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CONTRIBUIÇÕES PARA O CONTROLE DA INVASÃO POR *TUBASTRAEA COCCINEA* NA RESERVA BIOLÓGICA MARINHA DO ARVOREDO, SANTA CATARINA, BRASIL

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Contribuições para o controle da invasão por *Tubastraea coccinea* na Reserva Biológica Marinha do Arvoredo, Santa Catarina, Brasil

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RESUMO

Espécies exóticas invasoras são uma ameaça a biodiversidade global, causando ainda impactos econômicos e para a saúde humana. Prevenir que espécies exóticas sejam introduzidas é a forma mais efetiva de evitar futuros impactos. Quando a prevenção falha, detectar precocemente e agir rápido pode ser a única chance real de erradicação, especialmente no ambiente marinho. Mesmo que a erradicação não seja atingível, conter a espécie invasora em baixas densidades têm efeitos benéficos para o ecossistema. O conhecimento sobre a biologia da espécie invasora é essencial para definir e adaptar estratégias de manejo mais efetivas. O objetivo geral desse trabalho é propor estratégias de controle e monitoramento para a invasão do coral-sol *Tubastraea coccinea*, principalmente na Reserva Biológica Marinha do Arvoredo (Rebio), Santa Catarina, Brasil, limite sul de distribuição do invasor no Oceano Atlântico. No primeiro capítulo, nós descrevemos o histórico do manejo para combater o invasor na Rebio Arvoredo desde a sua descoberta na região. Nós também recomendamos os períodos e a frequência ideais para as atividades de controle serem mais efetivas, com base em informações da biologia reprodutiva e populacional do coral-sol. No segundo capítulo, a partir de simulações de dispersão de partículas, nós indicamos os locais mais prováveis para a ocorrência de novos focos de invasão do coral-sol no entorno da Rebio, além de investigar a possível origem da invasão. Visamos contribuir para um monitoramento mais efetivo (e menos oneroso), e principalmente para a detecção precoce do invasor em novos locais. Esse trabalho contribui com objetivos propostos no Plano Nacional de Prevenção, Controle e Monitoramento do coral-sol *Tubastraea* spp.

Palavras-chave: espécies invasoras marinhas; prevenção; manejo; reprodução; dispersão

ABSTRACT

Invasive species are a threat to global biodiversity, causing also impacts in economics and human health. Preventing exotic species from being introduced is the most effective way to avoid future impacts. When prevention fails, early detection and fast response may be the only real chance for achieve eradication, especially in the marine environment. However, even if eradication is not achievable, containing the invasive species at low densities has beneficial effects on the ecosystem. Knowledge about the biology of invasive species is essential to define and adapt effective management strategies. The main goal of this work is to propose control and monitoring strategies for the invasion of the sun coral *Tubastraea coccinea*, especially in the Arvoredo Biological Marine Reserve (Rebio Arvoredo), in Santa Catarina state, Brazil, southern boundary of the invader's distribution in the Atlantic Ocean. In the first chapter, we described control activities historic to combat sun coral in Rebio Arvoredo since its discovery. We also recommend timing and frequency for control activities to be most effective, based on information from reproductive and population biology of the sun coral. In the second chapter, based on dispersion models, we indicate the most likely location for the occurrence of emerging populations of sun coral in the surroundings of Rebio Arvoredo. We also investigated the possible origin of the invasion in the region. We aim to contribute to a more effective (and less costly) monitoring program, and mainly for the early detection of the invader in new sites. This work also contributes with the National Plan for the Prevention, Control and Monitoring for *Tubastraea* spp..

Palavras-chave: marine invasive species; prevention; management; reproduction; dispersion

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INTRODUÇÃO

O processo de invasão

Com os avanços tecnológicos e consequente aumento da conectividade global dos últimos séculos, espécies têm sido exportadas da sua área de distribuição natural em um ritmo acelerado (SEEBENS et al., 2017). As espécies podem ser transportadas de forma intencional, como plantas para cultivo ou animais de estimação, mas na maioria dos casos são transportadas acidentalmente (SIMBERLOFF et al., 2013). Cerca de 10% dessas espécies, se proliferaram desordenadamente, causando impactos econômicos, na saúde humana e nos ecossistemas, em um processo conhecido por invasão biológica (BLACKBURN et al., 2011; PYŠEK et al., 2020; ANTON, 2021)

A figura 1 ilustra as etapas do processo de invasão (BLACKBURN et al., 2011) e as estratégias de manejo (e seus custos) que devem ser adotadas em cada uma das etapas (HARVEY; MAZZOTTI, 2018). O processo inicia quando as espécies - ou qualquer parte delas que possam sobreviver e reproduzir, como sementes - são transportadas para fora da sua área de distribuição natural, passando a ser considerada uma espécie exótica no local receptor. Prevenir que isso aconteça é a melhor e mais barata estratégia de manejo para evitar futuros impactos. A partir do momento que a prevenção falha, a espécie chega ao novo local e consegue sobreviver, ela é considerada uma espécie exótica introduzida/casual. Detectar a espécie precocemente pode ser a única chance real de erradicação - a remoção completa da população. Caso ela consiga também reproduzir e formar populações viáveis, passa a ser uma espécie exótica estabelecida e a erradicação passa a ser cada vez menos provável e mais onerosa. Quando a espécie dispersa, sobrevive e reproduz em novos locais, ameaçando a diversidade biológica nativa, é considerada uma espécie exótica invasora (BLACKBURN et al., 2011). Nesse ponto, medidas de contenção que mantenham a população invasora em baixas densidades são essenciais para mitigar os impactos, e também para manter viva a chance de uma erradicação futura. Quando isso não é feito, a espécie se torna tão abundante que a erradicação não é mais possível, restando apenas conter a espécie para diminuir os danos (HARVEY; MAZZOTTI, 2018).

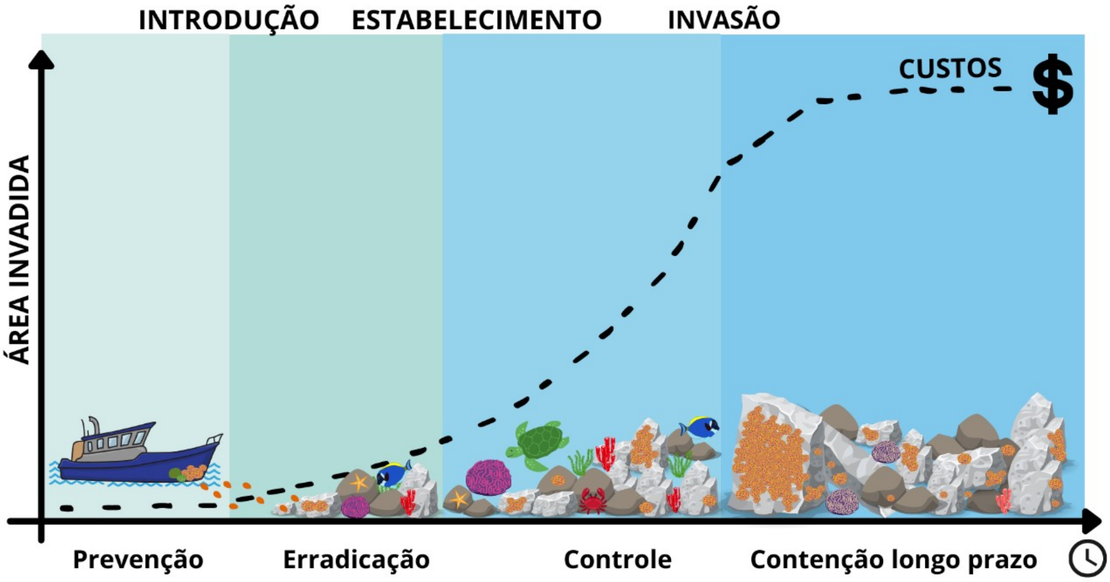

Figura 1 Ilustração do processo de introdução e estabelecimento de uma espécie exótica invasora e os custos e estratégias de manejo que devem ser adotadas em cada etapa (tons de azul) do processo. Adaptado de (BLACKBURN et al., 2011; HARVEY; MAZZOTTI, 2018)

Das milhares de espécies que são introduzidas, como saber quais são as que vão causar impactos? As pesquisas sugerem que o sucesso de um invasor está atrelado principalmente às características biológicas das espécies (invasividade), como a capacidade de se reproduzir assexuadamente, e também características do ambiente invadido (invasibilidade), como a riqueza de espécies locais (HUI et al., 2016). Além disso, o sucesso da invasão pode ser explicado pela pressão de propágulos (LOCKWOOD; CASSEY; BLACKBURN, 2005). A pressão de propágulos é a frequência com que uma espécie é introduzida em determinado ecossistema e pode ser dividida em dois componentes principais: o número de propágulo, que é o número de eventos de introdução; e o tamanho de propágulo, que é o número absoluto de indivíduos introduzidos em cada evento de introdução (LOCKWOOD; CASSEY; BLACKBURN, 2005). Há ainda o componente genético, que está relacionado ao tamanho mínimo viável de uma população necessária para sobreviver às estocasticidade ambientais e demográficas (LOCKWOOD; CASSEY; BLACKBURN, 2005). Em suma, uma espécie com alta fecundidade pode se tornar um invasor mesmo com uma baixíssima pressão de propágulos, enquanto uma espécie com características opostas pode se tornar invasora caso a pressão de propágulos seja alta.

O impacto causado pelas espécies invasoras

As espécies invasoras são consideradas a segunda maior causa de extinção de espécies (BELLARD; CASSEY; BLACKBURN, 2016). A introdução de gatos (*Felis catus*), por exemplo, está fortemente associada com a extinção de pequenos mamíferos e pássaros. Estima-se que anualmente cerca de 459 milhões de indivíduos nativos, apenas de mamíferos, são predados por gatos na Austrália (WOINARSKI et al., 2020). A Perca do Nilo (*Lates niloticus*) está relacionada com a extinção de cerca de 150 espécies de peixes endêmicos do Lago Vitória, na África (SIMBERLOFF et al., 2013)

Ao impactarem táxons específicos, as espécies invasoras desestruturam os mais diversos ecossistemas (ver exemplos em SIMBERLOFF et al, 2013). GRAHAM et al., 2018 detalharam como a introdução de ratos em ilhas desestrutura todo o fluxo de nutrientes nos ecossistemas. Os ratos predam os ovos de aves marinhas, diminuindo drasticamente a quantidade de guano depositado nas ilhas - fonte de nutrientes para as plantas - e escoado para os recifes adjacentes. Nos recifes de ilhas livres de ratos, os peixes crescem mais rápido, possuem maior taxa de herbivoria e biomassa, o que também contribui para o crescimento e resiliência dos corais. Os ecossistemas das ilhas livres de ratos têm duas vezes e meia mais nitrogênio acumulado do que as ilhas invadidas. Esses resultados mostram o impacto em cascata que uma espécie invasora pode causar no fluxo de nutrientes entre os diferentes ecossistemas.

Nem sempre a sociedade tem a percepção dos riscos que uma espécie invasora representa. A própria pandemia do Sars Covid-19, com impactos imensuráveis, pode (ou deveria) ser considerada uma invasão biológica (OGDEN et al., 2019; NUÑEZ; PAUCHARD; RICCIARDI, 2020). Os mosquitos *Aedes*, transmissores de graves doenças, são um problema em diversos continentes (HULME, 2014; AKINER et al., 2016). Além de vetores de doenças, insetos invasores também são pragas em cultivos, destroem estruturas humanas e florestas, alterando os ecossistemas e causando grandes prejuízos econômicos (DIAGNE et al., 2021). Apesar das estimativas dos prejuízos causados por espécies invasoras serem subestimadas, as cifras são assustadoras. BRADSHAW et al., 2016 estimaram que os prejuízos causados apenas por insetos invasores custam no mínimo 80 bilhões de dólares por ano globalmente. Apenas na indústria da pesca da anchova, estimou-se uma perda anual de 250 milhões de dólares com a introdução do ctenofáro *Mnemiopsis leidyi* no Mar Negro (ZAITSEV, 1992). Os custos já causados pelas espécies invasoras – considerando os danos e o manejo - chegam no valor de 1.288 trilhões de dólares (entre 1970 e 2017, DIAGNE et al., 2021).

Métodos e estratégias de manejo e seus desafios no ambiente marinho

Como exposto anteriormente (Figura 1), os custos para lidar com uma espécie invasora aumentam à medida que o tempo passa. A decisão sobre qual método de controle utilizar dependerá das peculiaridades de cada caso de invasão. No geral, os métodos tradicionais consistem na aplicação de substâncias químicas, controle biológico (a introdução de um inimigo natural da espécie invasora), e a remoção mecânica (SIMBERLOFF; PARKER; WINDLE, 2005). A aplicação de substâncias químicas e o controle biológico são amplamente utilizados no ambiente terrestre, principalmente na agricultura (MÜLLER-SCHÄRER; SCHAFFNER, 2008). Contudo, esses métodos normalmente são limitados no ambiente marinho, principalmente pela dificuldade de monitorar a especificidade com o hospedeiro/predador e pela rápida diluição na água (WILLIAMS; GROSHOLZ, 2008; GIAKOUMI et al., 2019;).

Em relação às estratégias de manejo, a adoção de medidas preventivas é essencial e obrigatório para cumprir diversos acordos internacionais (SIMBERLOFF; PARKER; WINDLE, 2005). O principal deles, tratado na Convenção da Diversidade Biológica (CBD), os mais de 160 países signatários se comprometeram em impedir que se introduzisse, além de controlar ou erradicar espécies exóticas que ameacem os ecossistemas, habitats ou espécies. A CBD se baseia no Princípio da Precaução, que diz que a falta de completa certeza científica não pode ser utilizada para adiar a tomada de medidas que evitem ou minimizem uma ameaça à biodiversidade.

No ambiente marinho, a maioria das espécies são introduzidas por conta do comércio internacional, seja por água de lastro ou incrustações (BAX et al., 2001). Nesse sentido, os estudos e tecnologias vêm evoluindo em métodos de prevenção. Na Austrália, as regiões portuárias estão sendo monitoradas utilizando Sequenciamento de Nova Geração em organismos incrustados em placas de assentamento (MARTINEZ et al., 2020). Também na Austrália, com base em informações biológicas da estrela invasora *Asterias amurensis*, foi sugerido que as embarcações abasteçam a água de lastro nos meses em que a estrela não está reproduzindo (DOMMISSE; HOUGH, 2004). Os mapas de distribuição potencial gerados pelos Modelos de Nicho Ecológico também podem ser utilizados para predizer o sucesso de uma espécie exótica em um novo local (JIMÉNEZ-VALVERDE et al., 2011). Estudos que contribuam para a prevenção do estabelecimento de espécies exóticas são importantíssimos para um manejo mais efetivo e barato.

Quando a prevenção falha, a detecção precoce e ação rápida pode ser a única chance de erradicar uma invasão, principalmente no ambiente marinho (SIMBERLOFF, 2021), onde detectar toda a extensão da invasão é quase impossível. São poucos os casos de erradicação de sucesso (ver SIMBERLOFF, 2021). Um bom exemplo é o da alga *Caulerpa taxifolia*. Uma pequena população da alga foi avistada na França, dando origem a um intenso debate sobre a origem, o que fazer e quem era o responsável por coordenar as ações de controle. Quando o imbróglio foi resolvido já era tarde demais. A alga acabou se disseminando por grande parte do Mediterrâneo, causando grandes impactos nos ecossistemas recifais (MEINESZ et al., 2001). Sabendo disso, os gestores ambientais da Califórnia agiram rapidamente quando a alga foi avistada nos anos 2000 (ANDERSON, 2005). Apenas 17 dias após a descoberta do foco de invasão, foi realizado o envelopamento (com lonas) do substrato onde encontravam-se as algas e injetado hipoclorito de sódio (NaClO). Apesar do impacto local na comunidade nativa, a alga foi erradicada com sucesso (ANDERSON, 2005).

Mesmo que a erradicação não seja possível, conter a população invasora em baixas densidades é essencial e pode ter efeitos benéficos locais similares a uma erradicação (GREEN ET AL., 2015). O engajamento da sociedade pode ser um importante aliado nesses casos. No caso do peixe-leão, além de campeonatos de captura, o uso do invasor na culinária também foi fomentado e o número de capturas aumentou (ANDERSON et al., 2017; MALPICA-CRUZ; CHAVES; CÔTÉ, 2016). O peixe-leão *Pterois volitans* - por conta da alta fecundidade e maturidade sexual precoce - em apenas 30 anos de invasão se espalhou por toda a costa leste americana, Golfo do México, Caribe e mais recentemente no Brasil (LUIZ et al., 2021). Dois indivíduos foram encontrados (e removidos) em Arraial do Cabo, em 2014 e 2016. Em 2020, foram registrados também no arquipélago de Fernando de Noronha e nos recifes mesofíticos abaixo da pluma do rio Amazonas, causando grande apreensão nas autoridades ambientais e comunidade científica (FERREIRA et al., 2015; LUIZ et al., 2021). Até novembro de 2021, aproximadamente 20 indivíduos já haviam sido removidos em Fernando de Noronha (divulgação Instagram Projeto Peld Iloc)

Nas últimas décadas, outro caso emblemático de invasão marinha no Atlântico é a dos corais do gênero *Tubastraea* Lesson, 1829: *T. coccinea* e *T. micranthus* são nativas do Indo-Pacífico, e *T. tagusensis* é nativa de Galápagos (CREED et al., 2017a). Dentre elas, *T. micranthus* é a que tem menor distribuição invasora. Avistada pela primeira vez em 2006, estima-se que foi introduzida no final dos anos 1990. Ainda é encontrada apenas em poucas plataformas de petróleo no Golfo do México, mas a expansão da sua invasão causa preocupação, visto que em experimentos em laboratório demonstrou ser agressiva (HENNESSEY; SAMMARCO, 2014; SAMMARCO et al., 2014). A espécie *T. tagusensis* foi avistada pela primeira vez no início dos anos 2000, no Rio de Janeiro (CASTRO; PIRES, 2001), e a invasão é restrita ao litoral brasileiro e Golfo do México (CREED et al., 2017; FIGUEROA et al., 2019). *Tubastraea coccinea* conta com populações esparsas ao longo de aproximadamente 8 mil km, entre o sul do Brasil e a Geórgia, nos Estados Unidos, passando por todo o Caribe e Golfo do México, além das ilhas Canárias (CREED et al., 2017a; CRIVELLARO et al., 2021; LÓPEZ et al., 2019; SOARES et al., 2020)

T. coccinea é o organismo de estudo da presente tese e as suas características biológicas e histórias de invasão merecem ser detalhadas.

Aspectos gerais da distribuição e ocorrência do coral-sol no Brasil

No Brasil, colônias de *Tubastraea* foram registradas pela primeira vez em uma plataforma de petróleo, na Bacia de Campos, norte do Rio de Janeiro (RJ), no final dos anos 1980 (CASTRO; PIRES, 2001). No final dos anos 1990, o primeiro registro foi feito em costões rochosos, em Ilha Grande (RJ), por onde se espalharam e dominam o bentos em muitos sítios, atingindo incríveis densidades de 200 colônias m^{-2} (CASTRO; PIRES, 2001; DE PAULA; CREED, 2004; PAULA; CREED, 2005). Foram então encontrados também no estado de São Paulo, em Ilhabela (MANTELATTO et al., 2011), na Bahia, em um naufrágio em Salvador (SAMPAIO et al., 2012), e no porto de Vitória, Espírito Santo, próximo ao importante ecossistema recifal tropical de Abrolhos (COSTA et al., 2014). Em 2012, o registro mais ao sul do Atlântico, na Reserva Biológica Marinha do Arvoredo, Santa Catarina (CAPEL, 2012). Foram registrados em plataformas de petróleo no Sergipe e Ceará, sendo o último o limite norte de distribuição da costa brasileira (BRAGA et al., 2021; SOARES et al., 2020). Mais recentemente, e veiculado pelas mídias, o coral-sol foi encontrado pela primeira vez nos estados de Pernambuco (2020) e Rio Grande do Norte (2021), em naufrágios. A situação deve se tornar ainda mais crítica, visto o grande número de plataformas que serão descomissionadas nos próximos anos, e do plano do atual governo federal de afundar até 1200 estruturas para formar recifes artificiais e fomentar o turismo (MIRANDA et al., 2020; SOARES et al., 2020; BRAGA et al., 2021).

Devido a sua coloração alaranjada e seus vistosos tentáculos amarelados, esses corais escleractíneos são popularmente chamados de coral-sol (em inglês, *suncoral* e *orange cup coral*) (Figura 2). São encontrados nos recifes e costões rochosos rasos, suportando até a emersão provocada pelas variações de maré e também as profundas plataformas fixas de petróleo (~110 metros) (CREED et al., 2017a). São comumente encontrados nas superfícies verticais e em cavernas/fendas (MIZRAHI; NAVARRETE; FLORES, 2014). Como são azooxantelados, não necessitam da luz e simbiose com algas para a nutrição. São corais ahermatípicos, que não formam recifes de corais, ou seja, necessitam de algum substrato para assentar, como os costões rochosos. Além dos substratos naturais, o coral-sol tem facilidade em se estabelecer em todo tipo de estruturas artificiais, em especial aquelas com baixa hidrodinâmica (CREED; DE PAULA, 2007; CREED et al., 2017a; TANASOVICI; KITAHARA; DIAS, 2020). Colônias já foram encontrados até em lixo à deriva, como isopor, plástico e chinelo de borracha, o que pode contribuir para introduções secundárias (MANTELATTO et al., 2020).

Figura 2 O coral invasor *Tubastraea coccinea,* popularmente conhecido por coral-sol por conta de seus tentáculos vistosos, ocupando uma fenda inacessível. Foto: Lucas Battaglin

Os modelos de nicho ecológico indicam que o coral-sol tem potencial de ocorrer ao longo de toda a costa brasileira (RIUL et al., 2013; CARLOS-JÚNIOR et al., 2015;). Em uma escala local, o coral-sol expande a sua distribuição a uma taxa de aproximadamente 2 km por ano (SILVA et al., 2014), e a temperatura pode influenciar em sua distribuição. Em Arraial do Cabo, o coral-sol não foi encontrado na região que sofre forte influência das águas frias da ressurgência (BATISTA et al., 2017). No mesmo trabalho, observaram em experimento de laboratório que todas as colônias expostas a temperaturas menores que 12.5ºC morreram em 48 horas, enquanto nenhuma morreu aos 15ºC, mesmo após 96 horas. Já no limite sul de distribuição do invasor, em Santa Catarina, ALMEIDA SAÁ et al., 2020 realizaram um experimento de maior duração. Colônias expostas a 16ºC morreram após 6 dias.

Aspectos biológicos do coral-sol

O sucesso da invasão do coral-sol pode ser explicado pelas suas características típicas de um *r*-estrategista (CREED et al., 2017; CAPEL et al., 2019). O coral-sol se reproduz sexuada e assexuadamente, sendo que grande parte das populações brasileiras são oriundas de poucos clones - encontrados também nas populações das plataformas de petróleo – e colônias com apenas 2 pólipos já estão maduras sexualmente (GLYNN et al., 2008; DE PAULA; DE OLIVEIRA PIRES; CREED, 2014; CAPEL et al., 2019). A reprodução é contínua, com picos de liberação de larvas que podem variar conforme as condições oceanográficas de cada região. O potencial reprodutivo das colônias é enorme. Já foram observados mais de 800 propágulos em um único pólipo (CRIVELLARO et al., 2021), e mais de 1,500 larvas liberadas por uma única colônia, em um dia (LUZ et al., 2020).

LUZ e colaboradores (2020) realizaram um experimento em laboratório para acompanhar a liberação de larvas e seu desenvolvimento. A maioria das larvas foram liberadas nas fases do Quarto Crescente (49%) e Lua Nova (31%). Os autores também observaram que as colônias liberam propágulos em diferentes estágios de desenvolvimento - de embriões até larvas maduras de aproximadamente 1mm de comprimento. A liberação de embriões pode ser um indício de aborto, visto que esteve relacionada com temperaturas mais altas. Embora os embriões tenham sido liberados em menor quantidade (442 de 18,139), e que a maioria morreu, sua liberação pode ser uma importante estratégia de longa dispersão. Os embriões recém-formadas são arredondadas e imóveis, enquanto as larvas maduras nadam ativamente, contraem e alongam o corpo e até “engatinham” pelo substrato. Normalmente assentam rápido (1-10 dias), mas permanecem viáveis por mais de quatro meses em condições artificiais (LUZ et al., 2020). Também podem sofrer metamorfose na coluna d'água e até formar agregados de larvas que assentam juntos, iniciando a vida bentônica já como colônia. Além de tudo, outra estratégia que pode contribuir para a dispersão e sobrevivência do coral-sol é o "polyp bail-out", possivelmente utilizada em condições estressantes, o pólipo abandona o esqueleto, assenta em um novo local e secreta um novo esqueleto (CAPEL et al., 2014).

Com esse arsenal de estratégias de vida que facilitam seu estabelecimento, o coral-sol tem causado impactos nos ecossistemas. O coral-sol possui defesas químicas que inibem seus competidores e possíveis predadores, como peixes (LAGES et al., 2010). Ao aumentarem em abundância e dominarem o ambiente bentônico, reduzem o recrutamento das espécies de coral nativas e perpetuam sua dominância no ambiente (MIRANDA et al., 2018). O coral-sol transforma as comunidades que eram predominantemente autotróficas em heterotróficas (LAGES et al., 2011; VINAGRE et al., 2018). Com isso, os peixes deixam de se alimentar em locais com alta dominância do invasor, impactando as cadeias tróficas (MIRANDA et al., 2018). Através da extrusão de filamentos mesentéricos, que servem também para a digestão intracelular, o coral-sol pode causar necrose e até excluir as espécies nativas (LAGES et al., 2010; SANTOS; RIBEIRO; CREED, 2013; HENNESSEY; SAMMARCO, 2014; ALMEIDA SAÁ et al., 2020). Também já foram avistados crescendo por cima dos mexilhões *Perna perna*, que são importante fonte de renda de pescadores artesanais (MANTELATTO; CREED, 2015). Além de tudo isso, o coral-sol se envolve em processo chamado de *invasion meltdown*, onde o coral-sol modifica o ambiente e facilita o estabelecimento de outras espécies invasoras, como é o caso do bivalve *Leiosolenus aristatus* (VINAGRE et al., 2018).

Métodos de controle do coral-sol

Existem diferentes métodos mecânicos e químicos para controlar o coral-sol. O melhor, é claro, é a prevenção. COUTO et al., 2021 elaboraram e aplicaram um protocolo para analisar o risco de invasão do coral-sol nas áreas protegidas marinhas do Rio de Janeiro. Os autores consideraram como fatores de risco a presença e quantidade de vetores, quantidade de substrato (costão rochoso) disponível para assentamento na área protegida, além das similaridades ambientais entre áreas doadoras e receptoras de larvas. O protocolo pode ser muito útil para definir estratégias de manejo mais eficientes de acordo com os fatores de risco que mais ameaçam cada região.

Já em relação às vias de fato, o envelopamento é capaz de eliminar o coral em duas semanas (MANTELATTO et al., 2015). Já a imersão em hipoclorito de sódio, ácido acético e água doce matam 100% dos corais em poucas horas (MOREIRA; RIBEIRO; CREED, 2014; ALTVATER et al., 2017). Contudo, não são métodos simples de serem aplicados em um ambiente complexo como os costões rochosos. Esses tratamentos podem e devem ser adotados em protocolos de biossegurança pré e pós fronteiras cccc.

A remoção manual, com auxílio da marreta e talhadeira, tem sido um método eficiente em controlar as populações de coral-sol em baixa densidade, sem causar danos em espécies não-alvo e contribuindo para a restauração das comunidades nativas (DE PAULA AF et al., 2017; CREED et al., 2021; CRIVELLARO et al., 2021; SAVIO et al., 2021). Porém, o método sofre com certas limitações. O coral-sol muitas vezes é encontrado em fendas e locais de difícil acesso (Figura 2), e o pior de tudo, tem uma alta taxa de regeneração - qualquer fragmento de esqueleto com tecido é capaz de regenerar e formar novos pólipos - prejudicando a efetividade das ações de erradicação (LUZ et al., 2018). Dentre “as luzes que surgem no fim do túnel” estão a recente descrição do genoma do coral-sol (SOARES-SOUZA et al., 2020), e também um possível uso comercial do invasor. O esqueleto do coral-sol já é vendido como artesanato, em locais altamente invadidos, no Rio de Janeiro, e as substâncias presentes no coral-sol são de grande potencial farmacêutico (CREED et al., 2017a; CARPES et al., 2020).

Apesar das limitações da remoção manual em erradicar o coral-sol, combater a sua invasão não é uma causa perdida (OIGMAN-PSZCZOL et al., 2017). Mais recentemente, com apoio técnico de especialistas de diversos setores, em 2018 o Ministério do Meio Ambiente oficializou o Plano Nacional de Prevenção, Controle e Monitoramento do coral-sol *Tubastraea* spp. (PNPCM). O próprio nome do plano já indica seus objetivos principais. Foram traçadas metas e diversos objetivos específicos a serem cumpridos em um horizonte de 5 a 25 anos (MMA 2018).

Contudo, antes mesmo do plano, muitos pesquisadores, gestores ambientais e voluntários vêm realizando um grande esforço conjunto para vencer essa batalha. Há o relato de ações de controle nos Estados Unidos, no Flower Garden Banks, onde foram removidas aproximadamente 400 colônias (PRECHT et al., 2014), entretanto as ações de combate se concentram no Brasil. Através da remoção manual, as iniciativas de manejo contabilizaram 232 mil colônias de coral-sol removidas no litoral brasileiro, entre 2006 e 2016 (CREED et al., 2017b). A grande maioria foi removida no Rio de Janeiro (226 mil), e na Bahia (5 mil). Entretanto, esse número já está bastante ultrapassado. Por exemplo, naquele período haviam sido removidas apenas 800 colônias em Santa Catarina e atualmente os números já ultrapassaram 14 mil colônias (CRIVELLARO et al., 2021).

Em Santa Catarina, encontra-se a população de coral-sol mais austral do Oceano Atlântico. O invasor é encontrado dentro e no entorno imediato da importante Reserva Biológica Marinha do Arvoredo (Rebio Arvoredo). A região é reconhecida como uma área de transição entre a fauna tropical e temperada, sendo o limite sul de distribuição de importantes espécies bentônicas tropicais, como o coral *Madracis decatis*, realçando a importância da área à conservação (SEGAL et al., 2017).

A Rebio Arvoredo é a nossa área de estudo e a invasão na região será detalhada a seguir.

Os “bastidores” da invasão do coral-sol na Rebio Arvoredo

Antes mesmo de ter sido registrado nos costões rochosos da região, o coral-sol era uma preocupação aos gestores do Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) da Reserva Biológica Marinha do Arvoredo, e também dos pesquisadores da Universidade Federal de Santa Catarina (UFSC). Em 2010, preocupados com potenciais impactos das atividades petrolíferas que ocorriam na Bacia de Santos, originou-se a construção do Projeto de Monitoramento Ambiental da Rebio Arvoredo e Entorno (MAArE), no contexto de um processo de licenciamento ambiental junto ao ICMBio (SEGAL et al., 2017). O projeto teve início em junho de 2013 e foi concluído em 2016. Durante esse período, foram realizadas cerca de 130 expedições a campo, para coleta de dados oceanográficos, químicos, físicos e biológicos - como o monitoramento de espécies invasoras.

Infelizmente, o coral-sol foi registrado nos costões rochosos da região durante as negociações, antes da implementação do projeto MAArE. Em janeiro de 2012, durante um mergulho turístico na Baía do Engenho, na Ilha do Arvoredo - porém fora da área da reserva. A descoberta foi realizada pelos instrutores de mergulho, e também biólogos, Cecília Pascelli e Edson Faria Junior (CAPEL, 2012). Em abril de 2013, também na Ilha do Arvoredo e fora da área da reserva, um novo foco de invasão foi encontrado no Saco do Farol (GREGOLETTO, 2013). Já no âmbito do projeto MAArE, em 2014, outro foco de invasão foi encontrado fora da UC, no Saco do Vidal. Também foi encontrado o primeiro foco de invasão dentro da área da reserva, na localidade do Rancho Norte. Devido ao grande tamanho das colônias encontradas nesse foco, o local é considerado o ponto inicial da invasão nos costões rochosos da região. Em 2015, ocorreu o primeiro registro fora da Ilha do Arvoredo e em um naufrágio, no Naufrágio do Lili, na ilha da Galé e dentro da UC (SEGAL et al., 2017).

Não é possível traçar a rota exata da introdução do coral-sol *Tubastraea coccinea* nos costões rochosos de Santa Catarina. É provável que a história está atrelada à plataforma de petróleo P-14, que operou entre o início dos anos 2000 até 2007, a cerca de 200km da costa catarinense. A população de coral-sol encontrada na Rebio Arvoredo é composta pelos mesmos clones encontrados nos corais da plataforma P-14 (CAPEL et al., 2019). Enfim, independente da origem, o problema estava dado e medidas de controle eram necessárias. Era consenso entre os gestores ambientais e pesquisadores a necessidade da continuidade de pesquisas com o coral-sol mesmo após o fim do projeto MAArE (2016).

Esse é o momento (2017) em que ingresso no doutorado no Programa de Pós-graduação em Ecologia, sendo orientado pela prof. dra. Bárbara Segal, co-orientado pelo pós-doc Thiago Cesar Lima Silveira e com grande contribuição e parceria da Dra. Adriana Carvalhal Fonseca, analista ambiental do ICMBio, loteada na Rebio Arvoredo. Desde então, iniciamos a formação de um grupo com a linha de pesquisa sobre o coral-sol no Laboratório de Ecologia de Ambientes Recifais (LABAR).

Os primeiros resultados do grupo vieram com o trabalho que avaliou o recrutamento da comunidade bentônica em estruturas artificiais dispostas nas três ilhas da Rebio (Arvoredo, Deserta e Galé) (BATTAGLIN, 2018). Apenas um recruta de coral-sol foi encontrado. Para onde as larvas estariam indo se não assentaram nem mesmo em blocos de assentamento dispostos ao redor dos principais focos da região? Em relação a reprodução do coral-sol na região, foi avaliado a variação no número de propágulos nos pólipos de colônias coletadas ao longo do ano (CUSTÓDIO, 2019). Esses resultados também fazem parte da publicação do primeiro artigo da presente tese e serão posteriormente explorados. Além disso, contribuímos com o experimento descrito em ALMEIDA SAÁ et al., 2020, em parceria com o Laboratório de Ficologia da UFSC (LAFIC). O trabalho descreveu as respostas fisiológicas do coral-sol e do zoantídeo *Palythoa caribaeorum* em diferentes temperaturas e em interação. Também em laboratório, a interação do coral-sol com a espécie de cnidário séssil nativo *Parazoanthus swiftii* (WINTER, 2019).

Em breve também serão concluídos os trabalhos de mestrado da Júlia Alvarenga - uma revisão com abordagem cienciométrica traçando paralelos com o Plano Nacional de combate ao coral-sol - e o trabalho de conclusão de curso de Millenne Ohanna, com modelos de nicho considerando variáveis antrópicas e avaliando o risco de invasão em Unidades de Conservação.

Estrutura da tese e objetivos

Conforme tratado anteriormente, a presente tese foi construída com base nas necessidades dos gestores da Rebio Arvoredo e nos resultados iniciais do nosso grupo de pesquisa. Dito isso, e em consonância com o Plano Nacional de Prevenção, Controle e Monitoramento do coral-sol, e também concordando com OIGMAN-PSZCZOL et al., 2017, de que o combate ao coral-sol não é uma causa perdida, o objetivo geral desse trabalho é propor estratégias de controle e monitoramento para a invasão do coral-sol *Tubastraea coccinea*, principalmente na Reserva Biológica Marinha do Arvoredo (Rebio), Santa Catarina, Brasil, limite sul de distribuição do invasor no Oceano Atlântico.

No primeiro capítulo, nosso objetivo foi indicar a frequência e períodos do ano ideais para a ocorrência de atividades de controle do coral-sol. Para atingir o objetivo, nós analisamos como as ações de controle impactam a cobertura e estrutura da população do invasor, e também, o quanto ele se reproduz ao longo do ano. Além disso, nós detalhamos o histórico das ações de controle na Rebio Arvoredo e destacamos seu importante papel em frear a expansão da invasão.

No segundo capítulo, nosso objetivo é indicar os locais mais prováveis para a ocorrência de novos focos de invasão do coral-sol no estado de Santa Catarina. Nós utilizamos um modelo de dispersão para simular a liberação de larvas a partir dos focos de coral-sol conhecidos na Rebio Arvoredo. Também, para investigar a possível origem da invasão na região, simulamos a liberação de larvas a partir das plataformas de petróleo e do porto de Itajaí. O modelo desenvolvido pode ser configurado para outras espécies e locais, sendo uma ferramenta de grande potencial de apoio às estratégias de monitoramento de espécies invasoras marinhas.

Ao longo dos dois dois capítulos são discutidas estratégias e recomendações que podem auxiliar no combate à invasão do coral-sol, e também de outras espécies invasoras marinhas.

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CAPÍTULO 1 Fighting on the edge: reproductive effort and population structure of the invasive coral *Tubastraea coccinea* in its southern Atlantic limit of distribution following control activities

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Fighting on the edge: reproductive effort and population structure of the invasive coral *Tubastraea coccinea* in its southern Atlantic limit of distribution following control activities

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Abstract

The detection and control of invasive alien species in marine ecosystems is especially challenging because it is difficult to visualize the full extension of an invasion, while control options are often limited. The invasive scleractinian coral *Tubastraea coccinea* have spread over 8,000 km of the Atlantic coastline, from Florida in the USA to southern Brazil, mainly in association with oil and gas platforms. This invasive coral threatens endemic species, reduces native coral recruitment, and modifies communities and trophic interactions, posing a relevant threat to shallow Atlantic reefs. The main aim of our study was to assess the effectiveness of an ongoing *T. coccinea* control program by analyzing the results of control interventions on population structure and cover of the target species in its southern Atlantic limit of distribution. We also describe the reproductive effort of *T. coccinea* in a 12-month time span. Between 2012 and 2019, almost 14,000 colonies were removed, most of them of small size (< 5 polyps). The highest reproductive effort was observed in September. Changes in *T. coccinea* cover, population structure and potential local propagule supply were observed. Control activities led to a reduction in up to half the cover of the invaded area, maintained the majority of the population in non-reproductive sizes, and consequently lowered the potential local propagule supply. Our paper highlights the fundamental role of control in preventing the local spread of *T. coccinea*. Recommendations on management frequency and timing are also discussed in order to contribute to the improvement of management efficiency.

Keywords: Marine invasion; Invasive species; Management; Mechanical control; Scleractinian corals; Propagules

Introduction

As a consequence of the expansion of international trade, the number of translocated and introduced species is continuously increasing (Seebens et al. 2017). Most introductions in marine ecosystems are related to shipping and aquaculture (Molnar et al. 2008), while the global artificialization of habitats is the main driver of success in marine invasions (Bishop et al. 2017). Invasive non-native species can alter ecosystem functions. The introduced clam *Corbula amurensis*, for example, has caused the decline of phytoplankton biomass, consequently reducing primary production in the San Francisco Bay in California, USA (Alpine & Cloern 1992). Moreover, invasive species can impact human health and the economy, as when human pathogens are dispersed by ballast water (Ruiz et al. 2000). An estimated loss of 250 million dollars/year in the anchovy fishery industry is correlated with the introduction of the ctenophore *Mnemiopsis leidyi* (Zaitsev 1992).

Prevention is the most effective strategy to avoid future impacts of biological invasions (Bax et al. 2001). When prevention fails, early detection and rapid response are the next best opportunity for eradication (Wittenberg & Cock 2001; Simberloff et al. 2013). A well-designed eradication program must have enough funds for long-term work and monitoring possible recolonization (Wittenberg & Cock 2001). Therefore, technical and financial limitations hinder the possibilities of eradication. In such cases, control efforts to reduce species abundance or limit spread can protect the natural ecosystem on a local scale as long as they are not discontinued, and may in due course increase the feasibility of eradication (Green et al. 2014).

There are several methods to contain spread using mechanical, chemical and/or biological control (Wittenberg & Cock 2001). Biological control requires close monitoring of host specificity, which can be limited in marine ecosystems. Chemical control has been successfully used under certain conditions (Mytilopsis *sallei* in Australia - Bax et al. 2002; *Caulerpa taxifolia* in California - Anderson 2005) that weighed the benefits against potential impacts such as fast dilution in water and impact on non-target species. Although mechanical control can be labor-intensive and time-consuming, it is highly specific to the target (Wittenberg & Cock 2001). Complementarily, information on the biology of the target species is important to support the definition of control strategies (Domisse & Hough 2004; Anderson et al. 2005). In Australia, a “ballast window” was defined for ships to fill up with ballast water only in larvae-free periods of the *Asterina* starfish in order to reduce propagule pressure and mitigate spread (Domisse & Hough 2004).

Two azooxanthallete scleractinian corals, *Tubastraea coccinea* Lesson 1829, native to the Indo-Pacific, and *T. tagusensis* Wells 1982, from the Galapagos Islands, successfully invaded Atlantic shallow reefs. These corals do not seem to have substrate settlement preferences (Creed & De Paula 2007). Their introduction has been mostly associated with structures translocated between regions, such as oil and gas platforms (please see Creed et al. 2017a for more details on *T. coccinea* invasion pathways). The invasion started in the Caribbean (1943) (Cairns 2000) and spread throughout the Gulf of Mexico (Fenner 2001), the Atlantic coast of Brazil (Castro & Pires, 2001), Florida in the USA (Fenner & Banks 2004), and the Canary Islands of Spain (López et al. 2019). The first record of the coral on the Brazilian coast was made on an offshore oil platform in the late 1980s, in the Campos Basin, in Rio de Janeiro (RJ) state (Castro & Pires 2001). It spread fast along natural substrates on the rocky shores of Ilha Grande, also in RJ state, in the 1990s (Castro & Pires 2001; De Paula & Creed 2004). Nowadays, several disjunct populations are present along 3,800 km of the Brazilian coastline, from North (Ceará state, Soares et al. 2016) to South (Santa Catarina state, Capel 2012).

These corals, popularly known as “sun corals”, are spreading fast (~2km/year, Da Silva et al. 2011) mainly due to early maturity, and sexual and asexual reproduction (Glynn et al. 2008; De Paula et al. 2014; Capel et al. 2017; Luz et al. 2020). In the Ilha Grande Bay (Rio de Janeiro state), *T. coccinea* reproduces many times throughout the year. Different stages of propagule development occur simultaneously in a polyp. Two reproductive peaks were observed, one from September to December and the other one from February to May (De Paula et al. 2014). Larvae were alive for ~4 months in artificial conditions (Mizrahi 2014; Luz et al. 2020), but they usually settle and metamorphose fast (1-3 days), displaying gregarious behavior near parental colonies (Glynn et 2008; De Paula et al. 2014; Luz et al.2020). Invasive *Tubastraea* corals impact trophic interactions (Miranda et al. 2018; Silva et al. 2019), modify communities (Lages et al. 2011), damage endemic species (Creed 2006; Santos et al. 2013; Barbosa et al. 2019), and reduce native coral recruitment (Miranda et al. 2018).

Several initiatives based on mechanical methods to control *Tubastraea* spp. have been locally implemented by environmental government agencies, non-governamental organizations, researchers and volunteers in Brazil (Creed et al. 2017b), as well as by local managers in the Flower Garden Banks Marine Sanctuary (Florida, USA) (Precht et al. 2014). Although a National Plan for Prevention, Control and Monitoring (NPPCM) for *Tubastraea* spp. was published in Brazil by the Ministry of Environment in 2018 (MMA 2018), no control actions have been implemented on a national scale so far. However, one of the goals of the NPPCM is to define priority areas for control and monitoring, as well as to eradicate small, isolated, and initial populations. Albeit manual removal using a chisel and hammer has proven effective to reduce *Tubastraea* spp. cover (De Paula et al. 2017), sun corals grow at high regeneration rates and can grow back from remaining tissue that is not completely detached from the substrate (Luz et al. 2018), which can undermine the effectiveness of control.

The main aim of our study was to assess the effectiveness of an ongoing *T. coccinea* control program by analyzing the results of control interventions on population structure and cover of the target species in its southern Atlantic limit of distribution. We also assessed the outcome of control activities conducted by local managers and volunteer researchers. In the same region, we investigated propagule production of *T. coccinea* for 13 months to determine the most appropriate time interval for control interventions. In addition, we combined information on reproduction and cover to estimate the potential of local propagule release. We assumed that control activities would reduce cover and maintain populations with small individuals, reducing the local population propagule supply. Considering the data available and the threat of invasion by *T. coccinea* in southern Atlantic ecosystems, we expect our study to contribute with relevant information to support and improve the ongoing control program.

Materials and methods

Study system

This study was carried out on rocky shores of the Arvoredo Marine Biological Reserve (Rebio Arvoredo from now on), a no-take, no-entry protected area (176km²) on the coast of Brazil, in the southwestern Atlantic (between 28º36'16.94" S and 28º13'43.18" S). Rebio Arvoredo comprises an archipelago formed by three islands (Arvoredo, Deserta, and Galé) of rocky shores surrounded by a highly productive pelagic ecosystem. Oceanographic conditions vary seasonally, with temperatures ranging from ~15 ºC to 29 ºC (Faria-Junior & Lindner 2019). In the summer, tropical hot and nutrient poor waters dominate the continental shelf. In winter, waters are cold, generating much higher primary production on the ocean surface due to the influence of the La Plata River and Patos Lagoon discharges (Freire et al. 2017). Given these conditions, Rebio Arvoredo plays a key biological role in the region. The area includes the most southern coralline algal bank on the Brazilian coast (Rocha 2004), serves as refuge to commercial fish species (Anderson et al. 2019), and is a transitional area between tropical and temperate fauna for many benthic species. The Reserve is the southern distribution limit of of *T. coccinea* in the Atlantic Ocean (Capel 2012; Lindner et al. 2017). This occurrence is at least 450km away from the nearest known population, located farther north (Alcatrazes islands, São Paulo state).

The first record of *T. coccinea* on the rocky shores of Arvoredo island was made in 2012, outside the limits of Rebio Arvoredo, in a site called Engenho (EG, Fig. 1) (Capel 2012). Subsequently, invasion patches were observed in two other sites, Saco do Farol (SF) and Saco do Vidal (SV), in 2013 and 2014, respectively (Fig 1). Still in 2014, the invader was found within the limits of Rebio Arvoredo in Rancho Norte (RN). Judging by the large size of colonies, this seems to be the site that was invaded first in the area (Fig S1a). In 2015, two colonies were found in a shipwreck by Galé Island (GI), also within the limits of Rebio Arvoredo. Currently, invasion patches are still scattered, outside and within the limits of Rebio Arvoredo. Invasion is generally restricted to vertical surfaces, caves and crevices. These substrates are mostly occupied by calcareous and turf algae, sponges, ascidians, the octocoral *Carijoa riisei*, the zoanthids *Parazoanthus swiftii* and *Palythoa caribaeorum* (only on horizontal surfaces, see

Almeida Saá et al. 2019), and the scleractinians *Astrangia rathbuni, Phyllangia americana* and *Madracis decatis* (a rare species) (Capel et al. 2012; Lindner et al. 2017).

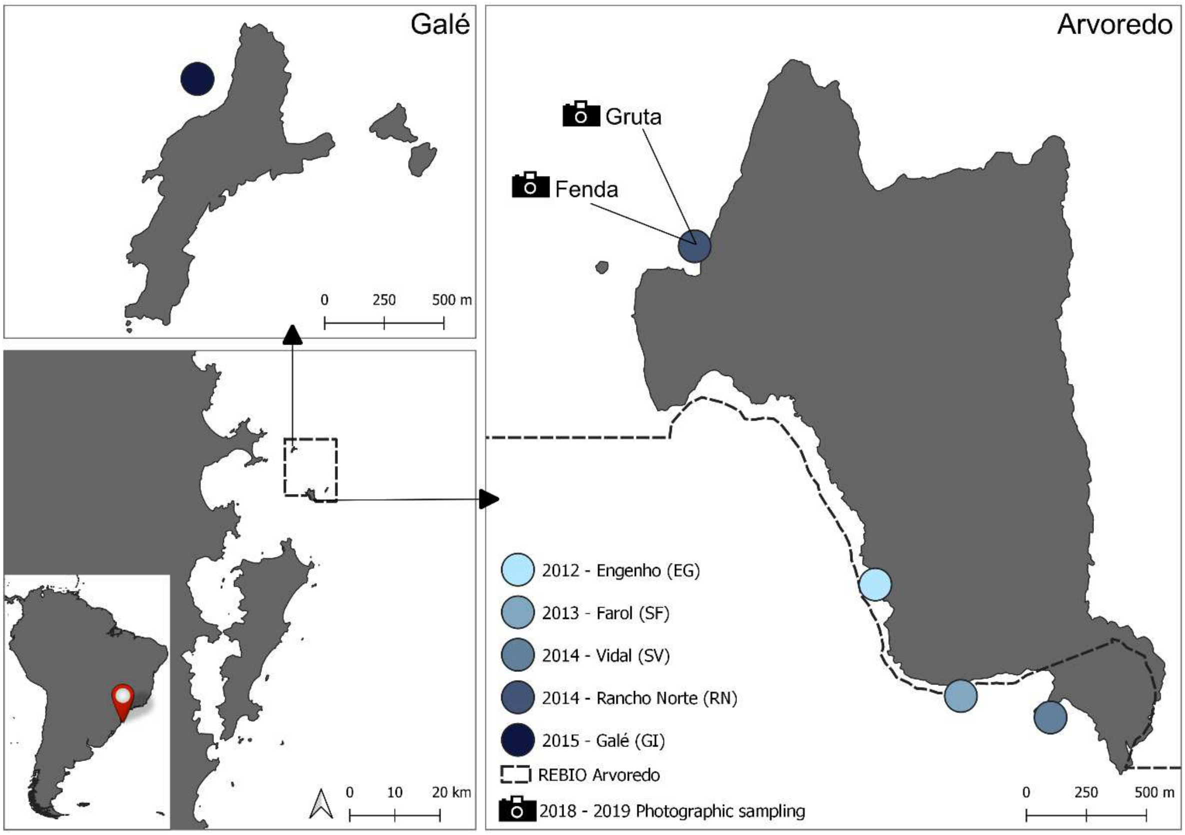

Figure 1. Map of the study area showing sites of occurrence of *Tubastraea coccinea* and areas of photographic sampling. Sites are chronologically ordered by successive observations of the invasive coral. The dotted line shows the limits of Rebio Arvoredo.

Control activities

In 2012, the federal environmental agency in charge of Rebio Arvoredo, Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), in partnership with researchers of the Federal University of Santa Catarina (UFSC), established a program to control and monitor invasions by *T. coccinea*. Current control activities consist in two 50-minute dives performed by two pairs of divers, each pair working on a site. While one diver manually removes colonies with a chisel and hammer, the other inserts them in a plastic bag to prevent dispersal of larvae or colony fragments. The removal of larger colonies was prioritized because of the larger number of polyps and likely higher reproductive potential. Control activities were undertaken outside (Engenho, Saco do Farol and Saco do Vidal) and within the limits of Rebio Arvoredo (Galé Island and Rancho Norte). The numbers of control actions in each site and of colonies removed since the beginning of the control program were recorded and analyzed. All colonies were classified in five size classes according to the number of polyps: I (1-5 polyps), II (6-10 polyps), III (11-20 polyps), IV (21-40 polyps), and V (41 or more polyps). Figures were produced using the package *ggplot2* (Wickham 2016) in RStudio software (2020).

Reproductive effort

To describe the yearly reproductive effort of sun corals, we collected five colonies of similar sizes in each campaign between January, 2018, and June, 2019 (January to April, and July to November, 2018, and January, February, April and June, 2019) Collections were made by scuba divers at 2-8 m depth on rocky shores of Arvoredo Island. Colonies were fixed in 4% formalin solution, decalcified in 10% formic acid and 2% formalin for 48h, then cleaned up in running tap water for 24h (Glynn et al. 2008; De Paula et al. 2014). We measured the diameter, maximum oral disc diameter and distance between the oral and aboral ends of polyps to evaluate colony and polyp area (circle formula) and polyp volume (cylinder formula). We dissected two central polyps (N=126) in each colony, and, when present, we counted all propagules under a stereomicroscope. As the development stages of embryos can only be differentiated through histological analysis (Glynn et al. 2008), we used the term propagule to refer to all stages. We only selected central polyps because larvae are more abundant in central polyps than on colony edges (Chornesky & Peters 1987). We extrapolated the number of propagules observed per polyp area to total colony area (propagules cm^2. $colony^{-1}$) in order to establish a correlation with cover (explained in the next section). We considered solely the central (fertile) part of the colonies for the extrapolation. Descriptive analyses were performed in RStudio software (2020) and figures were produced using the package *ggplot2* (Wickham 2016).

***T. coccinea* cover, population size structure and propagule supply**

Between January, 2018, and June, 2019, we monitored two invaded sites where frequent control actions were conducted in REBIO Arvoredo (Rancho Norte, sites “Fenda” and “Gruta”) approximately every four months (5 sampling efforts in Gruta and 6 in Fenda, Table S1). Both sites occupy an area of approximately five meters in length by one and a half in width at a depth of three meters. Accessibility to invasion patches for mechanical control differed between sites. Although a crevice in “Fenda” is inaccessible (Fig 6c), a vertical surface in this site is easier to access than in “Gruta”, where sun corals were growing on the negative surface of a cave. The invaded surfaces were photographed in the format of photo quadrats (25x25cm). To evaluate cover and assess population size structure, we outlined the area of each colony in ImageJ Software (Schindelin et al. 2012) on five photographs taken in each site (Ntotal=55). For this evaluation, we classified each colony according to five size classes based on surface area (<0.3cm^2; 0.3 - 1cm^2; 1-5cm^2; 5-10 cm^2; >10cm^2) and determined their relative frequency (%). Classes <0.3 cm^2 (recruit size 4mm, see Mizrahi 2008) and 0.3 - 1cm^2 represent non-reproductive individuals, since propagules were observed in colonies larger than 1.2 cm^2 or more (De Paula 2007). Descriptive statistics were performed in RStudio software (2020) and figures were produced using the package ggplot2 (Wickham 2016).

To estimate the local potential propagule supply of sun coral populations in our samples, we combined the data obtained on propagule production (propagules cm².colony^{-1}) and coral cover (cm²). We used the median of propagules per cm² from the month of September (200 propagules cm² colony^{-1}) to extrapolate to the coral cover (cm²) measured in each sample. Data from the month of September were used because it was the period of highest reproductive effort observed in our analysis. In the absence of control actions, all colonies would probably have reached an equivalent reproductive condition. Polyps located on the edge of colonies produce less larvae due to potential defense activity that is common along the edges (Chornesky & Peters 1987). Therefore, we measured the total area of 30 colonies on photographic samples and excluded the area of the peripheral (infertile) polyps from each of the colonies. We considered peripheral polyps as those not entirely inside the colony (with a free border). As a result, we obtained a fraction of 44.37% of potentially reproductive tissue in relation to total colony area. The cover of non-reproductive colonies/recruits (<0.3cm² and 0.3-1cm² classes) was excluded from the extrapolation.

Results

Control activities

Between February, 2012, and October, 2019, 59 control actions were conducted in Rebio Arvoredo, resulting in the removal of 13,986 colonies (Figure 2). The majority of these colonies belonged to the smallest size classes I (6872; 49.1%) and II (4611; 33%), with less colonies in classes III (1865; 13.3%), IV (468; 3.4%), and V (170; 1.2%). A considerable number of large colonies was eliminated shortly after discovery (Rancho Norte, site “Fenda”, 2014), with the removal of 108 and 75 colonies in classes IV and V, respectively. Only small colonies remain since then. Another large group of class V colonies was eliminated in Saco do Farol 2019 (43 colonies), and a few more colonies of size V (maximum 7) were removed in other 20 control efforts from scattered areas.

Rancho Norte was the site where more control actions (21) were conducted and the highest number of colonies was removed (6239), mainly because it contained the two largest invasion patches (in “Fenda” and “Gruta”). The highest number of colonies eliminated in a single control action was 876 (class I; 437; II: 264; III: 128; IV: 40; V: 7) at Engenho (2019). The smallest number of colonies eliminated refers to only two colonies immediately removed when discovered in a shipwreck by Galé island in 2015. Despite this early detection and rapid response effort, 23 colonies were found and eliminated in the same shipwreck in 2019. The years with the largest numbers of colonies removed were 2018 (4595) and 2019 (3805); conversely, 2012 (324) and 2015 (137) were the years with the lowest number of colonies removed. The years 2018 (15) and 2019 (11) were also those with more control campaigns, while 2013 (3) and 2015 (2) were the years with less control campaigns.

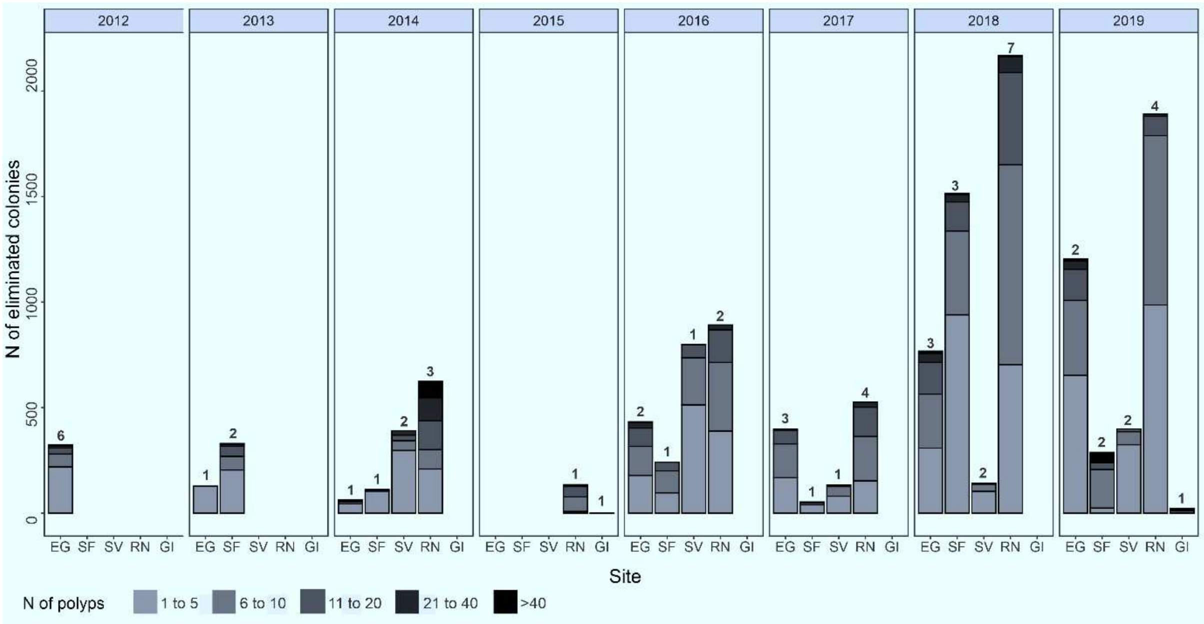

Figure 2 Number of control activities (labels on top of the bars) and colonies eliminated in each class of polyp numbers (vertical axis on the left) in each site. EG = Engenho; GI = Galé Island; RN = Rancho Norte; SF = Saco do Farol; SV = Saco do Vidal. Zero indicates the absence of control activities.

Reproductive effort

Samples were collected during 13 months, between January, 2018, and June, 2019 (Appendix Table 1). Colony diameter ranged between 2.1 and 7.3 cm (mean = 4cm ± 1.2), while polyp diameter ranged between 0.6 and 1.6 cm (mean = 1 cm ± 0.16). Polyp volume ranged between 250 and 5,069 mm^3 (mean = 1,205 ± 757 mm^3). The number of propagules per polyp varied widely (mean = 153.8 ± 165.6 SD). Propagules were present throughout the year except in January, 2018, and were observed in low numbers in August, 2018 (44 ± 56.3 SD propagules.polyp^{-1}), January, 2019 (39.8 ± 42.5 SD propagules.polyp^{-1}), February, 2019 (37.6 ± 26.8 SD propagules.polyp^{-1}) and June, 2019 (78.6 ± 47.7 SD propagules.polyp^{-1}) (Fig 3, Appendix Table 1). The absence and low number of propagules in summer (January and February) may indicate events of larvae release, as propagules were clearly observed in an advanced larvae development stage only in January, 2019, which coincides with the peak reproductive period observed in Ilha Grande Bay, in Rio de Janeiro (600km north of Santa Catarina). The highest numbers of propagules per polyp were observed in September (822 max; 500 ± 205 SD) and November, 2018 (453 max; 263 ± 102.3 SD). Polyps in October, 2018, also contained a large number of propagules (614 max; 191 ± 229.3 SD), with the exception of one colony in which no propagules were observed.

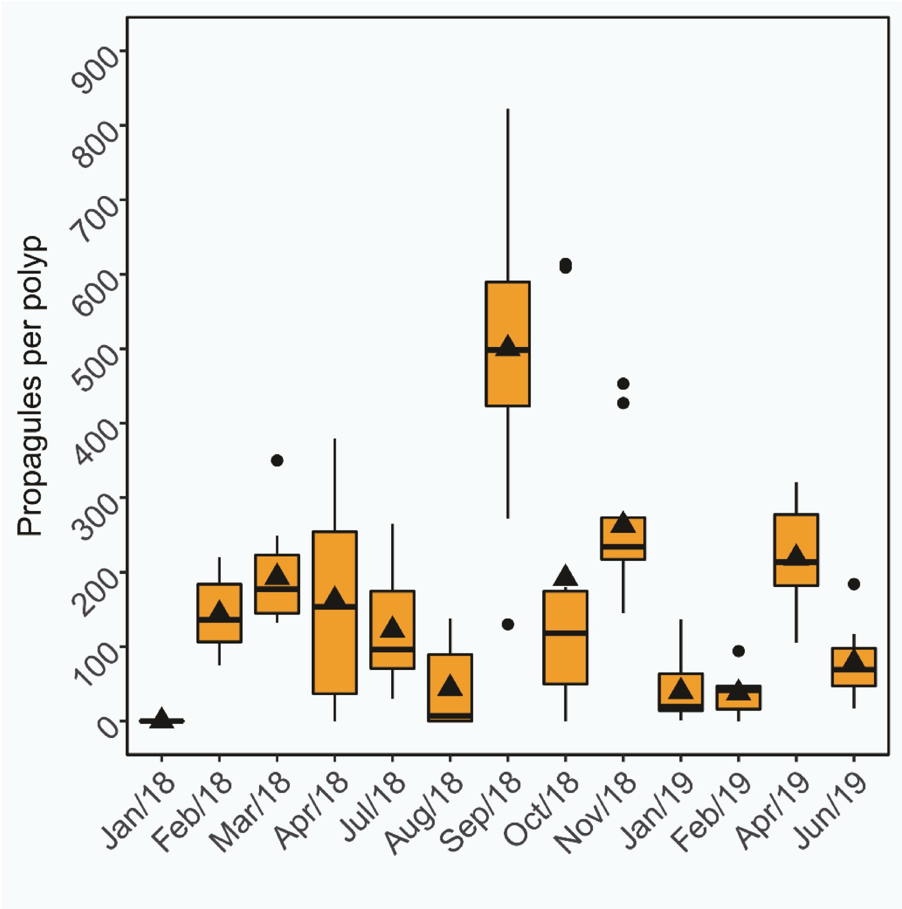

Figure 3 Variation and mean (black triangle) of *T. coccinea* propagules per month (2 polyps each, 5colonies/month). The horizontal black line inside box-plots represents the median.

Cover, population size structure and propagule supply

In both invaded areas, our first sampling effort (January 2018) was conducted 167 days after a control action. During the period of sampling, both areas were submitted to control actions six times, with similar total numbers of colonies removed (Fenda - 1673; Gruta - 1614). Most colonies eliminated (83%) contained between 1 and 10 polyps (classes I and II), with only three of them having more than 41 polyps.

Figure 4 shows the estimated propagule supply (4a), population structure (4b), and the number of eliminated colonies in each control action (4c) in Fenda. The highest mean cover 30.6 ± 10.35 SD % (Fig S2a) and mean estimated propagule supply of 37,913 ± 12,811 SD propagules per 0.06m² were observed in the first sampling effort (January, 2018). Population structure was almost evenly distributed (< 0.3 cm² - 11.5%; 0.3-1 cm² - 15.8%; 1-5cm² - 25.1%; 5-10cm² - 17.9%; and >10cm² - 29.4%), with by far the highest proportion of reproductive colonies observed. By January, 2018, 664 colonies had been removed in two control actions (classes I, 204; II, 285; III, 142; IV: 33). These efforts led to a reduction in cover from 30.6 ± 10.35 SD % to 5 ± 3 SD % (Mar 2018), or almost eight times less potential production of propagules (from 37913 ± 12811 SD to 5047 ± 3758 SD propagules per 0.06m²). Only

2.3% of colonies were larger than 5 cm². In August, 2018, mean cover was 4.9 ± 3.2 SD %, and propagule supply, 4,438 ± 4,545 SD propagules per 0.06m², with 80.4% of colonies probably non-reproductive and only 0.9% of colonies larger than 5cm². A low proportion of large colonies was also observed in the following control actions. Only 9 colonies with more than 20 polyps (class IV) were removed in control actions in May (5 colonies) and August (2 colonies), 2018, and in two actions in January, 2019 (2 colonies). In June, 2019, cover was 12.9 ± 7 SD %, propagule supply, 15,273 ± 8,639 SD propagules per 0.06m², and the proportion of reproductive colonies, 52.8%.

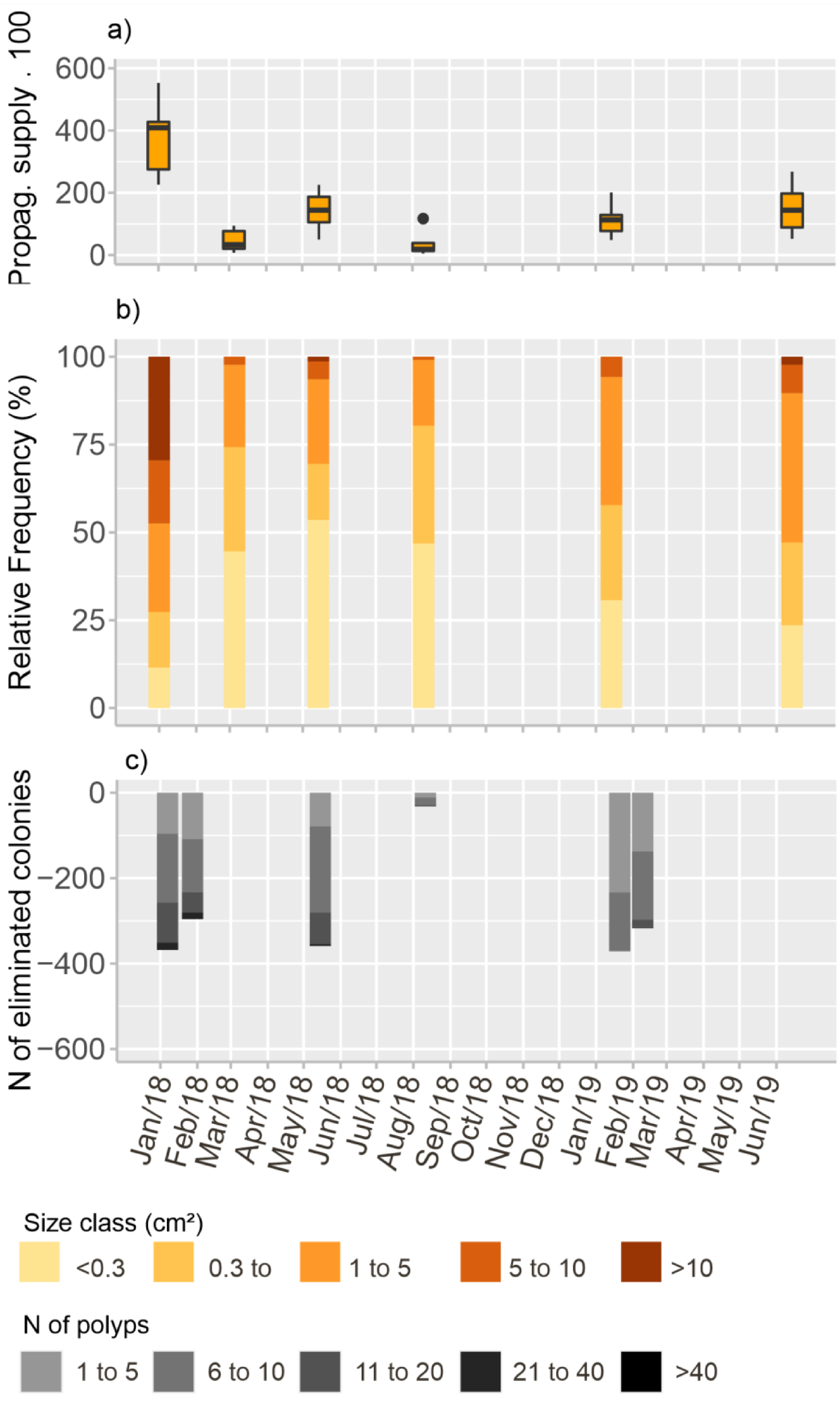

Figure 4 Changes in population structure after control actions in Fenda. (A) Estimated propagule supply (value of y axis was divided by 100 to adjust figure dimensions; the horizontal black line inside box-plots represents the median); (B) relative frequency of colonies in each size class, and (C) number of colonies eliminated in each class of polyp numbers per control action.

Figure 5 shows the estimated propagule supply (5a), population structure (5b), and the number of colonies eliminated in each control action (5c) in Gruta. In January, 2018, mean cover was 37.9 ± 10.6 SD % (Fig S2b), and propagule supply, 46,019 ± 12,811 SD propagules per 0.06m² (Fig 5b). These were smaller compared with colonies in Fenda (< 0.3 cm² - 12%; 0.3-1 cm² - 15.9%; 1-5cm² - 47.6%; 5-10cm² - 19.9%; and >10cm² - 4.5%). Afterwards, 955 colonies were removed in two control actions (classes I, 370; II, 366; III, 193; IV, 25; V, 1). In March, 2018, cover and propagule supply were 15.9 ± 2.6 SD % and 18,254 ± 2,342 SD propagules per 0.06m², respectively, with 72.8% of colonies non-reproductive. In the 2018 control actions (March and May), only 130 colonies were removed (classes I, 38; II, 71; III, 17; IV, 3; V, 1). There was an interval of 252 days between control efforts in 2018 (May) and 2019 (January), when the highest cover (41 ± 10.4 SD %), propagule supply (49,912 ± 12,947 SD propagules per 0.06m²), proportion of reproductive colonies (77.3%) and colonies larger than 10cm² (9%) were observed. Shortly after, 599 colonies (classes I, 226; II, 342; III, 28; IV, 3) were removed in two control actions conducted in January, 2019. In June, 2019, cover was 31.2 ± 5 SD %, propagule supply, 38,247 ± 6,130 SD propagules per 0.06m², and 73.3% of the colonies were reproductive.

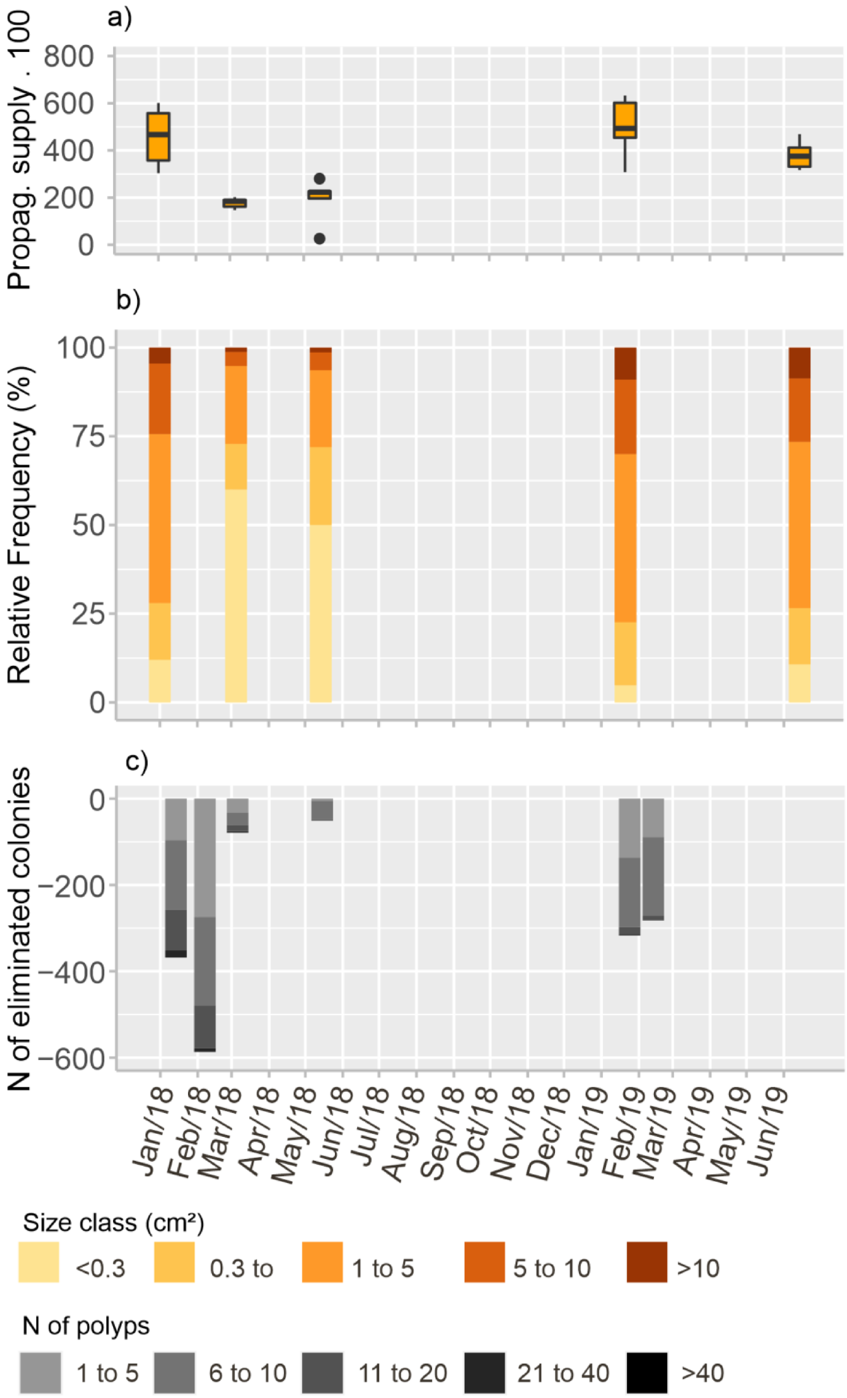

Figure 5 Changes in population structure after control actions in Gruta. (A) Estimated propagule supply (value of y axis was divided by 100 to adjust figure dimensions; the horizontal black line inside box-plots represents the median); (B) relative frequency of colonies of each size class, and (C) number of colonies eliminated in each class of polyp numbers per control action.

Discussion

Our results support the importance of ongoing control actions to slow the spread of *T. coccinea*. Even if manual removal is not the ideal control method because of the high regenerative capacity of *T.*

coccinea (Luz et al. 2018), the current advantage of manual removal is to restrain populations to a large proportion of small, non-reproductive individuals, therefore reducing propagule supply, and consequently restricting spread. The current status of relatively small invasion patches in the Arvoredo marine reserve and surroundings is due to the results of ongoing control. Although eradication is not feasible with the control methods currently in use, the maintenance of populations in restrained sizes with individuals in small size classes increases future possibilities of eradication (Myers et al. 2000), buying time until better solutions for more effective control are identified.

Some biological traits of *T. coccinea* explain its high invasiveness. The species reproduces mostly asexually (Capel et al. 2017), and colonies as small as two polyps are already mature (Glynn et al. 2008; De Paula et al. 2014). In artificial conditions, larvae can metamorphose in the water column and form clusters that settle and start benthic life as a colony (Mizrahi 2014; Luz et al. 2020). Although larvae of large colonies may be viable for a long time (~90 days, Luz et al. 2020), they usually show gregarious behavior and settle fast (1-3 days, Glynn et al. 2008; De Paula et al. 2014). The complexity of recruitment in corals is well known. Estimates show that only 1% of marine benthic invertebrates successfully survive the several bottlenecks in this early stage of life (Gosselin & Qian 1997). In this sense, considering our extrapolation of the propagule supply at the beginning of sampling, populations of *T. coccinea* in “Fenda” and “Gruta” may potentially produce approximately 80 thousand propagules. Considering a survival rate of ca. 1%, this means that a release event at that moment may generate almost 1,000 new settled individuals with capacity to establish new invasion patches on their own. The reproductive data generated in our study are extremely important for planning the timing of control activities, which should be conducted before reproductive peaks and before recruits or regenerative colonies reach maturity. Based on these data, we recommend that control activities are preferentially carried out between May and September in the southern Atlantic coast of Brazil. Although we cannot precise the relative contribution of larval recruitment versus regeneration for the maintenance of the *T. coccinea* population in the Rebio Arvoredo, it is important to highlight that limiting local production of propagules is key to contain spread to new sites and the establishment of new invasion *foci*.

Despite the high number of colonies removed (~14 thousand), the invasion observed in our study sites can be considered small compared to those in the Brazilian southeastern coast. In the Ilha Grande Bay (Rio de Janeiro), for instance, more than ~220,000 colonies had been removed in more than 150 control actions by 2017 (Creed et al. 2017b). Furthermore, a *T. coccinea* distribution and abundance survey in a port area influenced by upwelling in Arraial do Cabo (Rio de Janeiro) fifteen years after its first record showed that more than 50% of the total population was formed by colonies larger than 30cm² (Batista et al. 2017). During the 18 months in which we conducted sampling work, colonies larger than 5cm² never made up more than 50% of the populations. Sun coral is assumed to change communities completely when cover reaches 45% (Lages et al. 2011). Even with inaccessible crevices in Rebio Arvoredo (Fig S1c), there are not any known invasion patches in the region of our study with such levels of cover, which emphasizes the relevance of the ongoing control program to contain the invasion and consequential impacts on local communities and ecosystems.

De Paula et al. 2017 suggested that, after the first control effort of *T. coccinea*, follow-up within a 6-12-month interval may be sufficient. Our results corroborate this indication. From the discovery of invasion in Fenda (2014 Fig S1a) until now (Fig S1b), the effectiveness of control activities undertaken so far is palpable. Besides, immediately after control actions, regenerating colonies are flattened and virtually lack the calcareous skeleton (Fig S3b, S3e), becoming very difficult to detach from the substrate (Luz et al. 2018). Thus, the energy used on mechanical control should be invested when colonies have regenerated enough to be effectively removed, before reaching maturity. The combination of initial efforts of manual removal with a revisit to scratch/suction the remaining regenerating tissue may produce interesting results. Other methods to eliminate sun corals include the use of acetic acid (Creed et al. 2018), sodium hypochlorite (Altvater et al. 2017), freshwater (Moreira et al. 2014), and wrapping (Mantelatto et al. 2015), the last of which requires specific conditions or isolation of colonies for application and is extremely difficult to implement with success in tridimensional natural rocky reefs.

Regulatory frameworks for preventing the introduction and spread of sun corals must be established on all scales (global, regional and local) (Hewitt et al. 2008). There are 158 active offshore oil platforms, 23 drill ships, and expectations that 18 new structures will be installed by 2022 (Mafra 2018) in Brazil alone. A large part of these oil platforms (42%) are 20-25 years old, which means they must be decommissioned soon (Mafra 2018). Additionally, projections indicate that oil production will double in the next decade, generating more than 250 billion dollars in investments (MME 2018). The relevance of the expansion of these activities to the Brazilian economy is undeniable, but they are also a threat to marine ecosystems. While specific regulations on the decommissioning of such structures do not exist at present, the oil industry claims that having to clean all structures offshore would render the business unviable. The complexity of the issue must be acknowledged, but it is essential to prevent the transit of contaminated structures. There is an urgent need for the development of specific regulatory frameworks by policy makers. The commitment of the governments of Australia and New Zealand are good examples to follow (see Hewitt et al. 2009). In a similar way to using the “ballast window” proposed to reduce the spread of the starfish *Asterina* in Australia (Domisse & Hough 2004), structures potentially contaminated with *Tubastraea* corals should be moved only in periods of lowest reproductive potential (winter in the southern hemisphere). Furthermore, it is very important that these structures are immediately sent for clean-up (exposure to air or freshwater), avoiding docking for long periods in sheltered environments suitable to sun coral development.

In order to generate an effective response to marine invasions, different technical components must be integrated, such as data on the biology of the target species, agencies in charge of invaded areas, field expertise, and financial and human resources (Anderson et al 2005). Successful marine eradications have been achieved based on these premises (*Mytilopsis sallei* in Australia - Bax et al. 2002; *Caulerpa taxifolia* in California - Anderson, 2005). However, the early detection and rapid response of environmental agencies and scientists in the southern distribution limit of *T. coccinea* were insufficient for eradication to be achieved. This is explained mainly because sun corals have occupied crevices inaccessible to manual removal (Fig S1c), and most importantly, because a formal eradication program with sufficient funding to eliminate all individuals and monitor recolonization in the following years (such as recommended by Simberloff et al. 2005) has not been implemented. The recently published National Plan for the Prevention, Control and Monitoring for *Tubastraea* spp. (MMA 2018) must be put into action. The small, isolated invasion in the southern Atlantic limit of distribution in Rebio Arvoredo, an important Marine Reserve, must be prioritized for eradication. We agree with Oigman-Pszczol et al. (2017) on the claim that invasion by *T. coccinea* is not a lost cause.

Citizen-science may be helpful to increase *T. coccinea* control efforts. Positive results were obtained by citizen engagement in the detection and control of lionfish (*Pterois volitans*) in the Gulf of Mexico (see Scyphers et al. 2014). *Tubastraea coccinea* was actually first reported for Arvoredo island by recreational divers (Capel 2012). In 2013, the federal environmental agency (ICMBio), in partnership with the Marine Biodiversity Lab at UFSC, organized a workshop with staff from dive schools in the region to explain the threats and impacts of invasion by *T. coccinea* and provided training for the identification of colonies. Since then, some invasion patches around Arvoredo island were detected and reported by trained divers. However, controlling *T. coccinea* is not technically simple, requiring well-trained and qualified scuba divers to prevent the propagation of fragments. Creed et al. (2017b) involved local communities to collect corals by snorkeling and sell coral skeletons as a craftwork on a highly invaded site (Ilha Grande, RJ). Because invasion is restricted in Rebio Arvoredo, citizen engagement would be best used for the early detection of new invasion patches.

Given the challenges of controlling invasive marine species (Williams & Grosholz, 2008) and global predictions of increase in the number of non-native species (Seebens et al. 2017), our work provides relevant information to support and improve ongoing control of *Tubastraea* spp. Our data show that control efforts reduced the population propagule supply of *T. coccinea* by maintaining a large portion of the population in small, non-reproductive sizes. We also highlight the urgent need for new techniques that might lead to eradication. Furthermore, the NPPCM for *Tubastraea* spp. must be implemented and prioritize the southern Atlantic limit of distribution including Rebio Arvoredo. Finally, even in the lack of a formal eradication program with ensured funding, control activities have successfully slowed the spread of *T. coccinea.* With the use of more effective techniques and the commitment of federal policies, eradication can be feasible.

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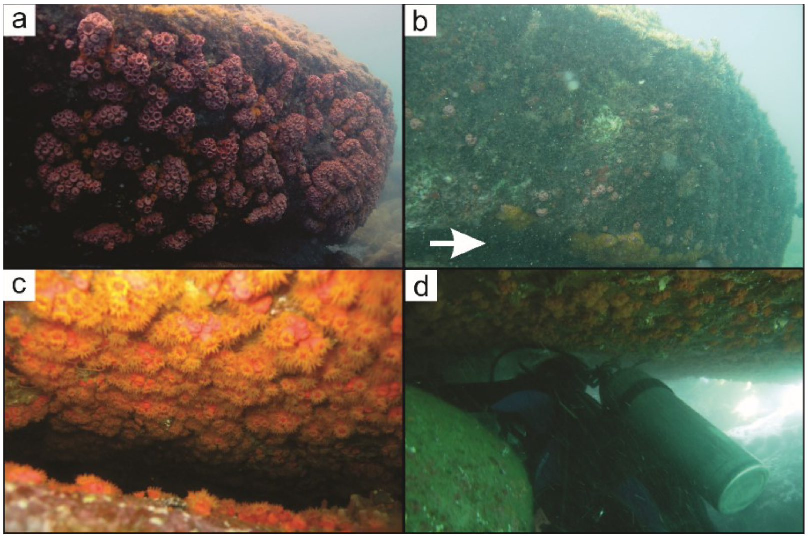

Figure S1 Sites invaded by *Tubastraea coccinea* in the Atlantic southern distribution limit. (A) The "Fenda" site upon discovery in 2014, considered the initial invasion focus due to the size of the colonies (photo credit: Edson Faria Junior). (B) The "Fenda" site in June, 2019, after 15 control actions. The white arrow indicates an (C) inaccessible crevice at Fenda (the word "fenda" in Portuguese means crevice). (D) The "Gruta" site (in Portuguese, the word “gruta” means cave) of difficult access for mechanical control.

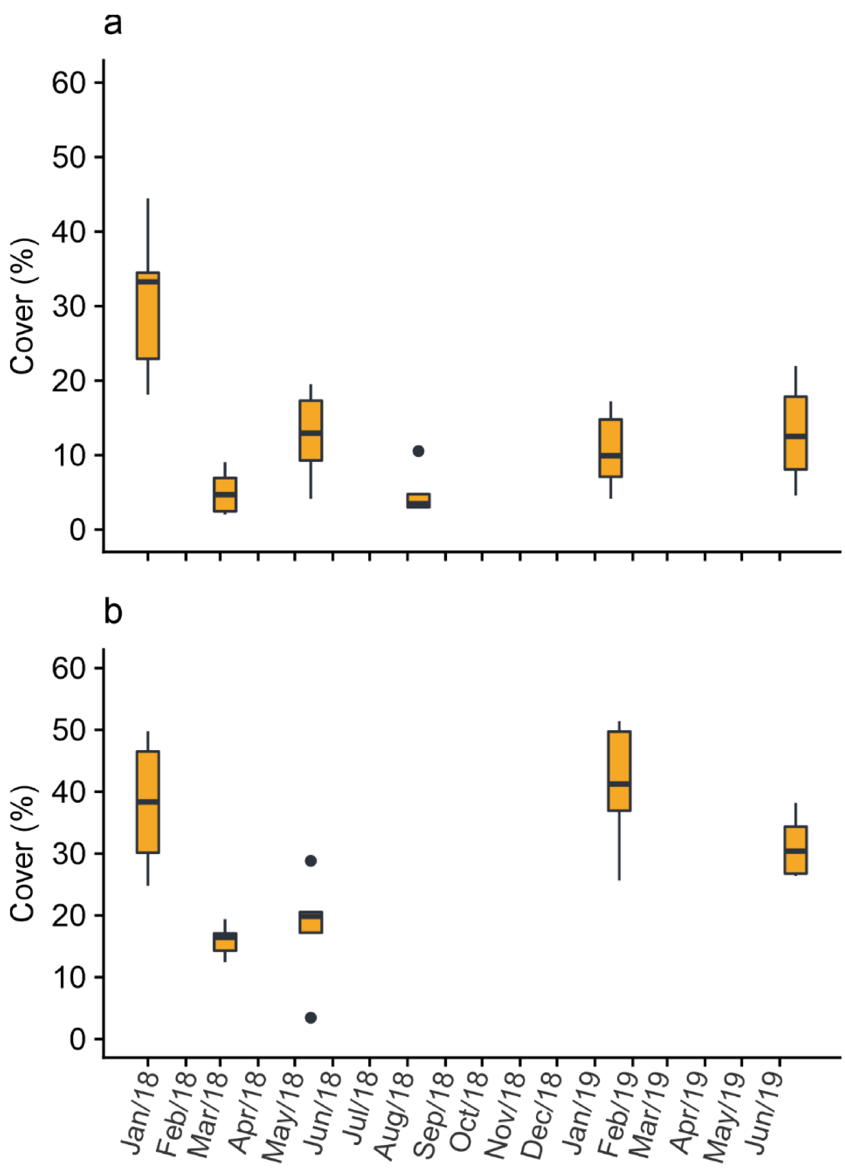

Figure S2 Variation of *T. coccinea* cover at (a) Fenda and at (b) Gruta. The horizontal black line inside box-plots represents the median.

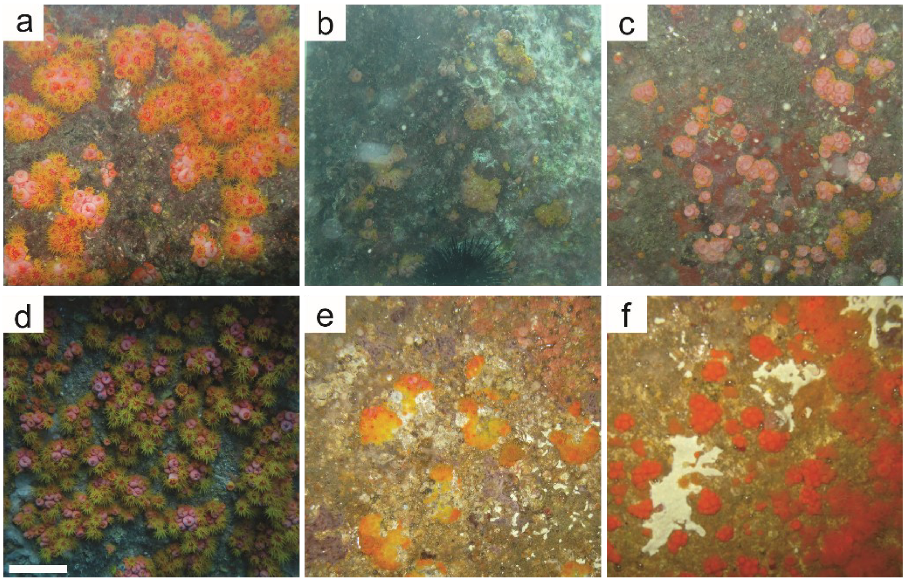

Figure S3 Invasion areas in Fenda (first row) and Gruta (second row) at January 2018 (a and d), March 2018 (b and e), and January 2019 (c and f). Scale bar (applies to all photos) = 5cm

Table S1 Sampling effort and coral measurements.

Month/Year	N colonies	Mean propagules per polyp /SD	Mean colony Diameter/SD (mm)	Mean Polyp Diameter/SD (mm)	Mean Polyp Volume/SD (mm^3)	Photographic Sample
Jan/18	5	0	23.7 ± 2.1	8.4 ± 1.3	566.3 ± 220.6	Fenda/Gruta
Feb/18	3	143.8 ± 56.1	46.6 ± 6.6	10.3 ± 1.1	773.5 ± 257.2	-
Mar/18	5	193.2 ± 68.2	49.3 ± 12.2	11.4 ± 1	1517.9 ± 535.9	Fenda/Gruta
Apr/18	5	162.5 ± 139	40.8 ± 7.9	10.1 ± 1.7	1142 ± 772.3	-
May/18	-	-	-	-	-	Fenda/Gruta
Jul/18	5	122.1 ± 76.6	24.1 ± 1.8	8.9 ± 1.1	852.1 ± 335.4	-
Aug/18	5	44.1 ± 56.3	29.3 ± 10.2	8.4 ± 0.8	543.5 ± 115	Fenda
Sep/18	5	500.2 ± 205.2	51.7 ± 7.4	11.9 ± 1.1	2153 ± 616.4	-
Oct/18	5	191.8 ± 229.3	43.8 ± 17.3	11.6 ± 2.1	1911.5 ± 1481	-
Nov/18	5	263.2 ± 102.3	44.2 ± 6.9	11.6 ± 1.1	1873.3 ± 481.8	-
Jan/19	5	39.8 ± 42.5	42.8 ± 7.4	9.9 ± 0.6	947.5 ± 268.2	Fenda/Gruta
Feb/19	5	37.6 ± 26.8	42.1 ± 8.9	10.2 ± 0.9	967.9 ± 265.4	-
Apr/19	5	219 ± 69.9	48.9 ± 4.3	11 ± 0.7	1445.9 ± 357.6	-
Jun/19	5	78.6 ± 47.7	36.5 ± 7.7	9.1± 0.9	800.4 ± 219	Fenda/Gruta

CAPÍTULO 2 - A tool for a war against time: dispersal simulation to support ongoing monitoring program of the invasive coral *Tubastraea coccinea*

(Artigo a ser submetido na revista Marine Pollution Bulletin e formatado conforme suas normas)

A tool for a war against time: dispersal simulation to support ongoing monitoring program of the invasive coral *Tubastraea coccinea*

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Abstract

Preventing, detecting, and monitoring invasive marine species is a big challenge as it is not possible to visualize all invasion extensions. Their early detection may be the only chance to achieve eradication. The Indo-pacific scleractinian coral *Tubastraea coccinea* invasion in the Atlantic dates from early 1940. Since then, disruptive populations were found along ~8.000 km of west Atlantic, and in the Canarian Islands of Spain (east Atlantic), mostly associated with the oil and gas industry. Their impacts have been noticed from endemic species to ecosystems. In Brazil, initiatives to control *Tubastraea* spp. have been done mostly by local environmental managers and researchers, but recently a National Plan for Prevention, Control and Monitoring (NPPCM) for *Tubastraea* spp. was approved. We applied an Individual-based Model within the invasion history of *Tubastraea*

coccinea in its southern distribution limit in the Atlantic, on the shores of the key Arvoredo Biological Marine Reserve. We indicated hotspots for the occurrence of new emerging invasion sites in the region and expect that ongoing monitoring programs early detect it. The model is easily replicated and might be a valuable tool for decision makers.

Key-words: *Tubastraea* – larval dispersion - Management - Prevention - Invasion - Conservation

Introduction

Invasive species impact the environment at all levels (species to ecosystems), and consequently human health, economics, and culture (1,2). It is estimated that its impacts already cost almost 1.3 trillion dollars in the world, between 1970 to 2017 (3). Furthermore, projections pointed out that the number of non-native species will increase 36% until 2050 (4). Therefore, invasive species must be a major concern for effective conservation (5).

Prevention is the only way to avoid invasive species impacts and when it fails, early detection and rapid response might be the last chance to achieve eradication - especially in the marine realm (6,7). The management of marine invasive species is extremely challenging mainly because you cannot see the real extension of the invasion. Control efforts are also logistically complicated by the requirement of favorable oceanographic conditions to scuba divers as well as limited time to work underwater. Traditional control methods, such as chemicals and biological control, are often limited by rapid dilution of water and the impossibility to closely monitor host specificity, respectively (6,7). Because of these obstacles, only a few attempts successfully eradicated marine invaders, and all of them were early detected populations occupying small areas (e.g. *Caulerpa taxifolia* in California; *Mitylopsis sallei* in Austrália; and *Unidaria pinnatifida* in New Zealand, 7). Managers also had enough financial and human resources, and knowledge about target species biology.

Scientists have been looking for solutions to increase early detection of invasive species (8). In marine ecosystems, citizen-science has been contributing with success in monitoring and controlling lionfish *Pterois volitans* in the Caribbean (9). There are also technological initiatives disposing settlement plates for biofouling in harbors areas and analyzing it with DNA metabarcoding (8). Correlative niche models can be applied to predict species invasion potential (10), and are constantly evolving to be more realistic, such as mechanistic models that incorpore physiological traits of species (11). However, decision makers managing invasive marine species are in a constant war against time and must act as fast as possible, like in oil spills. Individual-based models (IBM) have been applied in several ways (Tang & Bennett 2010), to predict oil spill (12), the dispersion of commercial marine organisms such as cod eggs (13), and also predict invasive aquatic species dispersal (14), but anyhow, as far as we know, IBM has not been much applied with marine invasive species.

Popularly known as “sun corals” - because their tentacles are flashy orange/red/yellow - *Tubastraea* spp. are native from the Indian and Pacific oceans and their introduction in shallow reef systems in the Atlantic Ocean is highly associated with the oil and gas industry (15). Nowadays they can be found in east Atlantic on the Canary Islands and along ~8.500 km of the west Atlantic Ocean - from Georgia state, in the United States of America, passing through the Gulf of México and Caribbean (where they were first notice), and in almost all the Brazilian coastline - (for detailed invasion pathways in the world please see Creed et al. 2017a). *Tubastraea* spp. impacts are noticed from species to ecosystems (16–19), and Brazil probably is the most affected country. Because of that, a National Plan for Prevention, Control and Monitoring (NPPCM) for *Tubastraea* spp. was published by the Ministry of Environment in 2018 (MMA 2018), but initiatives to control *Tubastraea* spp. have been done mostly by local managers and researchers (20). Control efforts results are undermined by sun coral's high regeneration capacity after manual removal (the most used and accessible method (21,22). Although it is not the ideal method to achieve eradication, it successfully contains invasive populations within colonies of restricted sizes, slowing down the invasion expansion and allowing native ecosystems recovery (22–24).

We used an IBM to simulate local spread of the invasive coral *Tubastraea coccinea* in its southern Atlantic limit of distribution, in a key Marine Reserve. We expect to support ongoing management programs in defining priority areas for the early detection of emerging invasions sites, contributing also with NPPCM for *Tubastraea* spp goals. We also investigated possible scenarios of the invasion origin and discussed the threat of oil and gas industry expansion in the region.

Material and methods

Study system

Our study was conducted in the southwest Atlantic Ocean along the coastline of Santa Catarina state, Brazil (Figure 1a). In this region there is the Arvoredo Biological Marine Reserve (Rebio Arvoredo), a no-take and no-entry protected area (176 km²) comprising an archipelago formed by three islands (Arvoredo, Deserta, and Galé) surrounded by rocky shores (Figure 1b). Seasonality is well defined with hot and nutrient poor waters in summer and cold and nutrient rich waters in winter (temperatures range from ~15 to 29 ºC) (25). These conditions make Rebio Arvoredo a transitional area between tropical and temperate fauna for benthic species and it has a crucial biological and social role in the region (25). This area is also the southern distribution limit of *T. coccinea* in the Atlantic Ocean. Sun coral was first registered on the rocky shores of Arvoredo island in 2012, by recreational divers in a site known as Engenho (Figure 1b, for a detailed invasion chronology history please see Crivellaro et al. 2021). Nowadays, as far as we know, sun corals are still restricted to the Rebio Arvoredo area with sparse invasion patches around Arvoredo island and in a shipwreck in front of Galé island.

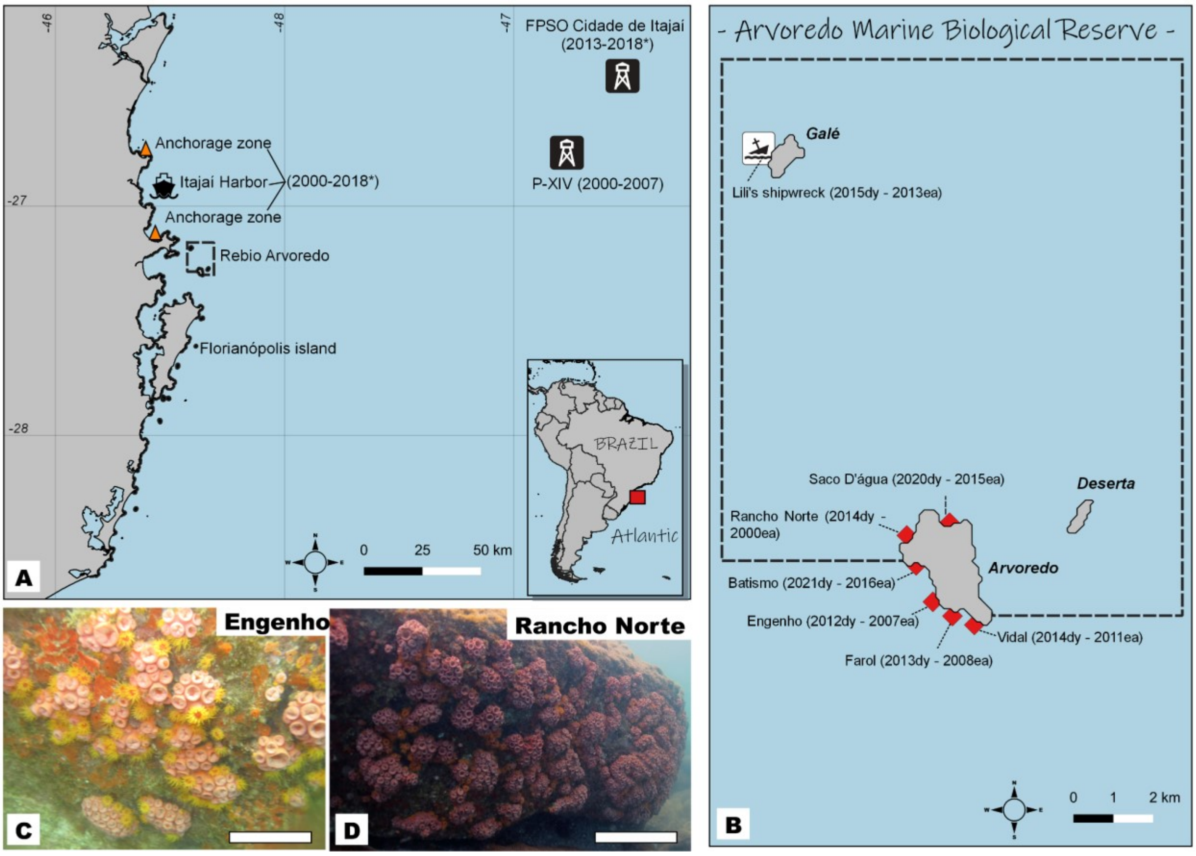

Figure 1 Map of the study area showing discovery year (dy) and the estimated arrival date (ea) of *Tubastraea coccinea* records, and also potential invasion source areas (A). The dotted line represents the limits of Rebio Arvoredo (A, B). Engenho was the first discovered site (C, scale bar ~ 10 cm), but Rancho Norte certainly represents the initial invasion site in the region (D, scale bar ~ 30 cm). 2018* = available data.

Although the first record on Rebio Arvoredo rocky shores was only in 2012, sun corals certainly arrived in the region earlier. The invasion is probably associated with the P-XIV oil platform as genetic studies found the same clones in the populations of P-XIV and Rebio Arvoredo (26), and sun corals were casually noticed in a research about the P-XIV fish community in 2000 (27). It could not be doubted that larvae drift directly from offshore to the rocky shores as larvae can stay viable for three months (in laboratory) (28). In addition, in 2013, FPSO Cidade de Itajaí also started to operate in the region and could be also a source of larvae.

We cannot discard the possibility of encrusted fishery vessels as a vector to the Rebio Arvoredo invasion. But its most probable invasion pathway is the use of Itajaí's harbor as logistical support to the oil industry. Itajaí harbor is ~50 km distant from Rebio Arvoredo and many vessels awaiting dockage use mostly two anchorage zones in the surroundings of the harbor. Environmental Agents already caught illegal dock cleaning in one of these areas, but it did not know if it was contaminated by sun corals (Adriana Carvalhal pers. comm.) Therefore, these areas represent a great risk to be a source of *T. coccinea* and other marine invasive species.

A three year (2013-2016) project named Environmental Monitoring of Rebio Arvoredo and surroundings (in Portuguese, MAArE) contributed to the discovery of most of the invasion sites in the region (25). The MAArE project monitored several sites, including the anchorage zone near Itajaí's harbor. However, since MAArE ends (2016) none monitoring activity occurred out of Rebio Arvoredo Islands and less sites inside the marine reserve are monitored either. Resources are limited and managers must prioritize activities to remove corals over monitoring.

Biophysical model

We simulated a *T. coccinea* larvae dispersal using the Phyton-based framework OpenDrift, an open software package for modelling the trajectories of objects (Lagrangian Elements) drifting in the ocean (29). We used daily means water velocity data from the global ocean reanalysis model GLORYS12V1 produced by the CMEMS Global Monitoring and Forecasting Centre (for detailed information https://resources.marine.copernicus.eu/product-detail/GLOBAL_MULTIYEAR_PHY_001_030/INFORMATION). Data were available from 1993 to 2018 on a regular grid (approximatively 8km).

We tried to bring realistic to the model being as simple as possible within the known biological information about *T. coccinea* and considering computer processing capability restrictions. We described our decisions in setting/producing (or not including) parameters in the following topics. The steps to build our simulations are available online (https://github.com/davivc/labar-coral-sol).

Classification of available rocky shores for settlement:

T. coccinea is an ahermatypic coral that requires a consolidated substrate to settle. They do not show preference for substratum type (30), but are mostly seen in calm waters of sheltered coves (31). We mapped rocky shores and classified them in relation to their wave exposure: Sheltered, when facing to west and protected from frontal east swell; and the ones not protected, Exposed. We outline and classify the rocky shores using Google Earth images in QGIS 3.12 (QGIS Development Team). We exported this layer as a shapefile and incorporate this information in the model. When drifted larvae interacts with Sheltered rocky shores it settles with success, and when it interacts with the Exposed ones, it deactivated.

Larvae speed:

Sun coral planulae swim actively in laboratory (28) but there is no information regarding its speeds. Coral larvae are poor swimmers and there are many complex variables that can influence larvae trajectories (e.g. wind, waves, tidal, reef complexity) (32,33) Hata et al. 2017 indicate that horizontal water currents are 1-4 higher in magnitude than the velocity of larvae. After some tests -- and as it was important for our purposes to retain larvae into our study domain -- we set larvae to dislocated with 25% of the water current velocity.

Larvae release starting period:

To set the date each site starts to seed, we estimated the arrival date of each invasion site assessing the number of polyps of the biggest colonies removed when each site was first discovered and controlled (Figure 1b, described in Crivellaro et al. 2021). As *T. coccinea* estimates to add 8 polyps/year (34), when a site had removed colonies of class V (40< polyps) we determine that it estimated arrival date (ea in Figure 1b) is five years older than the discovery year (dy, Figure 1b, Engenho, Farol, Saco d’água, and Batismo), class IV (21-40) three years older than dy (Vidal), class III (11-20) two years older than dy (Galé) (Table 1). We must make an exception regarding the Rancho Norte invasion site. This site was discovered only in 2014 but its density and size of the colonies clearly indicate that invasion in Rebio Arvoredo started there (Figure 1c,d). At least 75 colonies with more than 40 polyps were removed in the first control action in Rancho Norte while in other sites there were only 3 removed colonies with this same size. In this way, we determined Rancho Norte starts to seed in 2000, which is the year that *T. coccinea* was first reported in the P-XIV platform (27). We set the anchorage zone seed from 2000 until 2018 (last available data when we run the model), P-XIV from 2000 until 2007, and FPSO Cidade de Itajaí between 2013 and 2018.

Table 1 Date each site was first discovered and its estimated arrival date according to the size of removed colonies in the first control action (described in Crivellaro et al. 2021). *We starte

Site	**Discovery year**	**Number of polyps of the biggests colonies removed in first control action**	**Estimated arrival date**
Rancho Norte	2014	75 colonies with 40< polyps	2000
Engenho	2012	3 colonies with 40< polyps	2007
Farol	2013	3 colonies with 40< polyps	2008
Vidal	2014	22 colonies with 21 - 40 polyps	2011
Galé	2015	2 colonies with 11-20 polyps	2013
Saco d'água	2020	3 colonies with 40< polyps	2015
Batismo	2021	2 colonies with 40< polyps	2016

Larvae release quantity and frequency:

Tubastraea coccinea larvae release peaks normally occur during summer but they reproduce continuously (28,35), and we already observed recruits in the field in several periods along the year. Their reproductive potential is also impressive - ~1.500 larvae were released by one colony in just one day (28), and ~800 embryos were found in just one polyp (22). In addition, extrapolations with sun coral coverage in Rancho Norte estimated that this site may potentially produce 80 thousand propagules (22). Although there is considerable information regarding *Tubastraea* spp. reproduction, as water velocity data are daily means, incorporating real reproductive numbers would only overload computational processing capability. In this way, each simulation scenario we set just enough larvae to represent water current variability.

Dispersal simulations:

Our simulations had two main goals: (1) indicate where the most likely places are for the expansion of the invader in the region after almost 20 years of invasion; and (2) to speculate about possible invasion origins pathway. Therefore, we run our simulations separating our data into two sets:

Simulation 1: dispersal from known invaded sites on Rebio Arvoredo

We simulated *T. coccinea* larvae dispersal from the seven known invaded sites on Rebio Arvoredo, starting by each site's estimated arrival date (Figure 1b, Table 1). To simulate the dispersal within different ocean currents and to not discard any scenario, we separated our simulations by seasons. Also, we defined each site to seed one larva per hour.

Simulation 2: dispersal from oil platforms, Itajaí harbor and its anchorage areas

Although sun coral was never reported in Itajaí harbor and surrounds, its use as logistical support to the oil and gas industry might be an invasion pathway. We simulated *T. coccinea* larvae dispersal from the oil platforms P-XIV (2000-2007) and FPSO Cidade de Itajaí (2013-2018), and from three points that supporting vessels use to anchorage near Itajaí Harbor (2000-2018) (Figure 1a). As we used a larger domain in this simulation, we set each site's seed larvae every six hours and partitioned the model runs by year.

Simulation output:

Finally, after we set the domain, time period of each model run, and larvae velocity, number, and sources we are able to run the model. The model result displays the path and destination of larvae. If larvae status is “settled” it means it interacted with our Sheltered rocky shore layer, if the status is “died” it interacted with an Exposed rocky shore or land. There is also “missing” status when it went outside our study area and status “active” when it stills dispersing. Each time we executed the model we exported a csv file within this status. We merge the data in just one csv file and perform a kernel density map (0.1 º radius) using the accumulation of “settled” larvae within all data periods (2000-2018). We used QGIS software to produce maps and Rstudio to manipulate csv files.

Results

Simulation 1: dispersal from known invaded sites on Rebio Arvoredo

Our simulations results indicate the places that are most probable to occur new invasion populations of *T. coccinea,* after almost 20 years of invasion (Figure 2). Summer is the most probable scenario according to the known reproductive information of *T. coccinea.* However, in all scenarios most larvae settled on Rebio Arvoredo rocky shores and in the northeast portion of Santa Catarina island. The most remarkable differences between scenarios are that summer’s scenario larvae settled in the entire Santa Catarina island and in some sites ~100 km far south, and autumn’ scenario that larvae dispersed north in the surroundings of Itajaí Harbor and its anchorage zone. The northeast portion of Santa Catarina island was never monitored, either in MAArE project. This area poses the greatest risk of finding an emerging *T. coccinea* population and must be first prioritized in next monitoring activities.

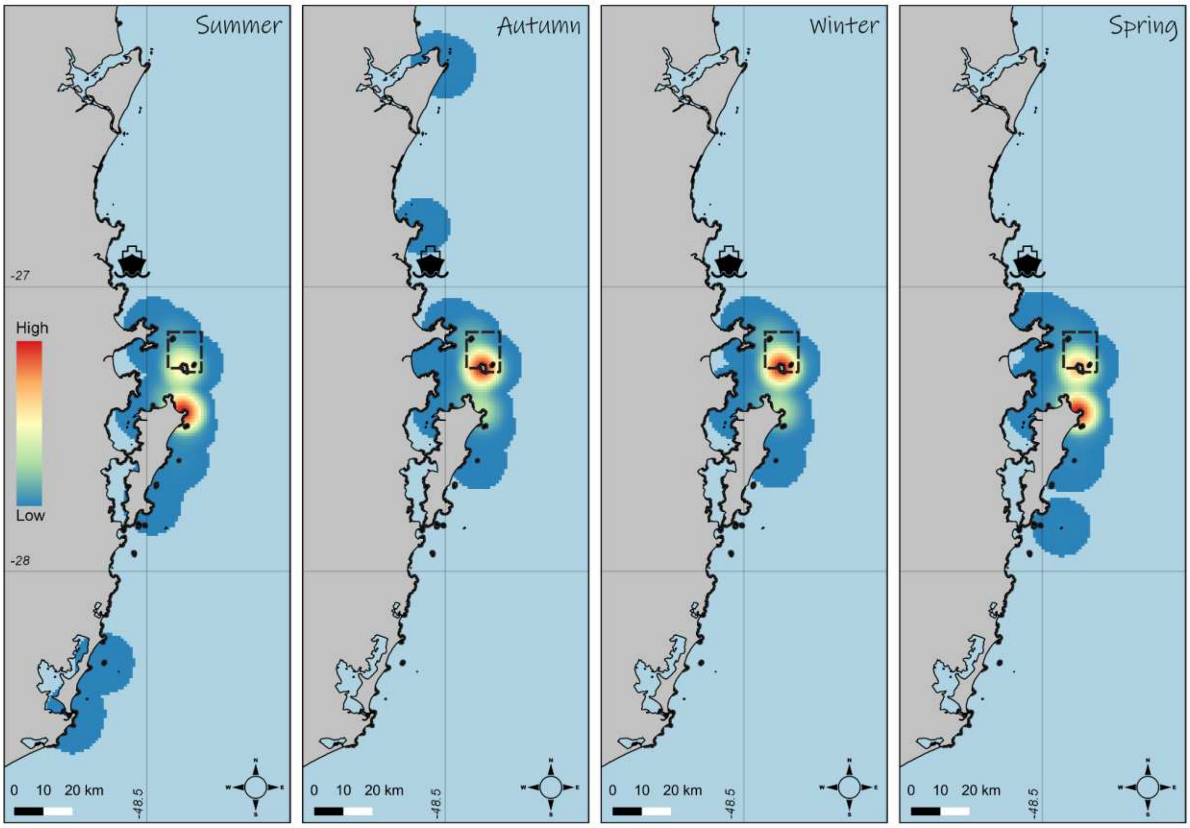

Figure 2 Kernel density showing hotspots of the accumulation of settled larvae each season from 2000 to 2018. Seed sources were the known invaded sites on Rebio Arvoredo. Gradient bar: High (red) = between 7,700 and 12,400 accumulated larvae; Low (dark blue) = between 1 and 1,100 accumulated larvae.

Simulation 2: dispersal from oil platforms, Itajaí harbor and its anchorage areas

Our simulations results indicated that oil platforms P-XIV and FPSO Cidade de Itajaí were not a source of larvae to Rebio Arvoredo rocky shores (Figure 3a). Itajaí harbor and its anchorage areas could be an invasion pathway (Figure 3b). Managers must prioritize monitoring these areas. If sun coral is found in these areas it increases the risk of the invasion spreading throughout the north of Santa Catarina state, and some islands of Paraná and São Paulo states.

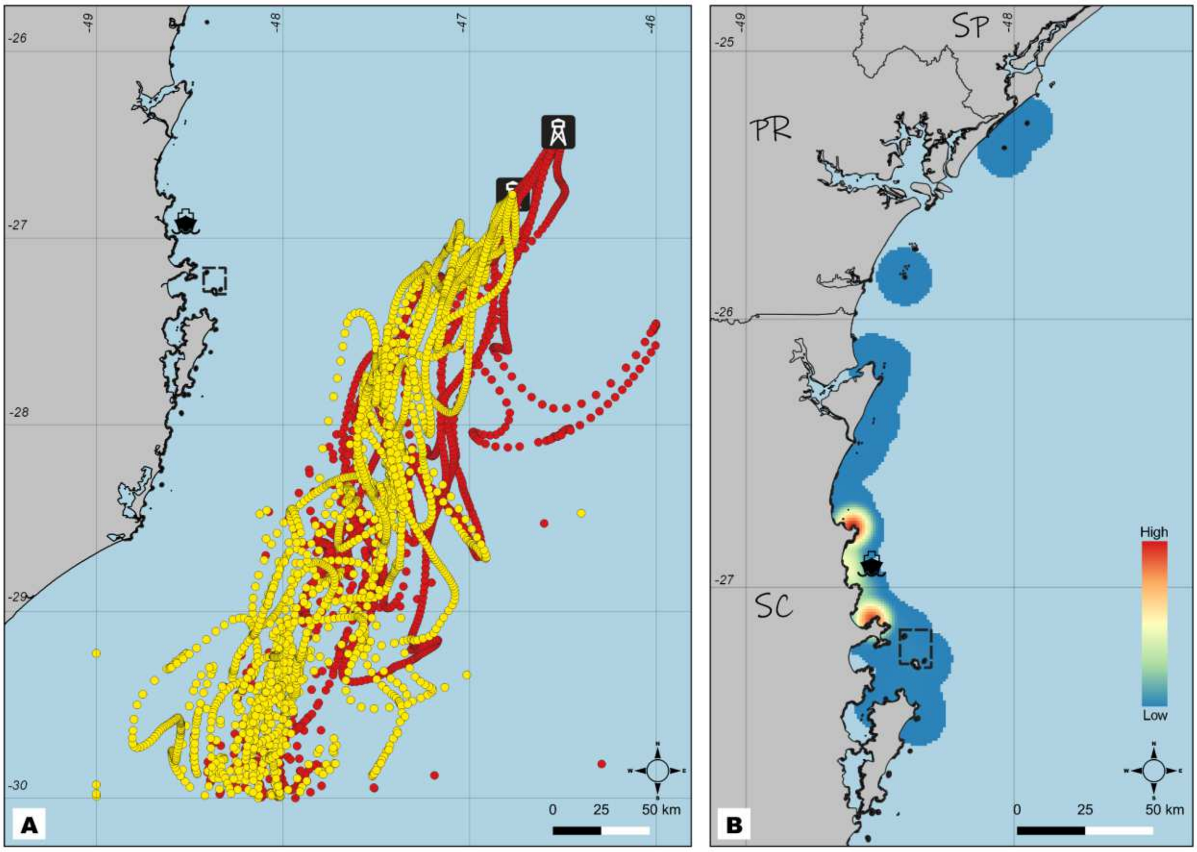

Figure 3 Larvae drift simulations from *oil platforms, Itajaí harbor and its anchorage area.* (A); Larvae dispersed from P-XIV oil platform (yellow circles), and from FPSO Cidade de Itajaí (red circles).(B); Kernel density showing hotspots of the accumulation of settled larvae from 2000 to 2018. Seed sources were the three anchor areas near Itajaí Harbor that supporting vessels use. SC: Santa Catarina; SP: São Paulo; PR: Paraná; Gradient bar: High (red) = more than 15,500 accumulated larvae; Low (dark blue) = between 1 and 2,100 accumulated larvae.

Discussion

Our simulations using individual based modelling consisted in a promising methodology to support the current monitoring program of *T. coccinea* in a key marine reserve in southern Atlantic distribution. In broad view, our method orientates best practices in defining priority areas for monitoring activities, which can improve prevention strategies and help to early detect small and isolated populations. These results are also in accordance with the goals of the National Plan for Prevention, Control and Monitoring for *Tubastraea* spp.. We encourage local environmental managers to apply our approach in other invaded locations, and with other species. We hope that our work will help local managers early detect marine invasive species, enabling the eradication of emerging invasive populations.

Bioclimatic niche models predicted that the entire Brazilian coastline has suitable conditions for *Tubastraea* spp. survival (36,37). In a local scale, Couto et al. (2021) analyzed the risk of invasion in Marine Protected Areas (MPA) of Rio de Janeiro state considering its distance from oil platforms and other potential source areas (38). The authors also measured the length of rocky shores in each MPA, highlighting our concern in consider available substrate for sun coral recruitment. One of our main concerns was to simulate realistic scenarios being as simple as possible. However, simulations could be improved in several ways, including other oceanographic (in situ) and biological data, and detailed information regarding potential vector traffic in the region. Future studies could also improve the model by evolving it to a forecast app, making it even more accessible allowing people within a minimum programming skill to replicate it. Our results can also improve other prevention methodologies. For example, settlement plates for eDNA analysis could be positioned in the most likely places for *Tubastraea* spp. dispersal.

Despite *Tubastraea* spp. larvae can be alive for a long time (~90 days in laboratory), they usually settle fast (1-10 days) in a gregarious behaviour (28,39). At Ilha Grande bay, in Rio de Janeiro state, and where *Tubastraea* spp. invasion probably started in the Brazilian coast, in 11 years sun corals expanded their range and abundance in ~2.1 km per year (31). Also in Rio de Janeiro state, on Cabo Frio, larvae seems to not be carried very great distances (40). Water currents on Rebio Arvoredo surrounds have a predominately southward flow that is strongly correlated with wind and local geological morphology, making the northern region of Santa Catarina island the main recipient of Rebio waters (41), and apparently also for *T. coccinea* larvae. Coral larvae are considered poor swimmers and recent data indicate that their ability to navigate between reefs is limited (32). Reefs systems may be self-seeding (42), and it is estimated that only 1% of larvae survive the recruitment process (43). During our simulations none of the drifted larvae from offshore oil platforms reached the coastline, but the traffic of potentially contaminated structures in Itajaí's harbor area is a constant threat and the most probable invasion pathway. *Tubastraea coccinea* known populations in our study area is still restricted to Arvoredo island and Galé shipwreck. However, it has been almost 30 years of oil industry operation in our study region, and we estimated that *T. coccinea* invasion on Rebio rocky shores may have started 20 years ago. According to the key invasion ecology concept of propagule pressure, the more a species is introduced into a location more populations will get established (44). There is an urgent need to improve monitoring activities.

Although larvae concentrated in the surroundings of Rebio Arvoredo it still represents a large area for monitoring with the current infrastructure and resources. In addition, current Brazilian Federal Government has been increasingly restricting resources for Environmental Agencies and conservation purposes. They actually have plans to sink 1200 artificial structures along the Brazilian coast to create reefs and promote tourism yet scientists warn that this will probably spread sun corals even more (45). Monitoring activities occur mostly only if there is time after the control activity ends, and around known invasion patches in Rebio Arvoredo islands. Activities normally are composed by only two pairs of scuba divers in two 50 minutes dives. Decision makers must prioritize monitoring the northern part of Santa Catarina Island and Itajaí's harbor surroundings. If there are no sources of larvae in these areas - and also in moving vectors - it may indicate that Rebio Arvoredo can be an isolated "closed" population, which increases eradication probability as its area might not be recolonized by outside sources (6). The engagement of society might be the solution to overcome resource restrictions and monitor a larger area. Citizen-science had success and detected 39 new records of *Tubastraea* spp. in Rio de Janeiro, a highly contaminated area (46). Engenho and Batismo sites on Rebio Arvoredo were also detected and informed to managers by recreational divers, but there is margin to improve the relationship with diving schools and tourists.

Frequently noticed by the media, the state of Santa Catarina is in a 30 year judicial battle in the Supreme Court with the state of Paraná because of the payments of royalties from the oil exploration of P-XIV and FPSO Cidade de Itajaí. Royalties were irregularly paid to Paraná and now Santa Catarina state claims a ~100 million dollars refund. Most of the region of our study area have oil fields that are Available in Permanent offer (Figure 4, data from National Agency of Oil and Gas), and some of the blocks are just ~50km away from Rebio Arvoredo. It is unquestionable the economic contribution of the oil and gas industry for Brazil’s development. However, the imminent expansion of this industry, and the decommissioning of many old platforms, represents a major threat to the conservation of natural ecosystems and the oil and gas industry must look for improving its prevention strategies.

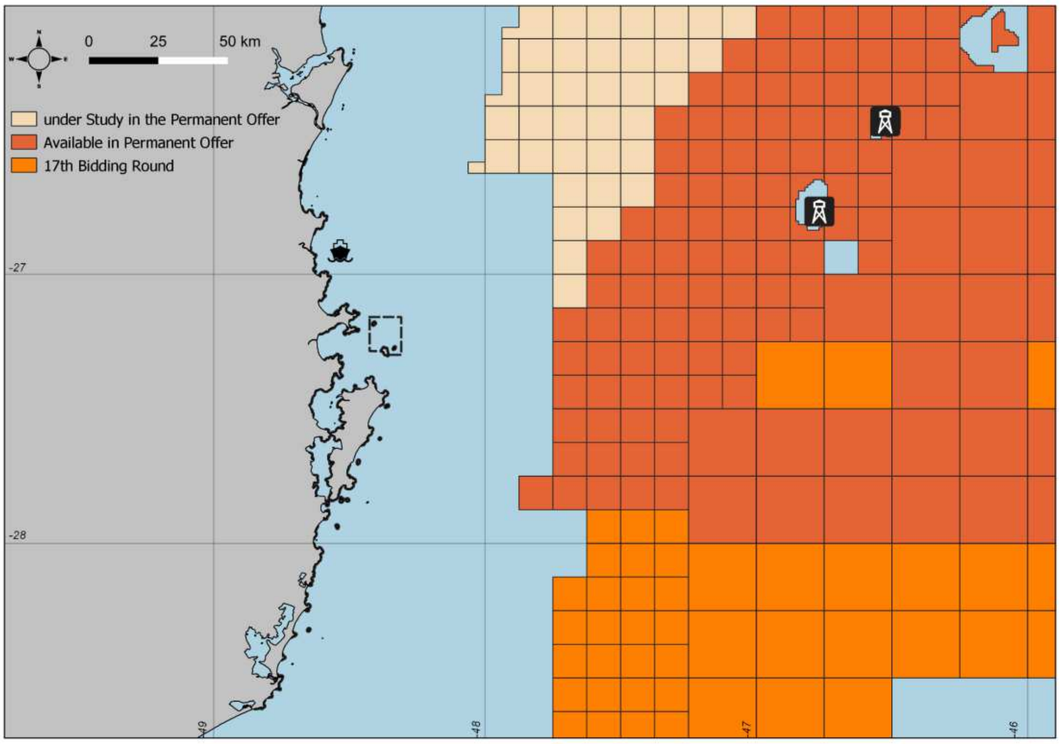

Figure 4 Oil fields with different sales status representing the imminent expansion of the oil and gas industry in our study area.

Early detection of marine invasive species might be the only chance to achieve eradication. The few attempts that successfully eradicated marine invasive species early detected the invader when they were restricted to small areas (6,7,47). Control activities performed on Rebio Arvoredo slowed down sun coral local spread by restricting colonies in small sizes and consequently reducing population reproductive potential (22). In its southern distribution limit on the Atlantic, *Tubastraea coccinea* known population is still restricted to Arvoredo island and Galé shipwreck, and it may be an isolated “closed” population. Rebio Arvoredo must be a prioritized area by NPPCM for *Tubastraea* spp. However, as time goes by, propagule pressure and the probability of *Tubastraea coccinea* gets new established populations increases. Our results indicated places that were never monitored before and must be prioritized in future monitoring activities. Our work provides a framework to support local managers monitoring programs to improve early detection of marine invasive species, in a war against time.

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CONCLUSÃO GERAL

Os resultados expostos na presente tese são fruto da grande parceria entre os gestores ambientais do ICMBio e o grupo de pesquisa do LABAR Coral-sol, da UFSC. Os nossos resultados já estão sendo utilizados, pelos gestores da Rebio Arvoredo, no planejamento das atividades de controle e monitoramento. Os nossos resultados também contribuem com os objetivos do Plano Nacional de Prevenção, Controle e Monitoramento do coral-sol (MMA 2018). Além disso, nosso modelo de dispersão de larvas é altamente dinâmico e pode ser facilmente aplicado para qualquer espécie e localidade, podendo ser uma ferramenta valiosa para tomadores de decisão.

Até o momento, os focos conhecidos de coral-sol em Santa Catarina continuam restritos à área da Rebio Arvoredo, espalhados principalmente pela ilha do Arvoredo, e em um naufrágio na ilha da Galé. Os esforços para controlar o coral invasor assim que ele foi descoberto foram (e continuam sendo) cruciais para frear a expansão da invasão na região. Apesar da remoção manual não ser eficiente o suficiente para se atingir a erradicação, o método restringe o tamanho das colônias, diminuindo consideravelmente o potencial reprodutivo da população e consequentemente sua disseminação. A busca por novas técnicas de controle é urgente.

A partir dos dados obtidos nos estudos aqui apresentados, é possível aprimorar a efetividade das ações de manejo, controle e monitoramento. Com base nos resultados sobre a biologia reprodutiva e mudanças na estrutura populacional do invasor após o impacto da ação de remoção, sugerimos que as atividades devem ocorrer principalmente antes do verão – que é o pico de liberação de larvas - e pelo menos a cada 6 meses, impedindo que as colônias regenerantes (e recrutas) não alcancem grandes tamanhos, mas permitindo que acresçam esqueleto o suficiente para serem removidas efetivamente, e não apenas “raspadas” (CRIVELLARO et al., 2021).

Com base nos nossos modelos de dispersão, alertamos para o iminente risco da invasão se espalhar para áreas não monitoradas, principalmente no norte da ilha de Santa Catarina e no entorno do porto de Itajaí (Capítulo 2 - CRIVELLARO et al., in prep.). Dessa forma, a Rebio Arvoredo e seu entorno devem ser consideradas áreas prioritárias para os programas de monitoramento e tentativas de erradicação de focos emergentes. Sua ocorrência ainda restrita à área da reserva aumenta muito as chances de erradicação. Medidas preventivas em relação ao tráfego de embarcações oriundas de áreas contaminadas são extremamente cruciais para o manejo da invasão do coral-sol.

Por fim, reforçamos Oigman-Pszczol e colaboradores (2017), de que o combate a invasão do coral-sol não é uma causa perdida!