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Anomalias térmicas e denso-dependência como fatores determinantes da dinâmica populacional do caranguejo-aratu, *Grapsus grapsus*, nas ilhas oceânicas brasileiras

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

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

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Coordenação do Programa de Pós-Graduação

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Prof.(a) Andrea Santarosa Freire, Dr.(a)
Orientador(a)

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Dedico este trabalho a todas as mulheres que me ensinam, me motivam e me inspiram, assim como o oceano.

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Durante o mestrado percebi que lar não é um lugar, e sim pessoas. Pessoas que te acolhem e te deixam fazer parte da vida delas; que ensinam ou aprendem algo novo com você; que compartilham as angústias, e melhor ainda, as conquistas. Eu tive a imensa sorte de ter vários lares nesses dois anos (e meio), lares com rostos, sotaques, hábitos e manias diferentes. Meus eternos agradecimentos a todos os lares que me receberam e me abraçaram, até mesmo em tempos de distanciamento. Esses lares foram a Lu, Maca, Mário, Pablo que compartilharam nasceres do sol nas dunas e fogueiras debaixo do abacateiro de casa. Minha família baiana Lai e Gab que viveram comigo os dias gloriosos de coleta de *Grapsus* e mergulhos na ilha da Trindade. A Pat, Igor e Fe que me deram teto e cama em Porto Alegre e as meninas da UFRGS que me acolheram durante a disciplina de Ecologia de Campo na FLONA São Chico. A minha amiga Cla que me ensinou a tomar café e me levou pra ver os botos-cinza e guarás de Cananéia. Minhas amigas de vida, que um belo dia resolveram tatuar uma gota mal feita pra simbolizar uma amizade. Minha orientadora Andrea, que me ensina a ser uma mulher do mar desde 2014 e me recebeu em sua casa sempre que precisei. Eu só precisava fazer o almoço todos os dias. E por fim, o lar mais importante de todos: minha mãe Carmen, que sempre foi meu melhor abrigo.

"Elas deixam ali uma nuvem de ínfimas esferas transparentes, um rio amplo e extenso, carregado de vida. É a contrapartida marinha da Via Láctea, o rio de estrelas que flui no céu." (CARSON, Rachel, 1941)

RESUMO

Nas últimas décadas, ondas de calor marinhas (OCMs) e anomalias positivas da temperatura superficial do mar (TSM), tornaram-se mais frequentes e intensas, causando declínios populacionais nos ecossistemas marinhos. Enquanto a temperatura do oceano atua como um filtro no efeito "gargalo" da sobrevivência dos estágios iniciais de crustáceos decápodes, a competição denso-dependente pode afetar o tamanho e a fecundidade nos adultos, impactando o recrutamento e a dinâmica populacional. Estudos sobre os efeitos da temperatura na fisiologia de invertebrados marinhos sugerem que espécies tropicais, que vivem próximo ao seu limite termal, são mais vulneráveis às mudanças climáticas do que seus análogos de ambientes mais frios. Neste trabalho, buscamos compreender os efeitos de anomalias térmicas do oceano e da denso-dependência na dinâmica populacional do caranguejo-aratu *Grapsus grapsus* em ilhas oceânicas brasileiras, localizadas em diferentes latitudes. Dados de contagem e captura-recaptura de curto prazo (2019), de fecundidade e de monitoramento populacional de longo prazo (2003-2019), coletados no Arquipélago de São Pedro e São Paulo (SPSP), Atol das Rocas (RA) e Ilha da Trindade (TRI), foram analisados usando um *'Integrated population model'*. O modelo que desenvolvemos integra quatro sub-modelos: 1) um *'dynamic N-mixture model'*; 2) um modelo Jolly-Seber de desenho robusto; 3) um modelo Log-Linear de Poisson; e 4) um *'state-space model'* que vincula o processo demográfico de curto prazo com a dinâmica populacional de longo prazo. Nossas hipóteses são que: a) os efeitos de OCMs e anomalias positivas da TSM no recrutamento são mais intensos em SPSP e RA (ilhas equatoriais) do que em TRI, localizada no Giro Subtropical do Atlântico Sul; e b) o recrutamento é afetado positivamente pelo tamanho do corpo e negativamente pela abundância de adultos. Apesar das tendências semelhantes de aumento de OCMs e anomalias da TSM em SPSP e RA, a população abundante de SPSP foi fortemente afetada, enquanto a população de RA, pouco abundante, não foi afetada por nenhuma variável. Em TRI, a frequência de anomalias positivas teve efeito negativo no recrutamento, porém nenhuma tendência foi observada para a variável. Além disso, observamos uma relação positiva do recrutamento com o tamanho corporal, e negativa com a abundância. Portanto, este estudo sugere que tanto processos denso-independentes quanto denso-dependentes atuam como agentes na dinâmica populacional do caranguejo-aratu nas ilhas oceânicas. Em um cenário de aumento da temperatura do oceano e de eventos extremos, compreender os fatores determinantes da dinâmica populacional é essencial para avaliar a vulnerabilidade climática de espécies marinhas com larga distribuição latitudinal. Efeitos aditivos ou sinérgicos entre adaptações às condições oceanográficas regionais e pressões denso-dependentes podem determinar a vulnerabilidade climática de cada população.

Palavras-chave: recrutamento, ondas de calor marinhas, vulnerabilidade climática, crustáceos; costões rochosos; Grapsidae.

ABSTRACT

In the last decades, marine heatwaves (MHWs) and positive sea surface temperature anomalies (ΔSST) have become more frequent and intense, causing population declines in marine ecosystems. While ocean temperature acts as a filter in the survival bottleneck of early life stages of decapod crustaceans, density-dependent competition can lead to smaller adults and thus reduced fecundity, affecting recruitment and population dynamics. Studies regarding the effects of temperature on the physiology of marine invertebrates suggest that tropical species that live near their thermal limit, are more vulnerable to climate change than their counterparts from colder regions. Here, we aim to understand the effects of ocean temperature anomalies and density-dependence on the population dynamics of the intertidal Sally lightfoot crab *Grapsus grapsus*, at three Brazilian oceanic islands, located in different latitudes. We jointly analysed short-term (2019) count and capture-recapture data, fecundity and long-term (2003-2019) population monitoring data collected at the St Peter and St Paul Arch. (SPSP), Rocas Atoll (RA) and Trindade Island (TRI), using an *'Integrated population model'*. We developed a model consisting of four sub-models: 1) a Dynamic N-mixture model; 2) a robust design Jolly-Seber model; 3) a Poisson log-linear model; and 4) a state-space model that links short-term demographic process with long-term population dynamics. Our hypotheses are that: a) the effects of MHWs and positive ΔSST on recruitment are stronger at SPSP and RA (equatorial islands) than at TRI, located in the South Atlantic Subtropical Gyre; and b) recruitment is positively affected by body size and negatively by adult abundance. Despite similar increasing trends in MHWs and ΔSST at SPSP and RA, the abundant SPSP population was strongly affected by the frequencies and intensity of MHWs and ΔSST, while the low abundant RA population was not affected by any variable. In TRI, the frequency of ΔSST negatively affected recruitment, even though no trend was observed. Moreover, we found a positive relationship of recruitment with body size, and negative with abundance. Therefore, this study suggests that both density-independent and density-dependent processes act as drivers of the population dynamics of the Sally lightfoot crab at the oceanic islands. Under a scenario of increasing ocean temperatures and extreme events, understanding the drivers of population dynamics is needed to assess the climate vulnerability of marine species with large latitudinal distribution. Additive or synergistic effects between adaptations to regional oceanographic conditions and density-dependent pressures may determine the climate vulnerability of each population.

Keywords: recruitment, marine heatwaves, climate vulnerability, crustacean, rocky shores; Grapsidae.

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number of larvae, respectively. The horizontal arrows represent the direction of the effect. The climate trends are represented by the thermometer with an arrow (increasing trend) or equal sign (no trend). The climate vulnerability is related to the climatic effects on each population SPSP= St. Peter and St. Paul Arch.; TRI= Trindade Island; RA= Rocas Atoll.....50

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INTRODUÇÃO GERAL

A ecologia de populações tem como objetivo entender os processos e fatores que regulam os parâmetros populacionais desde o nível genético até interações entre diferentes espécies. **Monitoramentos a longo prazo,** entre seus diferentes objetivos, buscam definir '*baselines'* das condições iniciais do ecossistema e entender as variações da **distribuição** – área de ocorrência e uso do habitat – e da **abundância** – tamanho ou densidade populacional – ao longo do tempo. Avaliar o estado de conservação de populações ou espécies-alvo, assim como suas respostas a distúrbios ambientais, naturais ou antrópicos, é essencial para o estabelecimento de estratégias de manejo eficientes (LINDENMAYER; LIKENS, 2009).

A **dinâmica populacional** de uma espécie é determinada por **processos estocásticos** e **determinísticos** que influenciam os parâmetros demográficos e o tamanho populacional**.** Os efeitos estocásticos ocorrem em decorrência de **eventos ao acaso,** não sendo possível determinar o estado atual ou futuro de uma população em função do estado no tempo anterior. Por outro lado, processos determinísticos, causados por **fatores denso-independentes** (e.g., variação da temperatura) ou **denso-dependentes** (e.g., recursos limitados), sempre levam ao mesmo resultado em função da condição inicial da população (Shaffer, 1981; Caughley, 1994).

Dentre fatores denso-independentes, a **sobre-exploração** e a **perda de habitat** têm causado um histórico de **declínios populacionais** e **extinções** de diversas espécies marinhas (HARNIK et al., 2012). Nas décadas pós-revolução industrial, o **aquecimento e a acidificação** dos oceanos, devido ao aumento da emissão de CO_2, também se tornaram uma ameaça global aos ecossistemas marinhos (HARNIK et al., 2012). Neste sentido, o aumento da temperatura do mar, considerando tanto **anomalias térmicas** quanto **ondas de calor marinhas** (OCMs) **(**HOBDAY et al., 2016; OLIVER et al., 2018) vêm causando mudanças

na distribuição de espécies e na estrutura de comunidades em diversos ecossistemas, como os recifes de corais, florestas de *kelps* e bancos de gramíneas (WERNBERG et al., 2013; HUGHES et al., 2018; HOLBROOK et al., 2020). A**s** OCMs são eventos prolongados de extremo aquecimento da temperatura do mar (HOBDAY et al., 2016) e já foram responsáveis por colapsos de estoques pesqueiros de diversas espécies de invertebrados (MILLS et al., 2013, CHANDRAPAVAN et al., 2019), com grande prejuízo social e econômico, principalmente, para comunidades de pescadores e populações tradicionais artesanais (DEFEO et al, 2013).

Em invertebrados marinhos com alta fecundidade e ciclo de vida complexo, como os **crustáceos decápodes**, o estágio larval é o período mais sensível à temperatura do oceano (AZRA ET AL., 2018). O efeito das variações da temperatura sobre a fisiologia do organismo dependerá da sua **tolerância termal** — intervalo de temperaturas em que o animal é capaz de sobreviver sem perdas funcionais — e da capacidade de se adaptar às novas condições ambientais (SOMERO, 2005). Nesse sentido, a temperatura do mar atua como um filtro no **efeito gargalo (*bottleneck*)** da sobrevivência entre os estágios larvais e juvenil. Quando o limite termal das larvas é excedido, funções metabólicas são comprometidas e ocorre estresse oxidativo (SCHIFFER ET AL., 2014). Porém, quando o aumento da temperatura não excede esse limiar, o desenvolvimento larval pode ser mais rápido (ANGER, 1991), diminuindo as chances de as larvas serem predadas no ambiente pelágico. Mudanças na temperatura também afetam a dispersão larval através de impactos na fenologia, na disponibilidade de alimentos, em comportamentos de natação e na duração pelágica larval, comprometendo o **recrutamento** e a **conectividade** entre populações (BASHEVKIN et al., 2020; LIMA et al., 2021).

O recrutamento de novos indivíduos para a população adulta também pode ser influenciado por **processos denso-dependentes.** A denso-dependência é um efeito auto-

regulador, no qual o **crescimento populacional** é regulado em função da abundância de indivíduos na população. Relações entre densidade de indivíduos e crescimento corporal, canibalismo, forrageamento e competição intraespecífica já foram observadas em diversas espécies de caranguejos (MANSOUR; LIPCIUS, 1991; PILE ET AL., 1996; FERNÁNDEZ, 1999; MOKSNES, 2004; MARKS et al., 2020). Em populações abundantes, em que existe forte competição por refúgio e alimento, os indivíduos tendem a ser menores e alcançam a maturidade sexual com menor tamanho (MOKSNES, 2004). Fêmeas menores produzem menos ovos, resultando em uma fecundidade reduzida (HINES, 1982). Portanto, o crescimento, a fecundidade e as interações denso-dependentes também atuam como fatores determinantes na dinâmica de populações naturais.

Frente a um cenário de aquecimento dos oceanos e aumento de eventos extremos da temperatura superficial do mar (TSM), é essencial compreender os fatores determinantes na dinâmica populacional de organismos marinhos. Para isso, usamos como modelo de estudo as populações do caranguejo-aratu *Grapsus grapsus* (LINNAEUS, 1758) de três ilhas oceânicas brasileiras. Dados de contagem, captura-recaptura e fecundidade coletados em diferentes escalas temporais foram combinados através de uma análise populacional integrada, conhecida como '*Integrated Population Models'* (BESBEAS et al., 2002)*,* para estimar parâmetros demográficos e os efeitos das OCMs e anomalias térmicas, assim como, do tamanho corporal e da abundância de indivíduos sobre o recrutamento das populações.

O Caranguejo-aratu e as Ilhas Oceânicas Brasileiras

O caranguejo-aratu é uma espécie dominante da zona entre-marés das ilhas oceânicas brasileiras - Arquipélago de São Pedro e São Paulo (SPSP), Fernando de Noronha (FN), Atol das Rocas (RA) e Arquipélago de Trindade e Martim Vaz (TRI) -, seus únicos locais de ocorrência no Atlântico Sul Ocidental. O caranguejo-aratu também ocorre desde o Golfo do

México ao Mar do Caribe, e no Pacífico, desde a Baja Califórnia (México) à costa nordeste do Chile e nas ilhas Galápagos. Os adultos e juvenis se alimentam de algas e pequenos peixes nas poças de maré, ovos e neonatos de tartarugas e de aves marinhas que nidificam nas ilhas (VINUEZA et al., 2006; GIANUCA; VOOREN, 2007), e são predados por polvos e moreias. Por outro lado, as larvas pelágicas são um importante recurso alimentar de peixes recifais planctívoros e espécies migratórias que visitam as ilhas (FREIRE et al., 2011). Assim, o caranguejo-aratu é um elo essencial entre a cadeia trófica marinha e terrestre, sendo considerado uma espécie-chave das ilhas oceânicas brasileiras. O monitoramento do caranguejo-aratu começou em SPSP em 2003 e a partir de 2012, com o início do Programa de Pesquisa Ecológica de Longa Duração das Ilhas Oceânicas (PELD-ILOC, https://peldiloc.sites.ufsc.br/pt/), as amostragens se estenderam às demais ilhas.

Ilhas oceânicas são consideradas laboratórios naturais para estudar processos ecológicos em nível populacional, pois possuem uma área terrestre reduzida com barreiras de dispersão limitando a conectividade entre populações. Além disso, apresentam uma biota com tamanhos populacionais reduzidos e, portanto, sensíveis a pressões ambientais, climáticas e antropogênicas (WOOD et al., 2017). Apesar do clima tropical oceânico (MOHR et al., 2009), TRI (~20° S) é a única ilha localizada no centro do Giro Subtropical do Atlântico Sul, onde há maior variação intra-anual da TSM em comparação às ilhas equatoriais (0-3° S). No inverno, TRI apresenta TSM entorno de 24° C, enquanto a média se mantém acima dos 26°C em SPSP e RA (Figs. S1 e S2, no material suplementar).

Em razão das diferentes condições de TSM, da diferenciação genética e das evidências de dispersão larval limitada entre as ilhas (TESCHIMA et al., 2015; BRANDAO et al., 2013; FREIRE et al., in press), as populações do caranguejo-aratu podem ter evoluído e se adaptado às condições locais, adquirindo tolerância térmica e capacidade de aclimatação específicas de cada população. Além disso, a dominância da espécie nos costões rochosos,

devido a predação e a competição interespecífica moderadas nas fases juvenil e adulta, podem resultar em pressões denso-dependentes, afetando o crescimento e o recrutamento de
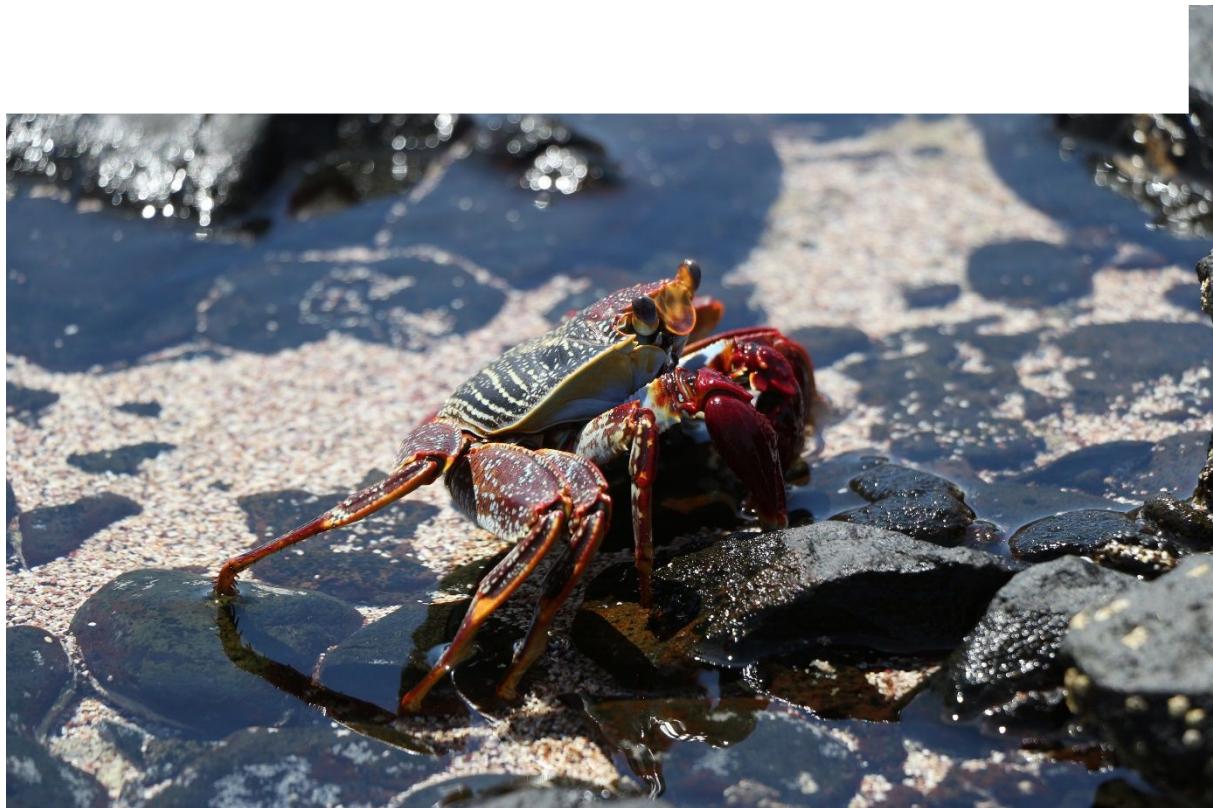
indivíduos para a população adulta. Portanto, as populações do caranguejo-aratu são um modelo ideal para avaliar efeitos ambientais e da denso-dependência na dinâmica populacional de um invertebrado marinho.

Uma abordagem integrada em estudos populacionais

Monitoramentos de longo-prazo são o principal meio de se obter dados para compreender relações demográficas em uma larga escala temporal (ZIPKIN; SAUNDERS, 2018). No entanto, balancear a efetividade do monitoramento com a sua viabilidade de execução representa um *trade-off* entre custo da coleta e precisão das estimativas. No geral, inferências demográficas, como a taxa de sobrevivência, requerem dados em nível individual, que são mais caros de se coletar (WILLIAMS et al., 2002). Além disso, métodos convencionais para estimar tendências populacionais usam apenas uma fonte de dados (e.g.

captura-recaptura, ocorrência ou contagem), muitas vezes acompanhada de um **viés amostral** (e.g., **detecção imperfeita** em contagens ou perda de marcas de identificação) (DENNIS et al., 2021). Estimativas enviesadas prejudicam a avaliação do estado de conservação das populações e resultam em medidas de manejo inadequadas (KÉRY et al., 2009). Para estimar parâmetros demográficos com maior precisão, modelos com abordagem integrada, como ***Integrated population models* (IPMs)**, combinam diferentes tipos de dados populacionais em uma única análise. Este método permite incorporar fontes de incerteza e estimar parâmetros latentes (BESBEAS et al., 2002; SCHAUB; ABADI, 2011), sendo utilizados até mesmo em estudos de espécies raras ou ameaçadas com dados esparsos e limitados (SCHAUB et al., 2007; WILSON et al., 2016).

O IPM que desenvolvemos consiste em quatro sub-modelos (Fig. 2, no artigo): (1) *dynamic N-mixture model* para os dados de contagem de curto prazo; (2) *robust design Jolly-Seber model* para os dados de captura-recaptura; (3) *Poisson log-linear model* para os dados de fecundidade; e (4) *state-space model* para os dados de monitoramento populacional (2003-2019). Os dados de contagem e captura-recaptura de curto prazo (1 e 2) foram coletados usando um desenho amostral com duas escalas temporais, conhecido como **desenho robusto de Pollock**. Com esse desenho, assume-se que a **população é fechada** entre ocasiões secundárias (pequena escala) e **aberta** entre ocasiões primárias (grande escala), o que permite estimar a probabilidade de sobrevivência e a taxa de recrutamento da população (Pollock, 1982).

Justificativa e Objetivos do estudo

Diversos estudos têm mostrado que espécies tropicais marinhas são mais vulneráveis a mudanças climáticas do que seus análogos da zona temperada, pois já vivem em temperaturas ambientais mais próximas ao seu limite termal e possuem menor capacidade de aclimatação

(SOMERO et al., 2005; VINAGRE et al., 2018; PINSKY et al., 2019). No entanto, estudos sobre tolerância termal e aclimatação em populações de espécies tropicais em larga escala latitudinal ainda são raros. Enquanto a maioria dos estudos envolve respostas fisiológicas, a complexidade de fatores atuando em nível populacional e a necessidade de dados de longo-prazo dificultam inferências de processos ecológicos em larga escala temporal (HARLEY et al., 2006). Nesse contexto, este estudo visa avaliar os efeitos de anomalias térmicas do oceano e da denso-dependência na dinâmica das populações do caranguejo-aratu nas ilhas oceânicas brasileiras SPSP, RA e TRI. Para isso, vamos 1) avaliar as tendências temporais da frequência e intensidade de OCMs e anomalias da TSM para contextualizar o cenário em cada ilha; 2) estimar parâmetros demográficos das três populações; 3) estimar os efeitos da frequência e intensidade de OCMs e de anomalias da TSM no recrutamento em cada população; e 4) estimar o efeito do tamanho corporal e da abundância de indivíduos no recrutamento.

Através da análise integrada usando dados de contagem, captura-recaptura e fecundidade, coletados em diferentes escalas, testaremos as hipóteses (Fig. 1) de que: a) os efeitos de OCMs e anomalias positivas da TSM no recrutamento são mais intensos em SPSP e RA (ilhas equatoriais) do que em TRI, localizada no Giro Subtropical do Atlântico Sul; e b) o tamanho corporal tem efeito positivo no recrutamento, enquanto a abundância tem efeito negativo. Este estudo contribuirá para a melhor compreensão dos mecanismos reguladores da dinâmica populacional de invertebrados marinhos; e servirá de suporte para medidas de manejo e conservação das ilhas oceânicas, que abrigam uma alta taxa de espécies endêmicas (PINHEIRO et al., 2018) e servem como reservatório de indivíduos de espécies exploradas pela pesca no entorno das ilhas, devido ao efeito de *spillover* (HALPERN et al., 2010).
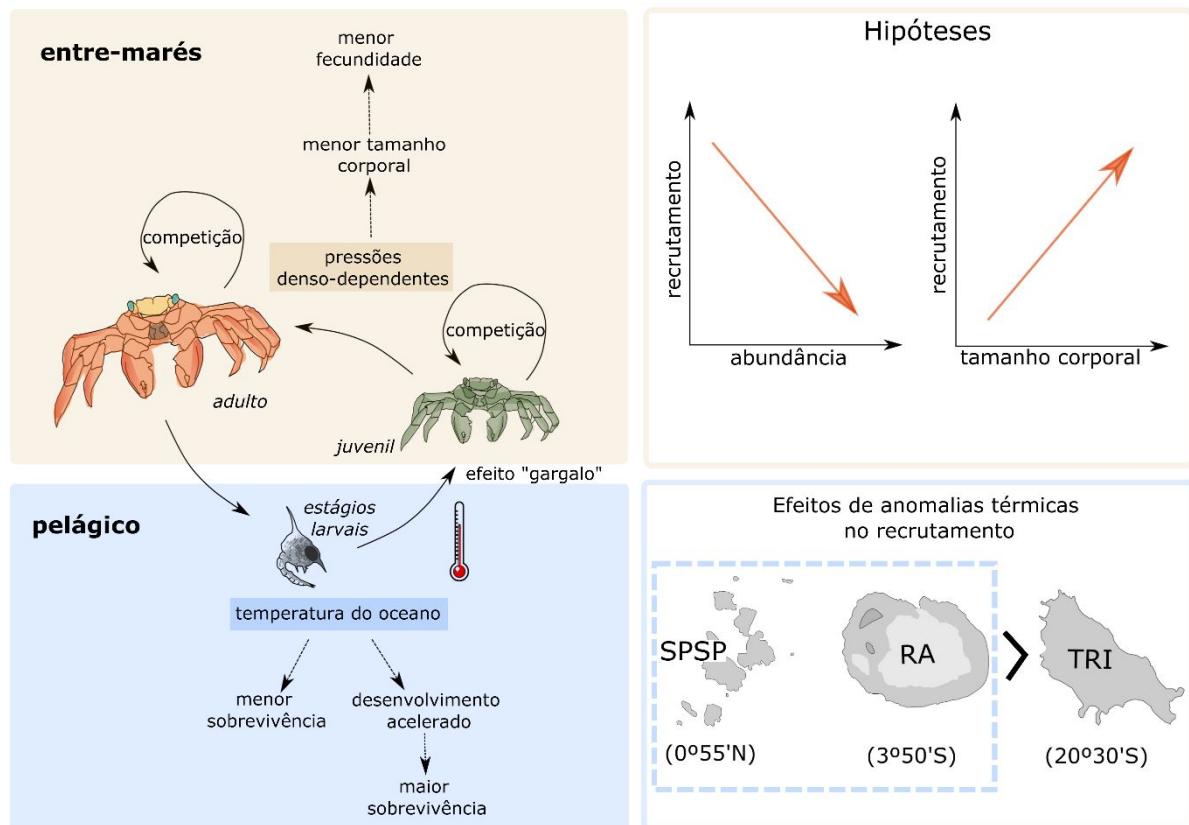
Figura 2. Esquema simplificado do ciclo de vida do caranguejo-aratu e das hipóteses testadas no estudo. SPSP= Arquipélago de São Pedro e São Paulo; RA=Atol das Rocas; TRI= Ilha da Trindade.

CAPÍTULO ÚNICO: OCEAN TEMPERATURE AND DENSITY DEPENDENCE AS KEY DRIVERS OF THE POPULATION DYNAMICS OF AN INTERTIDAL CRAB AT THE BRAZILIAN OCEANIC ISLANDS

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Abstract

1. In the last decades, marine heatwaves (MHWs) and sea surface temperature anomalies (ΔSST) have become more frequent and intense, causing population declines in marine ecosystems. Previous experimental studies have been suggesting that tropical marine species that live near their thermal limits, are more vulnerable to climate change than their counterparts from colder regions. For decapod crustaceans, ocean temperature acts as a filter in the survival bottleneck of early life stages, affecting recruitment. Still, density-dependent competition can lead to smaller adults and thus reduced fecundity.

2. Here, we aim to understand the effects of ocean temperature anomalies and density-dependence on the population dynamics of the intertidal Sally lightfoot crab *Grapsus grapsus*, at three Brazilian oceanic islands, located in different latitudes.

3. We jointly analysed short-term (2019) count and capture-recapture data, fecundity and long-term (2003-2019) population monitoring data collected at the St Peter and St Paul Archipelago (SPSP), Rocas Atoll (RA) and Trindade Island (TRI), using an Integrated population model. We hypothesized that: a) the effects of MHWs and positive ΔSST on recruitment are stronger at SPSP and RA (equatorial islands) than at TRI, located in the South Atlantic Subtropical Gyre; and b) recruitment is negatively affected by adult abundance and positively affected by body size.

4. Despite similar increasing trends in MHWs and ΔSST at the equatorial islands, the abundant SPSP population was strongly affected by MHWs and ΔSST, while the low abundant RA population was not affected by any variable. In TRI, recruitment was positively affected by MHW cumulative intensity and negatively affected by ΔSST. Moreover, recruitment was positively related to body size and negatively to abundance.

5. Climate vulnerability of each population might depend on synergistic interactions between local adaptation to regional climate and density-dependent pressures.

1. Introduction

Knowledge of the effects of environmental drivers and density dependent processes on demography is crucial for understanding population dynamics under climate change, which is one of the main threats to global biodiversity (Sala et al., 2000; Harnik et al., 2012). Changes in species distribution, phenology and physiology linked to anthropogenic climate change are well documented for different taxa in marine systems (Edwards & Richardson 2004; Doney et al., 2012), but few studies have addressed their impacts on species abundance. Sea surface temperature anomalies and marine heatwaves (MHWs) are expected to become more intense and frequent (Hobday et al., 2016; Oliver et al., 2018), causing impacts at the population level and altering ecosystem functions (Wernberg et al., 2013; Holbrook et al., 2020). Fishery collapse of lobsters, crabs, scallops and abalones have already been linked to warm events (Mills et al., 2013; Chandrapavan et al., 2019; Caputi et al., 2016).

For highly fecund organisms with complex life cycles such as decapod crustaceans, ocean warming and extreme climatic events are even more concerning, as their early pelagic stages (e.g., embryos and larval phases) are highly sensible to ocean temperature variations (Bartolini et al., 2013; Azra et al., 2018). Increasing temperatures can accelerate larval development, which reduces the time spent in high-risk pelagic environment, increasing larval survival and recruitment rate (O'Connor et al., 2007). Conversely, acute heat stress can lead to higher mortality of younger life stages (Pandori & Sorte, 2019). Increased temperatures combined with ocean acidification can also narrow larval thermal tolerance (Schiffer et al., 2014) and affect their capability to disperse and avoid predators through vertical swimming (Gravinese et al., 2019). This survival bottleneck process might affect settlement rate and thus, adult population dynamics, which are usually driven by density-dependent processes.

Evidence of density-dependent effects on survival, recruitment and growth of older life stages has been reported for several crustacean species, as the blue crab *Callinectes sapidus*, shore crab *Carcinus maenus,* and blue swimmer crab *Portunus armatus* (Mansour & Lipcius, 1991; Pile et al., 1996; Fernández, 1999; Moksnes, 2004; Marks et al., 2020). The negative effect of population density on growth has been linked to increased competition for shelter and food resources, and decreased activity of smaller crabs (Moksnes, 2004). In turn, reduced growth can lead to smaller size-at-maturity, fecundity-at-age and egg productivity (Hines, 1982; Ramirez Llodra et al., 2002; Goñi et al., 2003). Density-dependent cannibalism in younger-stage shore crabs also appears to drive recruitment (Fernández, 1999).

In the Southwestern Atlantic, the Sally lightfoot crab, *Grapsus grapsus* (Linnaeus, 1758) plays an important role in top-down control of the intertidal benthic community of the Brazilian oceanic islands, Saint Peter and Saint Paul Archipelago (SPSP), Fernando de Noronha Archipelago (FN), Rocas Atoll (RA) and Trindade Island (TRI). Adults and juveniles act as grazers on rocky shores, feed on small fishes in tide pools (Vinueza et al., 2006), and prey on eggs and neonates of turtles and boobies (Gianuca & Vooren, 2007). In the absence of intensive predation and interspecific competition, the populations thrive in the rocky shores, which might lead to high rates of body mutilation (Freire et al., 2011), suggesting density-dependent competition. Moreover, the pelagic larval stages are an important food resource for planktivorous animals that live nearby or visit the islands (Freire et al., 2011). Larval dispersal from SPSP to FN and RA (Freire et al., 2021), as well as evidence of larval retention and genetic differentiation between the equatorial populations (SPSP, RA and FN) and TRI (Brandao et al., 2013; Teschima et al., 2016) suggest that TRI and SPSP populations are most likely maintained by self-recruitment.

Warm-adapted intertidal species are expected to be more vulnerable to ocean warming than their counterparts from colder regions, as they already live closer to their thermal limits

and have limited acclimation plasticity (Stillman & Somero, 2000; Vinagre et al., 2018). TRI (~20° S) is the only island located within the South Atlantic Subtropical Gyre and exhibit a higher intra-annual sea surface temperature (SST) variability and lower annual mean and maximum SST (mean 25.3°C, max. 28.5°C) than SPSP and RA (mean ~27.5 °C, max. ~ 29.5°C) (Fig. S2-3). Given the differences in SST and the low connectivity between the equatorial islands and TRI, the Sally lightfoot crab populations might be adapted to regional conditions, resulting in distinct responses to ocean warming. Therefore, these populations are a good model to assess the drivers of population dynamics of a tropical marine invertebrate in different latitudes. In this study, we aim to 1) assess the temporal trends of MHWs and positive SST anomalies (ΔSST+) at the Brazilian oceanic islands; 2) estimate demographic parameters of the Sally lightfoot crab populations; and 3) estimate the effects of MHWs and ΔSST+, as well as body size and abundance on recruitment.

Estimating precise population parameters remains a challenge due to multiple sources of uncertainty related to data collection and stochastic processes (Saunders et al., 2018). Inference of demographic parameters often relies on individual-level data that are costly to collect (Williams et al., 2002). Integrated population models (IPMs) have been increasingly used to provide more accurate and precise demographic estimates by jointly analysing population and individual-level data (Schaub & Abadi, 2011). Here, we combined short-term count and capture-recapture data collected at TRI from Aug 2019 to Feb 2020; fecundity data collected at SPSP and TRI in 2004 and 2011, respectively; and long-term population monitoring data at the three islands from 2003 to 2019 (Fig. S1) in an IPM composed of four sub-models: (1) a dynamic N-mixture model for short-term replicated count data; (2) a Jolly-Seber robust design model for capture-recapture data; (3) a Poisson regression model for fecundity data; and (4) a dynamic N-mixture model that links the short-term and long-term demographic processes. Our IPM allow us to test the hypothesis that: a) the effects of MHWs

and ΔSST+ on recruitment are stronger at SPSP and RA (equatorial islands) than at TRI; and b) recruitment is positively affected by body size and negatively by abundance.

2. Material and methods

2.1 Study sites

The Brazilian oceanic islands – Saint Peter and Saint Paul Archipelago, Rocas Atoll and Trindade Island – are the only sites where the Sally lightfoot crab inhabits in the South Atlantic Ocean, which have been systematically monitored. The islands encompass no-take Marine Protected Areas (MPAs) restricted to the ICMBio team (Brazilian Environmental Agency), Brazilian Navy and authorized researchers (Fig. 1).

The islands are influenced by the warm oligotrophic water of the South Equatorial Current (SEC) system which bifurcates into the North Brazil Current (NBC) and the Brazil Current (BC). SPSP is under the influence of the northern branch of the SEC, while the NBC flows northward close to RA and FN. The BC flows south towards TRI, which is located in the centre of the South Atlantic Subtropical Gyre (SASG), specially under the sluggish flow of the southern branch of SEC (Stramma & England, 1999, Freire et al. in press). The mean SST ranges from ~26ºC to ~29ºC throughout the year in the equatorial islands, whereas in TRI it ranges from ~22ºC (late austral winter) to ~29ºC (late austral summer) (Fig. S3). Here, we considered TRI as a 'subtropical island' due to its location in the SASG and SST features.

Saint Peter and Saint Paul Archipelago (0°55' N, 29°20' W, <1 km2 land area) is a set of 15 islets in the equatorial Atlantic about 1,010 km from the northeastern coast of Brazil (Becker et al., 2001). The region is under the influence of the Intertropical Convergence Zone (ITCZ) from January to May (rainy season), favouring larval retention near the island (Díaz et al., 2009). Increased primary productivity around SPSP is attributed to the Island Mass Effect (Doty & Oguri, 1956) and resurgence of deep cold waters (Campelo et al., 2019).
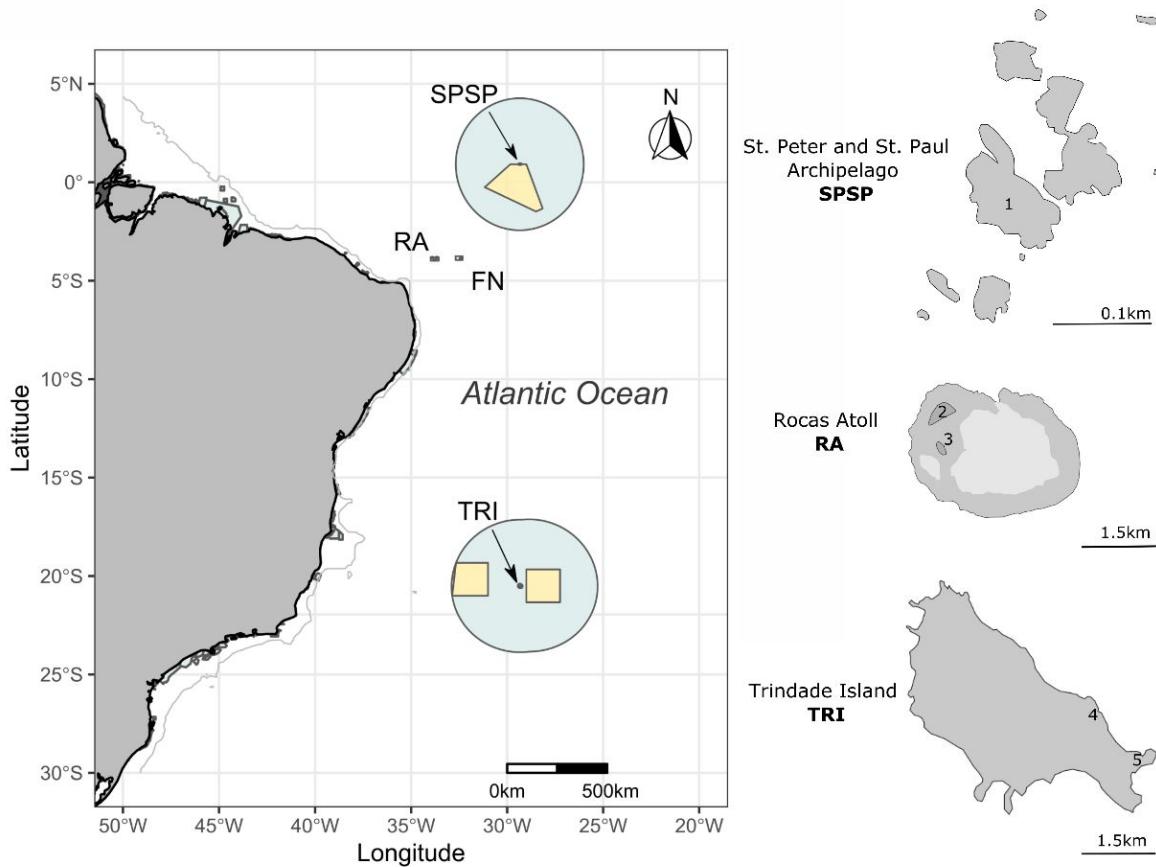
Figure *1*. Location of the oceanic islands and the large marine protected areas of Brazilian waters (light blue). Detail of the islands with the sites selected for this study (1= Ilha Belmonte; 2= Ilha do Farol; 3= Ilha do Cemitério; 4= Praia das Andradas; 5= Praia das Tartarugas). Yellow polygons represent no-take MPAs. Rocas Atoll is totally no-take MPA, the inner lagoon is light grey.

Rocas Atoll (3°50'S, 33°49'W, 7.5 km^2) is the only atoll in the South Atlantic, located 266 km off the Brazilian coast (Kikuchi & Leão, 1997) and 124 km west of FN. The semidiurnal tides with high tides reaching up to 3.8m, leads to only two small sand islands permanently emerged (Gherardi & Bosence, 2001), where surveys have been conducted.

Trindade Island (20°30 S, 29°20 W, 13.5 km²) is an emerged tip of the Vitória-Trindade Seamount Chain, 1,140 km off the eastern coast of Brazil (Protrindade, 2017). Winds prevailing from NE to E lead to a greater exposure of the eastern side to waves and erosion of the rocky shore. Surveys have been usually conducted between July and October, when swells occur more frequently and air temperatures are lower (Pedrosa et al., 2017).

2.2 Data collection

The Sally lightfoot crab monitoring has been carried out since 2003 at SPSP and since 2011 at RA and TRI by different projects (detailed in Freire et al., 2011 and Teschima et al., 2016). Since 2012, the Long-Term Ecological Research of Brazilian Oceanic Islands (PELD-ILOC/ CNPq, https://peldiloc.sites.ufsc.br/) has been monitoring the marine wildlife of the oceanic islands through yearly scientific expeditions to each archipelago. Unfortunately, the expeditions were interrupted due to the COVID-19 pandemic. Data collection is represented in Figure S3 and described below as 'Short-term data' and 'Long-term data'.

2.2.1 Short-term data

The short-term data consist of replicated counts and capture-recapture data collected using a classical robust design at the rocky shore of 'Praia dos Andradas' in TRI (Fig. 1) from August 2019 to February 2020 during two expeditions of two months (Aug–Oct and Dec–Feb). The sampling structure consisted of eight primary occasions, each of which consisted of three to four secondary occasions (days). Within each expedition, the time interval across primary occasions was always a two-week interval, while between expeditions there was an interval of eight weeks. The surveys were always conducted in the morning, during the low tide in full and new moon, to have access to the greater rock exposure of spring tides.

We conducted the counts through visual census wherein one observer walked along the rocky shore counting the crabs in three transects of 20m x 2m ($40m^2$) arranged parallel to the shore. Then, we captured individuals randomly by hand or using nets, identified the gender, and measured the largest width of their carapace (CW) with a vernier calliper (0.05 mm). We photographed the posterior region of the carapace for individual identification based on the spotted pattern of each individual. The capture effort was standardized in two-hour periods of fieldwork by three people. To avoid stressing the crabs, we limited five individuals to be measured at time and released them right after the sampling, before capturing more crabs. We used the Wild-ID software for post processing photo-identification and pattern matching (Bolger et al., 2012). A catalogue of individuals was created for each sex, but only data from females (n=161) was used in analysis, due to changes in the method of male identification.

We also used CW and estimated number of eggs carried by females to estimate fecundity rate. Ovigerous females were collected at SPSP in 2004 (n=67) and at TRI in 2011 (n= 37). In the laboratory, the egg mass was removed, fixed in 70% alcohol and threated as described by Greco & Rodríguez (2004).

2.2.2 Long-term data

The long-term population monitoring was also performed through the visual census described above. However, the transects were spatially replicated according to the accessible area of the rocky shore on each island. The area covered by each transect has only been standardized at $40m^2$ since 2012. We selected data from the sites (sites 1-5 in Fig. 1) visited more often over the years, resulting in a total of 471 transects (SPSP=247; RA=91; TRI=133).

Crabs were also collected as described above, but individuals were not identified. We used the maximum female's CW (SPSP=251; RA=142; TRI=210) at each island and occasion to estimate the effect of body size on recruitment. We decided to use maximum values over

the averages intending to minimize sampling bias related to protocol changes over the years, such as collecting smaller individuals in the early years of survey for sexual maturity analysis (Freire et al., 2011).

2.3 Ocean temperature data and analysis

We used data of daily 0.25º-resolution Optimum Interpolation Sea Surface Temperature (OISST v2.0) based on Advanced Very High Resolution Radiometer (AVHRR) Satellite data (Reynolds et al., 2007) from the National Oceanic and Atmospheric Administration's (*NOAA/ OAR/ESRL PSL, Boulder, Colorado, USA*, from their website: ftp://ftp.cdc.noaa.gov/Datasets/noaa.oisst.v2.highres/). We extracted data for each island from 1982 to 2019 and calculated the frequency and cumulative intensity of marine heatwaves and the frequency and average of positive sea surface temperature anomalies (ΔSST+) (calculated as Hobday et al., 2016). Here, MHW is considered as a prolonged anomalously warm water event persisting for at least five days and with SST warmer than the 90th percentile of a 30-year historical baseline period, while ΔSST+ are deviations above the long-term mean (Hobday et al., 2016). We applied the nonparametric Mann-Kendall trend test from the R package 'Kendall' (McLeod, 2015) to detect trends in time series. Then, to analyse the influence of the SST-derived covariates on the recruitment, we calculated and averaged an 18-month period prior to sampling, considering an approximate duration of one year and a half for the larvae to become adults (Madeira, 2008; Freire et al., 2011). Due to the presence of multicollinearity between variables, checked using the variance inflation factor (VIF), we selected the MHWs frequency (MHW^{freq}), MHWs cumulative intensity (MHW^{int}) and ΔSST+ frequency ($\varDelta SST^{freq}$) as covariates for the recruitment process.

2.4 Integrated population model

Our IPM was composed of four sub-models (Fig. 2): (1) Dynamic N-mixture model 1; (2) Jolly-Seber robust design model; (3) Poisson regression model; and (4) Dynamic N-mixture model 2. Under a robust design (sub-models 1 and 2), the population is assumed to be closed within a primary occasion and opened across primary occasions which yields the estimates of apparent survival probability and recruitment rate (Pollock, 1982). To integrate the sub-models using data in different scales, we assumed that bi-weekly recruitment (γ^{BW}) and bi-weekly apparent survival (φ^{BW}) were constant across populations and years. We assumed that only recruitment between yearly surveys depends on the effects of SST-derived covariates and density-dependence. Parameter notation and definitions are listed in Table S1

2.4.1 Dynamic N-mixture model 1

We adapted the original dynamic N-mixture model (Dail & Madsen, 2011) to estimate apparent survival and recruitment from the short-term counts sampled at TRI in 2019, while accounting for unequal time intervals I_{p-1} between primary occasions $p = 1, 2,..., P$ (sampling design in Fig. S3). In the first primary occasion, the number of individuals $n_{j,1}$ at site $j=1,2,...,$ J (J=3 fixed transects) was assumed to follow a Poisson distribution with an expected initial abundance λ such that

$$n_{j,1} \sim Poisson(\lambda) \tag{1}$$

For subsequent primary occasions ($p \geq 2$), we assumed that the number of survivors $s_{j,p}$ from the last primary occasion followed a Binomial distribution such that

$$s_{j,p} \sim Binomial(n_{j,p-1}, \varphi_{p-1}) \tag{2}$$

where the apparent survival probability φ_{p-1} was a function of a bi-weekly apparent survival probability φ^{BW} and the time interval between two consecutive primary occasions I_{p-1} such

that $\varphi_{p-1}=\left(\varphi^{BW}\right)^{I_{p-1}}$. The number of recruits $g_{j,p}$ was assumed to follow a Poisson distribution such that

$$g_{j,p} \; Poisson\left(n_{j,p-1} \times \gamma_{p-1}\right) \tag{3}$$

where the recruitment rate γ_{p-1} was a function of bi-weekly recruitment rate γ^{BW} and the time interval such that $\gamma_{p-1}=\gamma^{BW} \times I_{p-1}$. Note that because immigration from other islands to TRI is unlikely to happen, the number of recruits is likely to represent local recruitment only. Eventually, the abundance was calculated by summing up the survivors and recruits:

$$n_{j,p}=s_{j,p}+g_{j,p} \tag{4}$$

We then linked the count data $y_{j,p,s}$ in transect j, primary occasion p and secondary occasion s, to the abundance estimate with

$$y_{j,p,s} \; Binomial\left(n_{j,p},\Theta\right) \tag{5}$$

where the detection probability Θ was assumed to be constant and equal for all individuals.

2.4.2 Jolly-Seber robust design model

We adapted the Jolly-Seber robust design model (Gibson et al., 2018) to estimate survival probability from the capture-recapture data. We organized our data into an individual encounter history format. The likelihood of this model was governed by two parameters, apparent survival probability φ_{p-1} and capture probability ρ. To account for the different numbers of secondary occasions within each primary occasion, we used $1-\left(1-\rho\right)^{n_p^{capt}}$ for primary occasion p, in which n_p^{capt} was the number of secondary occasions.

2.4.3 Poisson regression model

We modelled the number of eggs, E_f, for each female f as a Poisson distribution such that

$$E_f \; Poisson\left(\mu_f\right) \tag{6}$$

where the fecundity rate μ_f was a function of the carapace width of each female cw_f given by

$$\log\left(\mu_f\right) = \alpha^{fec} + \beta^{fec} \times cw_f \tag{7}$$

We assumed coefficient β^{fec} to be the same across populations and over years. Thus, β^{fec} makes the connection between the Poisson regression model and the following model.

2.4.4 Dynamic N-mixture model 2

The dynamic N-mixture model 2 has a similar structure of the dynamic N-mixture model 1 but the former explains population dynamics over a longer time period (i.e., over years). The unequal time intervals $I_{i,t-1}^{\dot{c}}$ between time $t = 1,..,T$ at each island i are in terms of the number of two-week periods. The abundance index in the first year $N_{i,1}$ was modelled with a Poisson distribution such that $N_{i,1}\ Poisson(\Lambda_i)$, where Λ_i was the expected initial abundance at each island. From the second year on (i.e., $t \geq 2$), we modelled the abundance index as the sum of the numbers of survivors $S_{i,t-1}$ and recruits $G_{i,t-1}$ from the last year such that $N_{i,t} = S_{i,t-1} + G_{i,t-1}$. The number of survivors was modelled with a Binomial distribution such that

$$S_{i,t}\ Binomial\left(N_{i,t-1}, \phi_{i,t-1}\right) \tag{8}$$

where $\phi_{i,t-1}$ is the apparent survival probability, which is a function of the constant bi-weekly survival probability φ^{BW} (section *2.4.1*) and the time interval $I_{i,t-1}^{\dot{c}}$ between surveys $\phi_{i,t-1} = \left(\varphi \dot{c}\dot{c} BW\right)^{I_{i,t-1}^{\dot{c}}} \dot{c}$. The number of recruits was modelled with a Poisson distribution such that

$$G_{i,t}\ Poisson\left(N_{i,t-1} \times \Gamma_{i,t-1}\right) \tag{9}$$

where recruitment rate $\Gamma_{i,t-1}$ was assumed to be influenced by the abundance, maximum carapace width (*CW*), and SST-derived covariates such that

$$\log\left(\Gamma_{i,t-1}\right)=\log\left(\overline{\Gamma}_{i,t-1}\right)+\beta^{dd}\times\log\left(N_{i,t-1}\right)+\beta^{fec}\times CW_{i,t}+\beta_{i,1}\times MHW_{i,t}^{freq}+\beta_{i,2}\times MHW_{i,t}^{\int\dot\iota+\beta_{i,3}\times\Delta SST_{i,t}^{freq}\dot\iota}$$

(10)

where the mean recruitment rate $\overline{\Gamma}_{i,t-1}$ was calculated as a function of the bi-weekly

recruitment rate γ^{BW} (section *2.4.1*) such as $\overline{\Gamma}_{i,t-1}=\gamma^{BW}\times I_{i,t-1}^{\dot\iota}$. The coefficient β^{dd} was the

effect of density dependence and β^{fec} was the effect of body size, which was assumed to be

the same as in the Poisson regression model (section *2.4.3*). The island-specific coefficients

$\beta_{i,1}$, $\beta_{i,2}$, and $\beta_{i,3}$ were the effects of the standardized covariates $MHW_{i,t}^{freq}$, $MHW_{i,t}^{\int\dot\iota\dot\iota}$and

$\Delta SST_{i,t}^{freq}$, respectively. Covariates are normally standardized to have 0 mean and unit standard

deviation (*sd*). However, to link long-term population process to our fine-scale demographic

parameters, we standardized these covariates x using the value from the TRI island ($i = 3$) in

year 2019 ($t = 12$) such that $x_{i,t}^{st}=(x_{i,t}-x_{3,12})/sd\left(x_{i,t}\right)$. We also calculate population growth

rate as $N_{i,t}/N_{i,t-1}$.

We then linked the count data $Y_{i,t,k}$ in island i, time t and sampling replicate k, with the

abundance index with a Poisson distribution such that

$$Y_{i,t,k}\ Poisson\left(N_{i,t}\times a_{i,t,k}\times\Theta\right)$$

(11)

where $a_{i,t,k}$ was the surveyed area, θ the detection probability, which was assumed to be the

same as in the dynamic N-mixture model 1 (section *2.4.1*).

Figure *2*. Graphical representation of the IPM characterized by four sub-models: (1) a Dynamic N-mixture model for the short-term count data (blue); (2) a robust design Jolly Seber model for the capture-recapture data of female crabs (green); (3) a Poisson regression model for fecundity data (red); and (4) a state-space model for the long-term data, including the counts, body size and climate time series. Squares represent data input (y=short-term counts; c= adult females capture histories; Y=long-term counts; MHW and ΔSST = SST-derived covariates; CW= long-term carapace width data; ne= number of eggs per female; cw= female's carapace width). Rhombus represent state variables (s/S=number of survivors; g/G=number of recruits; n/N=abundance index; z=alive state;). Opens circles represent estimated parameters associatedwith observation processes (Ω=capture probability; Θ= detection probability). Shaded circles represent estimated population parameters (φ= adult
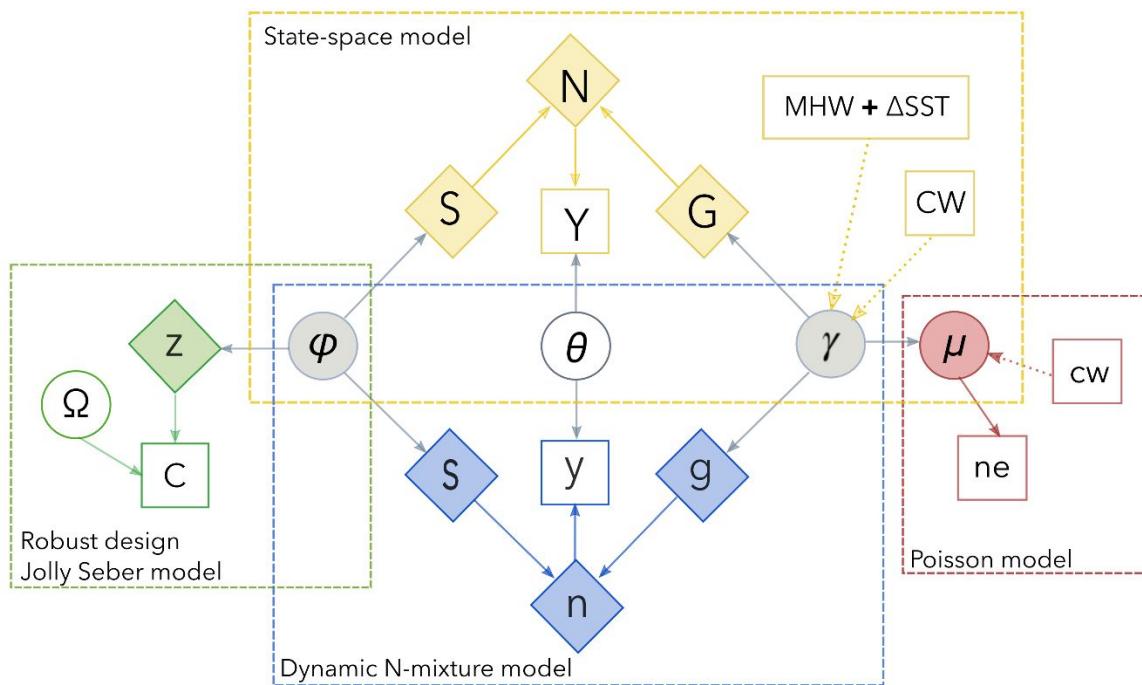
apparent survival; γ=recruitment; μ=fecundity rate). Additional parameters and hyperparameters accounting for spatial and temporal variation in model components are not shown.

2.4.5 Model implementation

We fitted the model under a Bayesian framework with a Markov chain Monte Carlo algorithm implemented with JAGS 3.3.0 (Plummer, 2003) called from R (R Core Team, 2020) using the 'jagsUI' package (Kellner, 2015). We assume vague prior for all parameters and posterior distributions of the parameters were generated by 80,000 iterations of three chains after an adaptive phase of 40,000 iterations, a burn-in of 20,000 samples and thinning of 4. Convergence of the MCMC algorithm was considered achieved when Rhat values were <1.1 for the MCMC chains of all parameters (Gelman & Hill, 2006).

2.5 Demographic relationship analysis

The relationships between maximum CW and log-transformed abundance estimates were fitted using simple linear regressions, as wells as the relationship between log-transformed number of eggs and female's carapace width.

3. Results

3.1 Ocean temperature trends

We found positive trends ($p < 0.05$) in historical series (1982-2019) of MHWs frequency and cumulative intensity (Fig.3), as well as in frequency and mean of $\Delta SST+$ in SPSP and RA (Fig.4). However, no trends were found in TRI ($p > 0.05$). Since the start of monitoring in 2003, most of the maximum values of the MHW properties (Table 1) were recorded during the 2010 event, which was the longest-lasting marine heatwave that reached the Brazilian oceanic islands (TRI=91 days along the year; SPSP=17 days; RA=14 days).

Table 1. Maximum values observed for marine heatwave properties in each island and their year of occurrence. SPSP= St. Peter and St. Paul Arch.; RA= Rocas Atoll; TRI= Trindade Island.

	SPSP	RA	TRI
Frequency (events per year)	11 (2010)	10 (2010)	8 (2003)
Duration (days per year)	17 (2010)	21 (2009)	91 (2010)
Intensity (mean per event [ºC])	1.27 (2015)	0.96 (2019)	1.41 (2010)
Cumulative intensity (Intensity x Duration)	21.8 (2010)	21.3 (2009)	140 (2010)

(a)
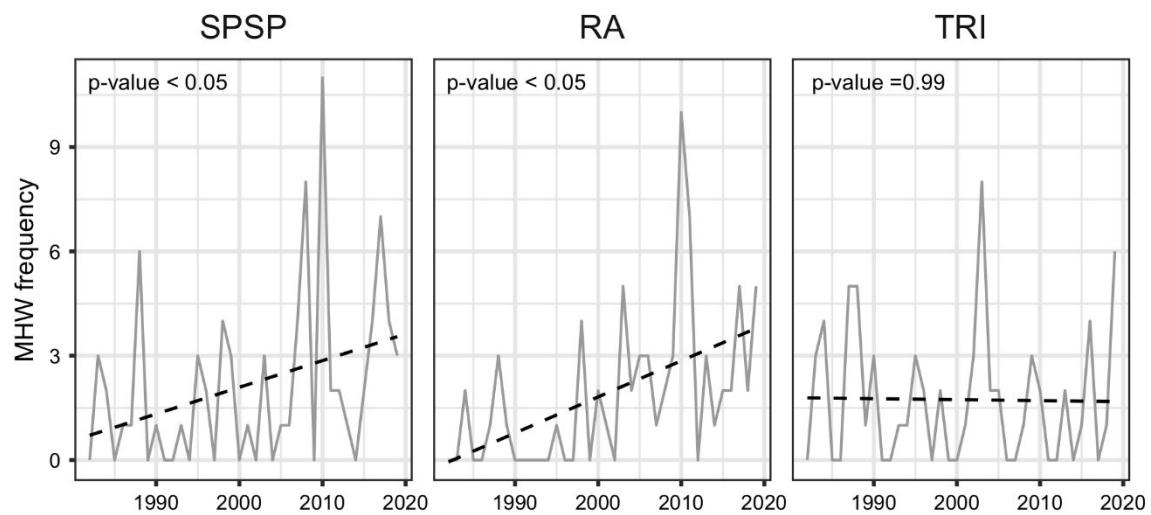
(b)
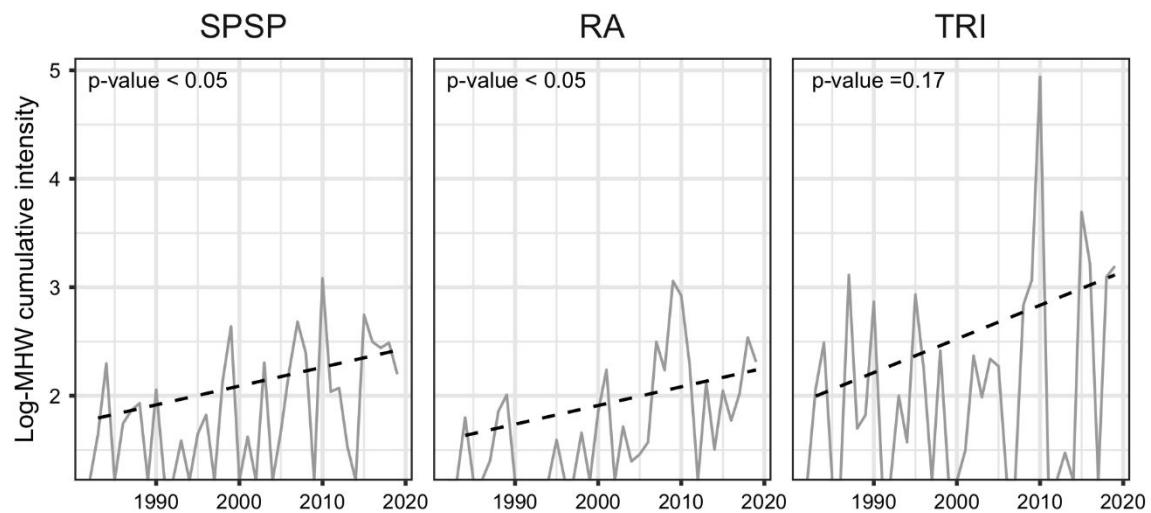
Figure *3*. Annual frequency (a) and cumulative intensity (b) of marine heatwaves (MHW) in each island, from 1982 to 2019. The fitted trends and corresponding p-values based on Mann-Kendall tests are shown.

(a)

(b)
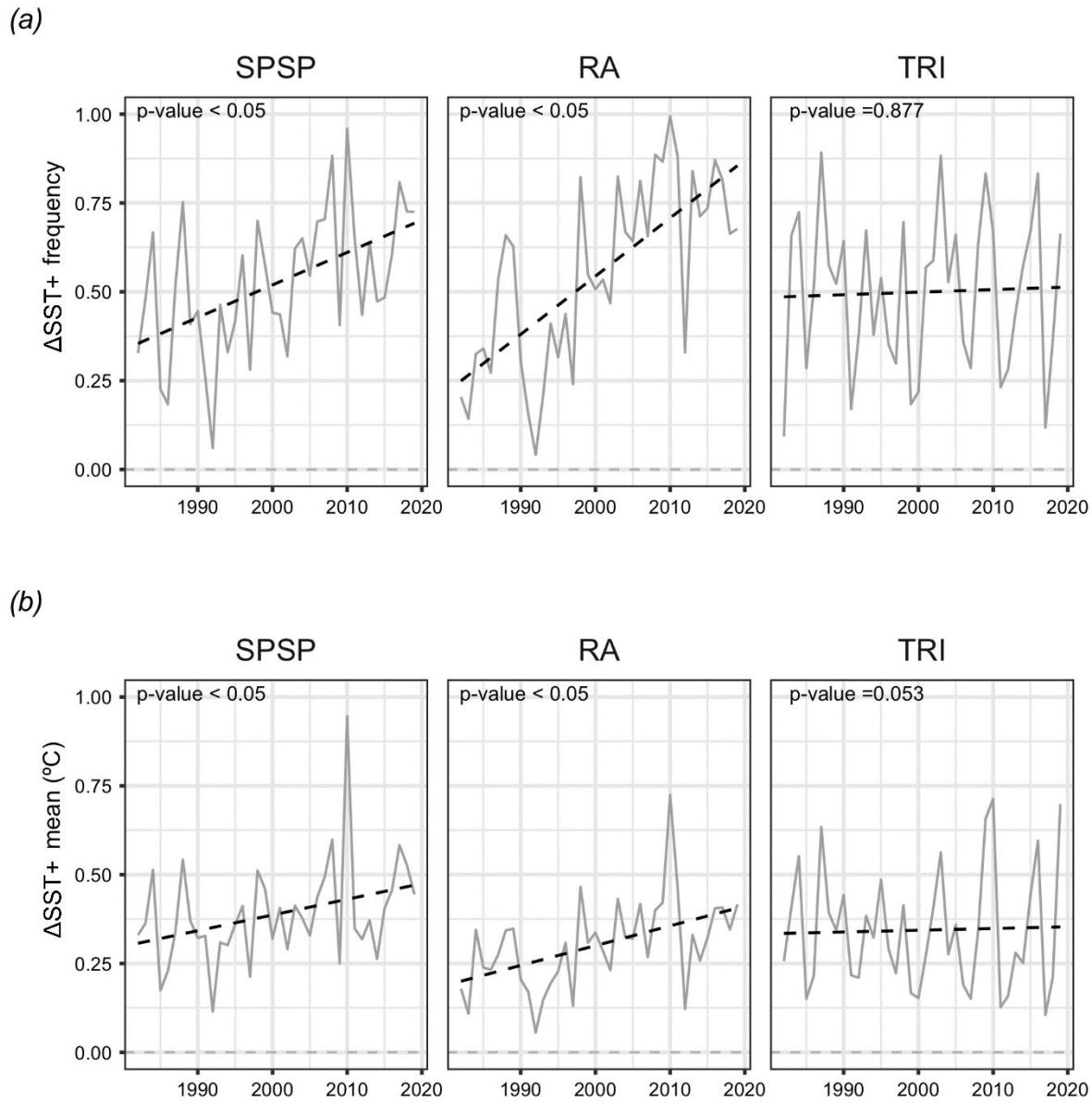
Figure *4*. Annual frequency (a) and mean positive sea surface temperature anomalies (ΔSST+) (b) in each island, from 1982 to 2019. The fitted trends and corresponding p-values based on Mann-Kendall tests are shown.

3.2 Demographic and population estimates

The short-term parameter estimates showed a high bi-week apparent survival probability [φ^{BW} = 0.71 (95% CI: 0.67, 0.75)] and a low bi-week recruitment rate [γ^{BW} = 0.32 (0.28, 0.35)]. Considering an interval of one year (~26 bi-weeks), the recruitment contributes almost

entirely to the abundance index, since the probability of adult annual survival was calculated as 0.72^{26} and was less than 0.001. No trend was observed for recruitment in a broad time scale (Fig. 5a, b), suggesting that the populations are not declining or increasing (Fig. 5c, d). The detection probability averaged 0.23 (0.20, 0.25) and the capture probability averaged 0.40 (0.38, 0.42).

The detection probability averaged 0.24 (0.21, 0.27) and the capture probability averaged 0.40 (0.38, 0.42).

The SPSP population presented the largest mean abundance [N= 71.15 (95% CI: 62, 81.7)] compared to RA [N=11.8 (95% CI: 9.6, 15.2)] and TRI [N= 34.6 (95% CI: 29.3, 44.3)] and also had a higher abundance variability (Fig. 5b). Conversely, the RA population was the most stable population, with the lowest abundance variability. Increase in the abundance of SPSP always followed peaks in the recruitment index with time lags of 1-2 years (Fig 5a, b). The only evident peak in recruitment and population growth rate was in 2011 at RA and TRI (Fig. 5a, c), which was the first year of monitoring in both islands.
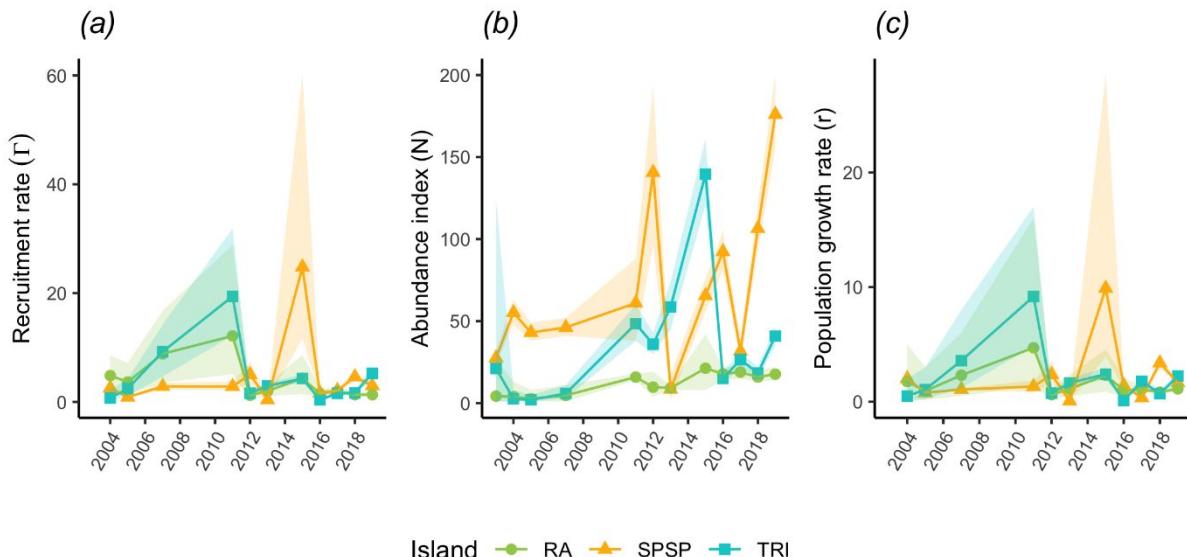
Figure 5. Annual estimates (means ± 95% credible intervals) of recruitment rate (Γ) (*a*), abundance index (N) (*b*) and population growth rate (*c*) for each population.

3.3 Effects of SST and density-dependence on demography

Our results revealed a spatial variation of the climatic effects on recruitment among the islands (Fig. 6). In SPSP, the positive effect of MHW frequency [$\beta_{1,1}$ = 1.18 (95% CI: 0.98, 1.39)] on recruitment was strongly opposed to MHW cumulative intensity [$\beta_{1,2}$ = -1.06 (95% CI: -1.30, -0.84)] (Fig. 6a-d). In TRI, MHW^{int} had a slight positive effect [$\beta_{3,2}$ = 0.21 (95% CI: 0.10, 0.31) on recruitment. The ΔSST^{freq} had a negative effect at SPSP [$\beta_{1,3}$ = -0.66 (95% CI: -0.89, -0.43)] and TRI [$\beta_{3,3}$ = -0.63 (95% CI: -0.80, -0.46)] (Fig. 6e-f). In RA, MHW^{freq} (95% CI: -0.60, 0.26), MHW^{int} (95% CI: -0.06, 0.57) and ΔSST^{freq} (95% CI: -0.70, 0.6) had no effects on recruitment. All the parameter estimates are found in the Table S2.

We found a strong negative relationship between maximum body size and abundance index (slope= -3.63 ± 0.82) among the populations (Fig.7a). Despite the latitudinal proximity and similar temperature variation of SPSP and RA, there is a great difference in the maximum body sizes between these populations. The low abundant population of RA has the largest crabs, while the highly abundant population of SPSP has smaller crabs. TRI showed intermediate conditions of body size and abundance. As expected, we found a positive relation between number of eggs and female body size (slope= 0.06 ± 0.005) (Fig. 7b) with larger females from TRI producing more eggs than smaller females from SPSP. Recruitment index was positively related to body size [β^{fec} = 0.37 (95% CI: 0.37, 0.37)] and negatively related to abundance [β^{dd} = -0.53 (95% CI: -0.62, -0.45)] (Fig. 7c-d).

(a) Effect of MHW frequency

(b)

(c) Effect of MHW cum. intensity

(d)

(e) Effect of ΔSST+ frequency

(f)
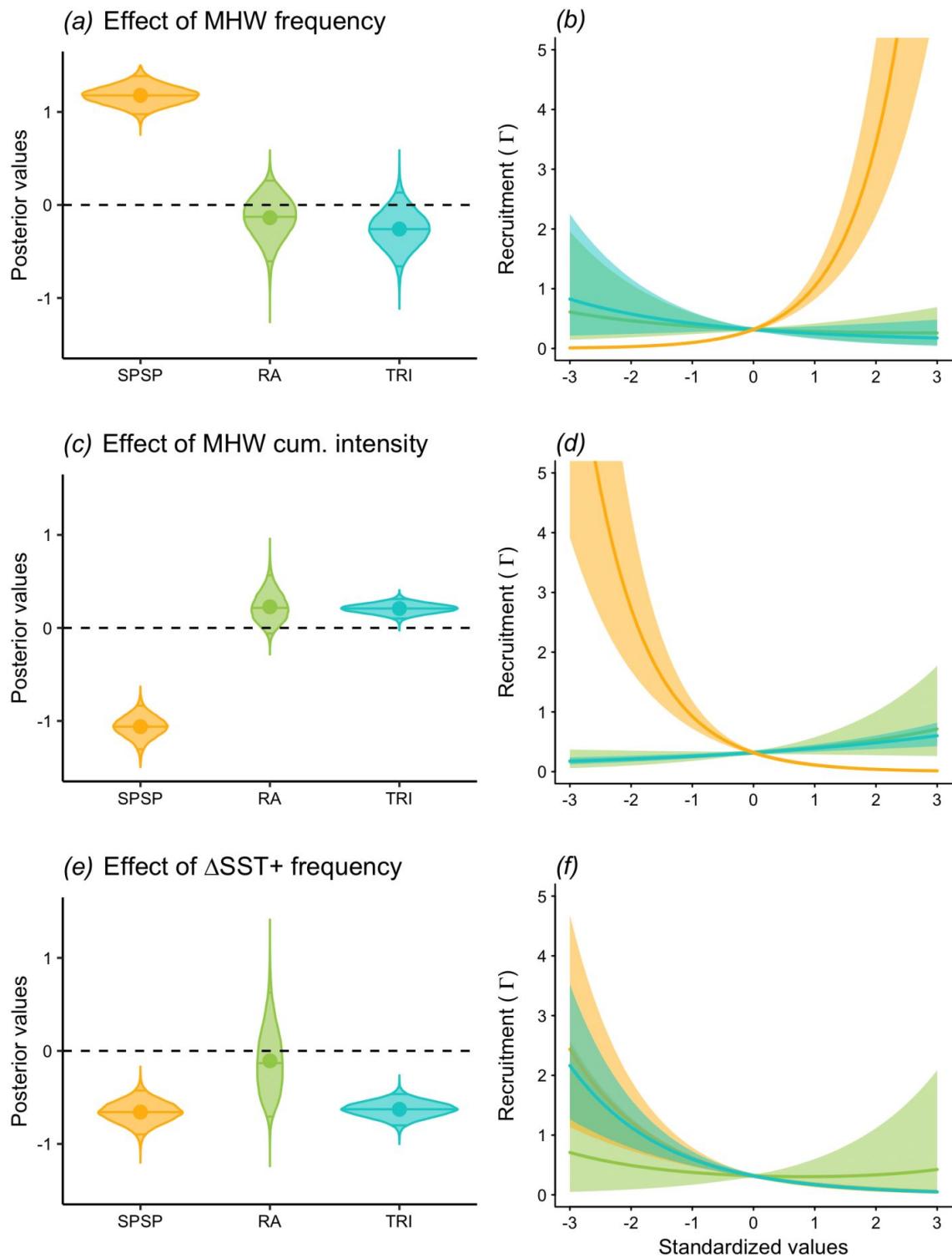
Figure 6. Violin plots representing the estimated effects on recruitment (mean, 95% CI) *(a, c, e)* and response curves *(b, d, f)* of marine heatwaves frequency *(a-b)*, cumulative intensity *(c-d)*, and frequency of positive sea surface temperature anomalies *(e-f)* for each island.

(a)

(b)

(c)

(d)
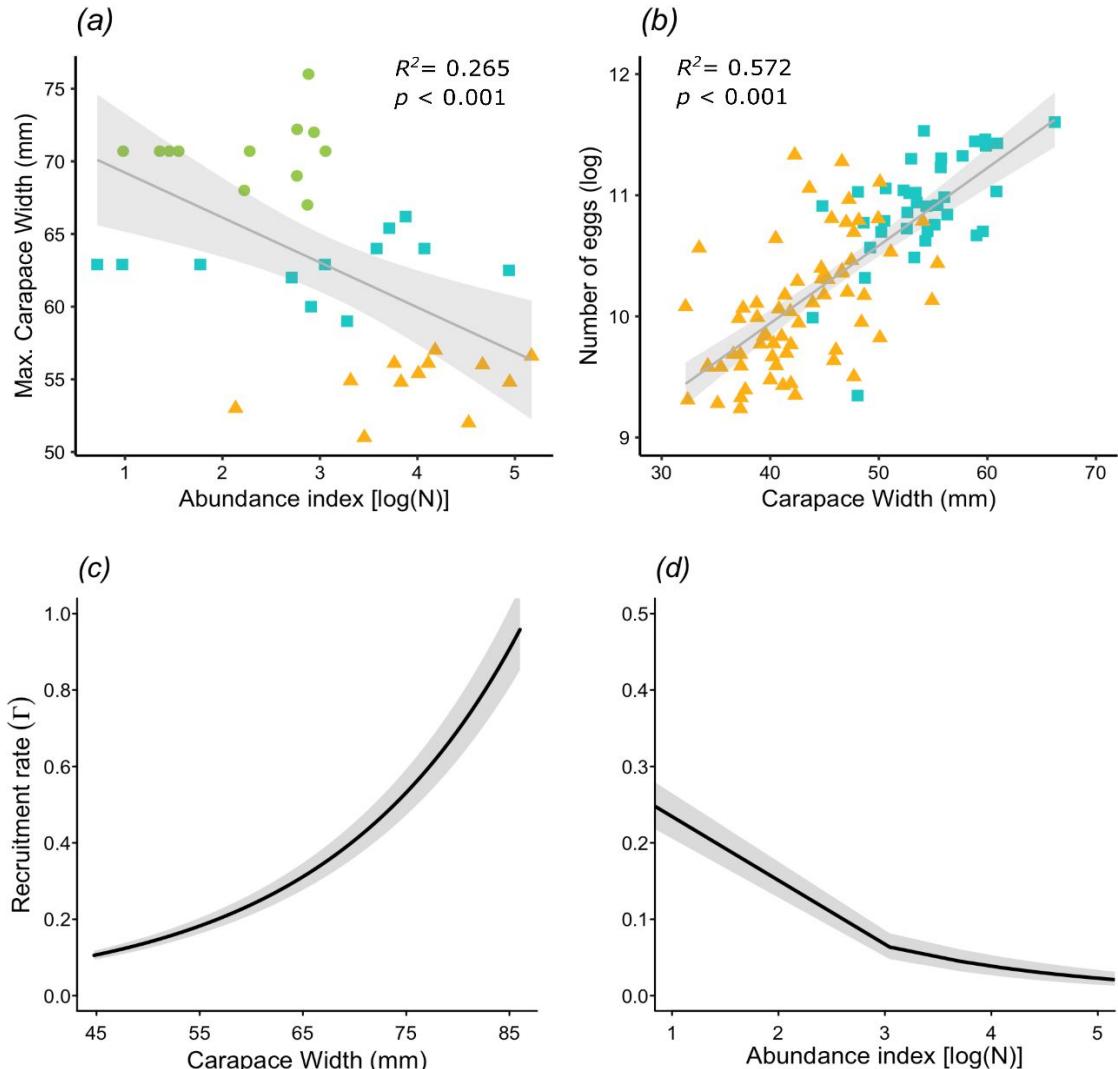
Fig

ure 7. Demographic relationships between female's maximum carapace width and abundance *(a)*; number of eggs and carapace width *(b)* and response curve of recruitment rate to variation in carapace width *(c)* and in abundance *(d)*.

4. Discussion

Using an integrative framework, we estimated demographic parameters and the effects of marine heatwaves and sea surface temperature anomalies, as well as density-dependent processes, on wild populations of a marine invertebrate, the intertidal rocky crab *Grapsus grapsus*, that inhabits remote islands in the Atlantic Ocean. Increasing frequency and intensity of MHWs and ΔSST+ were observed only at the equatorial islands SPSP and RA. However, no long-term declining trends in abundance and recruitment in these populations or in TRI suggest that they are still able to withstand increased temperatures or recover after warm events. We also found that density-dependent pressures act as driver on recruitment. Interestingly, the population with highest density and smallest crabs, SPSP, was the most affected by the SST-derived covariates, while no effect was observed for RA, the population with lowest density and largest crabs. Therefore, we suggest that a synergistic interaction between climate and density-dependent pressure might be driving the responses to climate change differently across populations (Fig. 8) and should be investigated in further studies.

Despite the lack of information about thermal tolerance and phenotypic plasticity throughout the ontogenetic development of tropical species at large latitudinal scales, some studies have predicted a higher vulnerability to climate change for tropical marine species than their temperate counterparts (Vinagre et al., 2018; Pinsky et al., 2019). Warm-adapted intertidal species may not be able to adjust its upper thermal limits to increasing temperatures, as they have limited acclimation plasticity and already live closer to their thermal limits (Stillman & Somero, 2000; Madeira et al., 2012). Indeed, the positive trends of ocean temperature anomalies at the equatorial islands SPSP and RA (Fig. 3-4) point out a potential vulnerability of these populations to climate change. However, TRI and SPSP were both

negatively affected by the frequency of ΔSST+, highlighting that populations locally adapted to subtropical climate can also be vulnerable to long-term warming (Fusi et al., 2015).
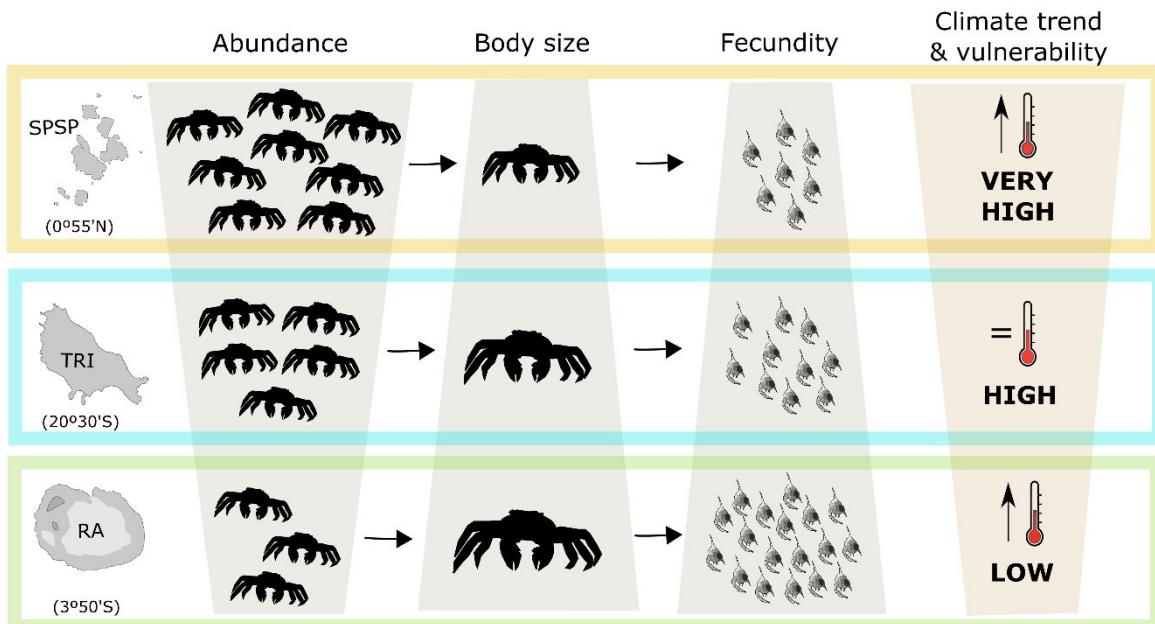
Figure 8. Infographic of the key findings of our study. The relationship between abundance, body size and fecundity are represented by the number of crabs, the size of the crab and the number of larvae, respectively. The horizontal arrows represent the direction of the effect. The climate trends are represented by the thermometer with an arrow (increasing trend) or equal sign (no trend). The climate vulnerability is related to the ocean temperature effects on each population SPSP= St. Peter and St. Paul Arch.; TRI= Trindade Island; RA= Rocas Atoll.

The negative effect of MHW cumulative intensity on the recruitment of SPSP population might be due to an increase in larval mortality when upper thermal limit was exceeded during extreme warm events. Conversely, the positive effect of MHW frequency reflects the larval ability to cope with more frequent warm events when thermal threshold is not exceeded. Increasing temperature within the thermal tolerance window leads to faster larval development (Anger, 1991), reducing the predation risk and increasing larval survival. The factors linked to the absence of effects in RA might be: 1) weak density-dependent pressure

given the low and stable abundance; 2) increased zooplankton biomass and planktonic productivity were observed during thermal stress (Campelo et al., 2019), which means greater food availability for larvae; and 3) RA is the only island totally protected by a no-take MPA. Evidence of the combined effects of climate and density on demographic fluctuations have shown that climatic effects were stronger at high densities (Aanes et al., 2000; Barbraud & Weimerskirch, 2003).

The negative relation between abundance and body size across populations suggests a density-dependent growth, although changes in body size were not related to density of crabs within each population (Fig. 7a). The low abundant RA population has the largest females, whereas the highly abundant SPSP population has the smallest females. TRI has intermediate abundance and body size dimensions, despite the Bergmann's rule that body size increases with latitude (Blackburn et al., 1999). Compensatory increases in growth and size-at-maturity have been observed in declining populations of exploited lobsters as response to higher per capita food availability (Pollock, 1995, DeMartini et al., 2003). While larger females produce more eggs, increased competition at high density populations leads to smaller body sizes and consequently, lower fecundity (Hines, 1982). High densities can also affect recruitment through cannibalism and shelter availability (see review in Wahle, 2003). Therefore, density-dependent growth and competition can be driving recruitment and population dynamics of the Sally lightfoot crab at the oceanic islands.

Several species of crabs, lobsters and prawns constitute large and valuable fisheries, which have been impacted by increased mortality, spread of diseases (Pearce & Balcom, 2005), and phenological and physiological changes (Mills et al., 2013) linked to anomalous warm events. Despite the commercial and ecological importance of crustaceans worldwide, we found no previous research using an integrative approach to estimate demographic parameters and the effects of drivers affecting crustacean populations. The use of IPMs to

study invertebrate populations is still rare, probably due to the difficulty to mark individuals (Dennis et al., 2021). Frisch & Hobbs (2007) used the exoskeleton color patterns to identify individuals of white-clawed crayfish and they showed that the marks were resistant to ecdysis and stable through time. The natural marks on the carapace of the Sally lightfoot crab seemed to resist through a six-month period, but further research considering sex and age/size-classes is needed to confirm whether this approach is useful for longer periods.

The lack of information on larval abundance and survival, settlement rate and adult survival in each island were important limitations to estimate more reliable demographic parameters. However, this study showed that combining multiple types of data at different scales can be useful to estimate demographic parameters, even when survey data is limited. Thus, our model can be considered a starting point for future population studies of short-lived and highly fecund organisms. This approach seems promising for long-term monitoring data, in which field team and goals often change over time, potentially increasing bias on estimates and when funding resources are limited.

To improve understanding of population dynamics and the drivers regulating the demographic fluctuations of the Sally lightfoot crab, we recommend investigation of critical thermal window across life stages for different locations; population-specific acclimation responses; and the effects of primary productivity and CO_2 concentration, which are known to affect survival and development of crustacean larvae (Anger, 1991; Schiffer et al., 2014). Sexual maturity and fecundity analysis of the RA population would also help to understand the mechanisms driving the recruitment success; and capture-recapture surveys at SPSP and RA would allow site-specific estimates of adult apparent survival and detection probability.

To conclude, intertidal zone and tide pools are probably the first habitat where impacts of climate change and ocean warming on marine assemblages become visible (Vinagre et al., 2018). The monitoring of the Sally lightfoot crab is the only population assessment of an

intertidal species at the Brazilian oceanic islands, which are home to several marine endemic species (Pinheiro et al., 2018). Here, we provide a better understanding of the ecological mechanisms that regulate the populations of a marine invertebrate with a complex life cycle and evidences that thermal stress can be threatening the marine biodiversity of the oldest (RA) and largest MPAs (SPSP and TRI) of the Brazilian waters, which serve as reservoirs of species exploited beyond these areas due to the spillover effect (Halpern et al., 2009).

Ethics statement

Funding statement

Acknowledgments

Author contribution

TM and AF designed the project, NC provided and explained the climate data, TM and QZ analyzed the data, TM wrote the manuscript, and TM, QZ and AF discussed the results and revised the manuscript.

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Supplementary material
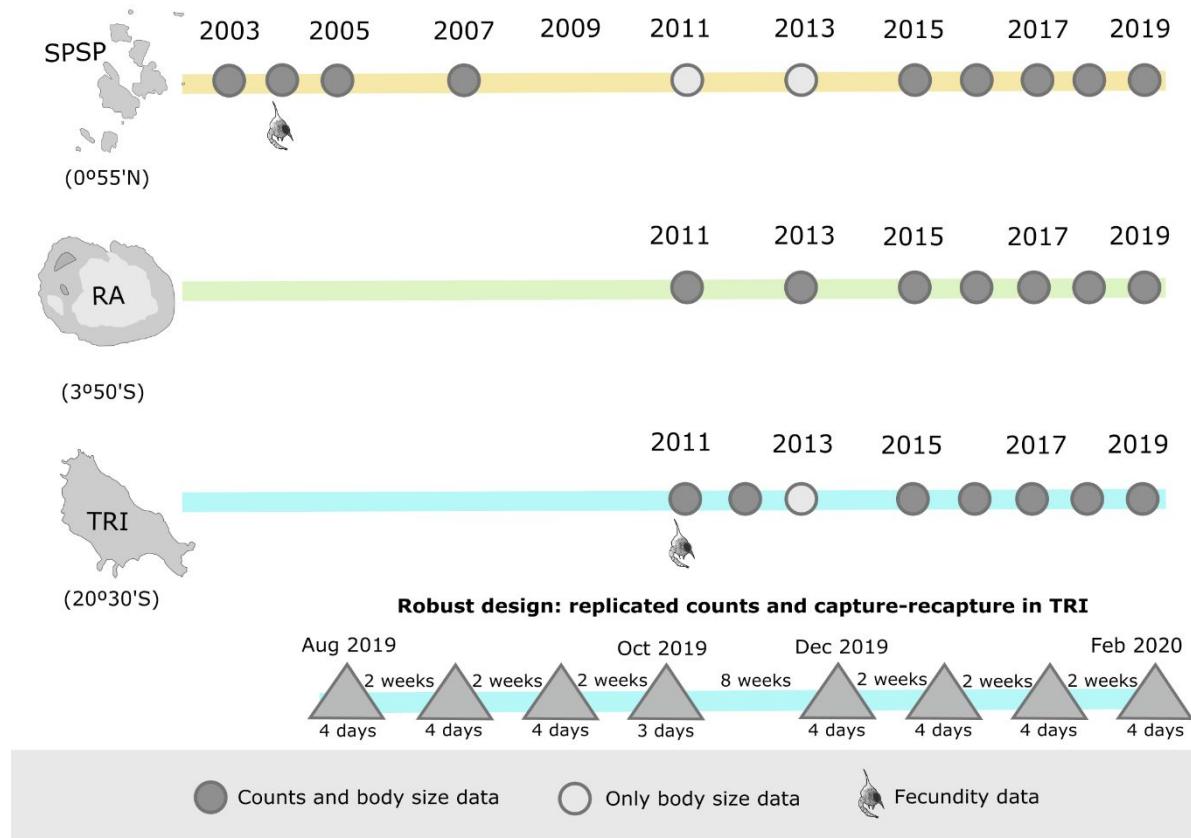
Figure S1. Timeline of the Sally lightfoot crab monitoring data and short-term count and capture-recapture data collected at Trindade Island used in the integrated population model.
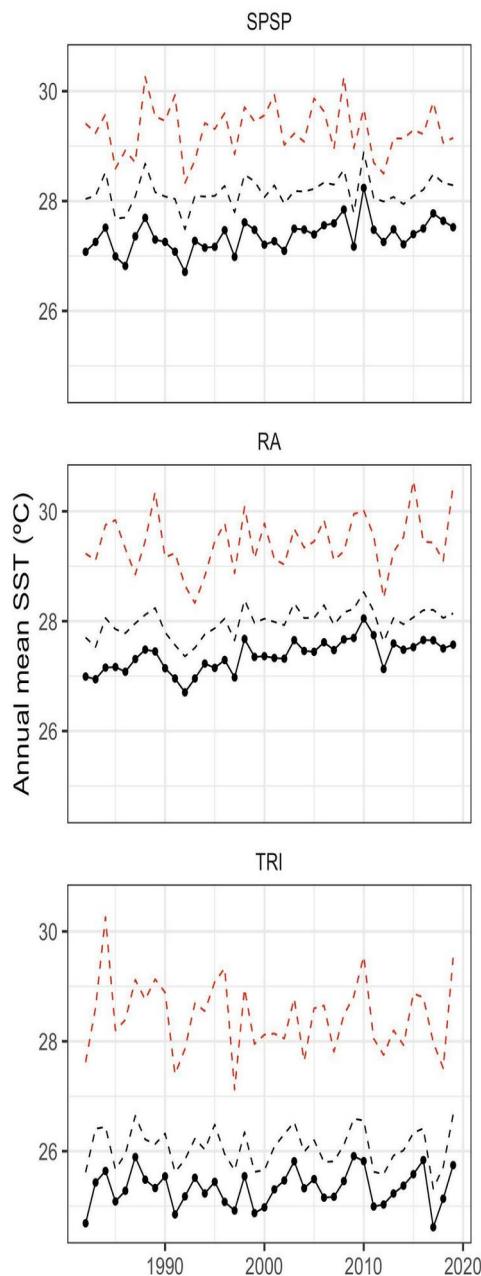
Figure S2. Mean annual sea surface temperature (SST) (continuous line), mean annual maximum monthly SST (black dashed line) and annual maximum SST (red dashed line) for each island, from 1982 to 2019. A greater climatic variability is observed at TRI (~20º S) compared to the equatorial islands. SPSP= St. Peter and St. Paul arch.; RA= Rocas atoll; TRI= Trindade Island.
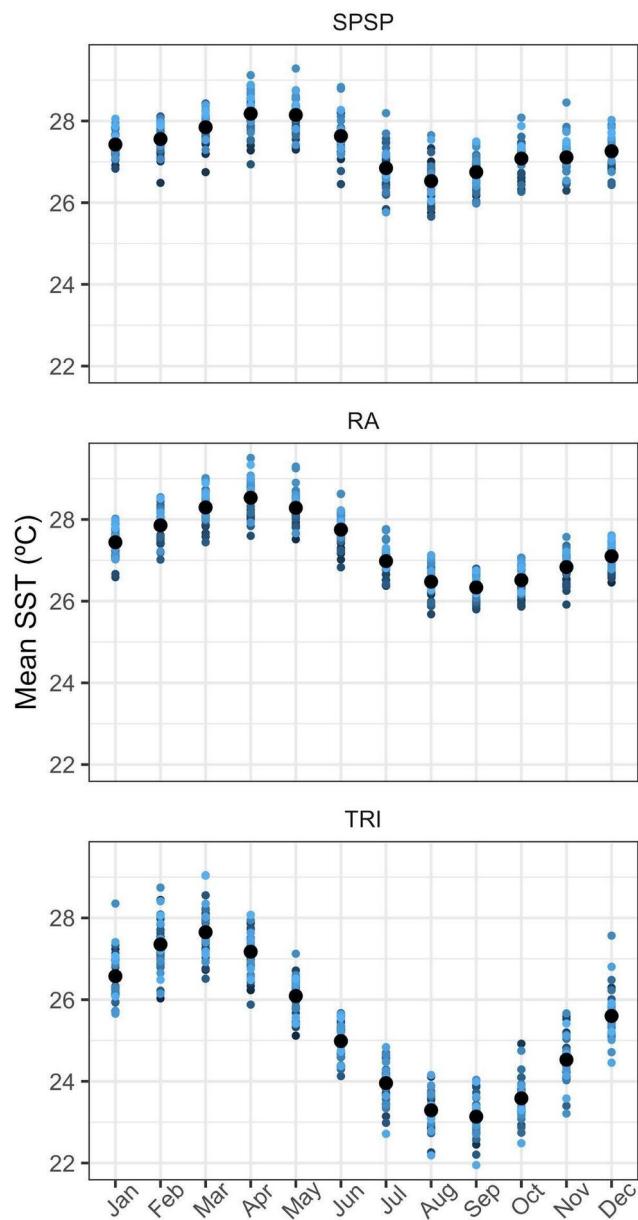
Figure S3. Intra-annual variation of SST. The blue dots represent the average for each year in the historical series (1982-2019). The most recent years are in light blue. SPSP= St. Peter and St. Paul arch.; RA= Rocas atoll; TRI= Trindade Island.

Table S1. Notations (in equations and model code) and definitions for parameters indicated by their respective sub-models. DN1=Dynamic N-mixture model 1; DN2=Dynamic N-mixture model 2; JSRD= Jolly-Seber robust design model; PR=Poisson regression model. Lowercase Greek letters (λ, γ, φ) describe parameters of ecological processes at fine temporal scales. Uppercase Greek letters (Λ, Γ, ϕ) describe parameters of long-term ecological processes at each island.

Equation	Code	Definition	Sub-models
λ	lambda0	Expected initial abundance	DN1
γ_p	gamma	Recruitment rate for each primary occasion p	DN1
φ_p	phi	Apparent survival probability for each primary occasion p	DN1 & JSRD
γ^{BW}	gamma_bw	bi-weekly recruitment rate	DN1 & 2
φ^{BW}	phi_bw	bi-weekly apparent survival probability	DN1 & 2
Θ	p_det	Detection probability of individuals	DN1 & 2
ρ	p_cap	Capture probability of individuals	JSRD
β^{fec}	beta_fec	Effect of the carapace width on fecundity rate	PR & DN2
Λ_i	lambda0_ss	Expected initial abundance at each island i	DN2
$\Gamma_{i,t}$	gamma_ss	Recruitment rate at island i and time t	DN2
$\phi_{i,t}$	phi_ss	Apparent survival probability at island i and time t	DN2
β^{dd}	beta_dd	Effect of abundance on recruitment rate	DN2

Table S2. Posterior estimates, standard deviation, credible intervals and Rhat values for the constant effects of body size (β^{fec}) and abundance (β^{dd}); island-specific effects of MHW frequency (β_1), cumulative intensity (β_2), and frequency of positive SST anomalies (β_3) on recruitment.

Parameters	mean	sd	2.5%	50%	97.5%	Rhat
β^{fec}	0.37	0	0.37	0.37	0.37	1
β^{dd}	-0.53	0.04	-0.62	-0.53	-0.45	1
$\beta_1 random\,effect$	0.26	1.08	-1.72	0.27	2.20	1
$\beta_{1,SPSP}$	1.18	0.10	0.98	1.18	1.39	1
$\beta_{1,RA}$	-0.14	0.22	-0.60	-0.13	0.26	1
$\beta_{1,TRI}$	-0.26	0.20	-0.66	-0.26	0.13	1
$\beta_2 random\,effect$	-0.20	1.00	-1.93	-0.21	1.61	1
$\beta_{2,SPSP}$	-1.06	0.12	-1.30	-1.06	-0.84	1
$\beta_{2,RA}$	0.23	0.16	-0.06	0.22	0.57	1
$\beta_{2,TRI}$	0.21	0.05	0.10	0.21	0.31	1
$\beta_3 random\,effect$	-0.46	0.54	-1.30	-0.50	0.56	1
$\beta_{3,SPSP}$	-0.66	0.12	-0.89	-0.66	-0.43	1
$\beta_{3,RA}$	-0.11	0.35	-0.70	-0.13	0.62	1
$\beta_{3,TRI}$	-0.63	0.09	-0.80	-0.63	-0.46	1

CONSIDERAÇÕES FINAIS

Compreender a dinâmica de populações naturais é um desafio. Alterações desde o nível fisiológico ao populacional ocorrem em função de fatores que atuam de maneira isolada ou interagindo entre si. Este é o primeiro trabalho a apresentar tendências de ondas de calor marinhas e anomalias térmicas do oceano em duas ilhas oceânicas equatoriais e no Arq. de Trindade e Martim Vaz (Figs. 3-4), e a investigar seus efeitos sobre a dinâmica populacional do caranguejo-aratu *Grapsus grapsus.*

De fato, as ilhas equatoriais apresentaram fortes tendências de aumento da frequência e intensidade das anomalias térmicas, enquanto nenhuma tendência foi observada em TRI. Eventos de branqueamento de corais e impactos na biomassa de zooplâncton em decorrência de anomalias térmicas já foram registrados nas ilhas equatoriais brasileiras (GASPAR et al., 2021; CAMPELO et al., 2019). Estudos recentes apontam uma maior vulnerabilidade climática em espécies tropicais do que em espécies análogas de regiões mais frias (VINAGRE et al., 2018; PINSKY et al., 2019). Assumindo que este padrão também se aplicaria a populações em diferentes latitudes, esperávamos que as populações de SPSP e RA seriam mais afetadas do que TRI. No entanto, nossa primeira hipótese não foi corroborada, sugerindo que mesmo populações adaptadas a condições semelhantes podem responder de maneiras distintas as mudanças no ambiente. A população mais afastada do equador, TRI, não é menos vulnerável ao aumento da temperatura do oceano do que as equatoriais. Portanto, generalizar os impactos climáticos em organismos marinhos somente em função da distribuição latitudinal, pode ser precipitado e prejudicial para a manutenção de populações com características diferentes.

A hipótese dos efeitos do tamanho corporal e da abundância sobre o recrutamento também foi corroborada, concordando com as relações já bem estabelecidas em crustáceos decápodes (HINES, 1982). Este estudo não buscou investigar interações entre os efeitos da TSM e da denso-dependência. Porém, a população mais abundante foi a que sofreu maiores efeitos das OCMs e anomalias térmicas, enquanto a população com menor abundância, praticamente não foi afetada, independentemente da posição latitudinal. Portanto, recomendamos que futuros estudos considerem potenciais interações entre fatores denso-independentes e denso-dependentes.

Apesar de registros recentes do caranguejo-aratu na costa brasileira indicarem capacidade de dispersão por meios naturais ou antrópicos (MACEDO et al., 2021), futuros cenários de aquecimento e mudanças nas correntes do Atlântico Sul preveem aumento da mortalidade e redução das distâncias percorridas por larvas de peixes, na ausência de aclimatação (Lima et al., 2021). A redução da conectividade prevista por esses autores, mesmo entre as ilhas oceânicas equatoriais, tornará as populações do caranguejo-aratu e de outros animais marinhos ainda mais vulneráveis a eventos extremos. Nesse contexto, áreas marinhas protegidas (MPAs) previnem o efeito sinérgico entre impactos climáticos e outros fatores causadores de declínios populacionais (HARLEY; ROGERS-BENNETT, 2004). Para populações com abundância reduzida, a conectividade entre MPAs é um amortecedor contra eventos catastróficos, diminuindo o risco de colapso populacional sob o efeito de Alle (WHITE et al., 2021).

A população de RA é a menos abundante, a mais estável e menos suscetível aos efeitos da temperatura do oceano. Esse resultado pode ser uma evidência da efetividade da MPA que protege integralmente o único atol do Atlântico Sul. Além disso, correntes oceânicas favorecem o transporte de larva de SPSP e FN para RA (CAMPELO et al., 2019), enfatizando a necessidade de uma rede de MPAs efetiva entre as ilhas oceânicas. Este

trabalho servirá como um *baseline* para a continuidade do monitoramento do caranguejo-aratu – interrompido pela pandemia de COVID-19 – que será retomado em breve, juntando esforços com as entidades governamentais responsáveis pelo manejo das MPAs nas ilhas oceânicas.

Viva o GRAPSUS!

TEXTO DE DIVULGAÇÃO

Sob futuros cenários de aumento da temperatura do mar, frequência e intensidade de eventos extremos e mudanças das correntes oceânicas no Atlântico Sul, as populações de animais marinhos que vivem em ilhas isoladas podem estar ameaçadas. Mudanças comportamentais, na duração do desenvolvimento e nas taxas de sobrevivência já foram observadas como efeitos da variação da temperatura em invertebrados marinhos, através de experimentos. No entanto, respostas em populações naturais podem depender de uma série de fatores que regulam o crescimento de uma população, como por exemplo, a denso-dependência. Durante o mestrado em Ecologia no PPGECO/UFSC, a aluna Thais Macedo investigou os efeitos de anomalias térmicas do oceano e de fatores denso-dependentes nas populações do caranguejo-aratu *Grapsus grapsus* do Arquipélago de São Pedro e São Paulo, Atol das Rocas e da Ilha da Trindade. O estudo mostrou que a abundância de caranguejos é negativamente relacionada com o tamanho dos indivíduos, e as fêmeas maiores apresentam uma maior produtividade de ovos (i.e., taxa de fecundidade). Por outro lado, os efeitos das anomalias térmicas do oceano foram mais intensos na população mais abundante (SPSP), enquanto a população menos abundante (RA) não foi afetada. Esse resultado se deu independente da tendência de aumento de anomalias térmicas em ambas as ilhas. Apesar da única ilha localizada mais ao sul (TRI) não ter apresentado tendências de aumento de anomalias, a população foi afetada negativamente, sugerindo que a vulnerabilidade climática não depende, exclusivamente, da localização geográfica das populações. Portanto, concluiu-se que tanto fatores ambientais

quanto denso-dependentes atuam na regulação dessas populações. Avaliar a vulnerabilidade climática de espécies-chave é essencial para o manejo e conservação de áreas marinhas protegidas, onde a interação entre efeitos climáticos e outros tipos de impacto é minimizada. Para isso, deve-se considerar as respostas fisiológicas e populacionais, assim como, o grau de exposição à ameaça.
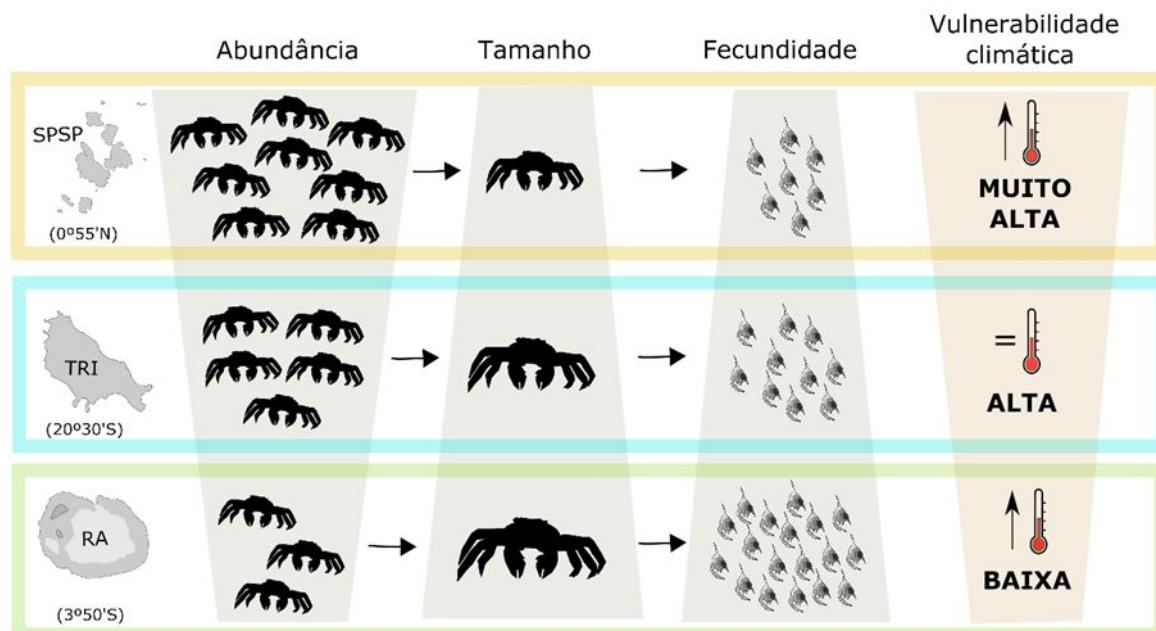
Figura 9 traduzida para acompanhar o texto de divulgação.

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