando se considera o grande número de espécies e a variabilidade da resposta deles a cada condição ambiental. Alguns mecanismos fisiológicos de algas coralinas, como a calcificação, ainda não são completamente compreendidos (NASH et al., 2019), e estudos sobre o a viabilidade de esporos em cenários de mudanças ambientais também são escassos (PAGE; DIAZ-PULIDO, 2020). E um fator muito importante para estimarmos a futura distribuição de bancos de rodolitos, a capacidade de dispersão desses organismos, é dificilmente considerada e investigada (CORNWALL; DIAZ-PULIDO; COMEAU, 2019). Todas essas são informações cruciais para de fato serem criadas predições mais precisas sobre esse importante grupo de organismos, podendo guiar ações de manejo e conservação desses ecossistemas.

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