Antonella Carolina Almeida Saá

# DESVENDANDO INTERAÇÕES: A TEMPERATURA E A COMPETIÇÃO COM ESPECIES NATIVAS, PODEM AFETAR O RENDIMENTO DO INVASOR CORAL SOL *Tubastraea coccinea* (Lesson 1829)?

Dissertação submetida ao Programa de Pós-Graduação em Oceanografia da Universidade Federal de Santa Catarina para a obtenção do Grau de Mestre em Oceanografia.
Orientador: Prof. Dr. Paulo Antunes Horta Jr.
Co-orientadora: Prof$^{a}$. Dr$^{a.}$ Nadine Schubert
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Florianópolis
2019

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Almeida Saa, Antonella C.
DESVENDANDO INTERAÇÕES: A TEMPERATURA E A COMPETIÇÃO COM ESPECIES NATIVAS, PODEM AFETAR O RENDIMENTO DO INVASOR CORAL SOL *Tubastraea coccinea* (Lesson 1829)?/ Antonella C. Almeida Saa; orientador, Paulo Horta, coorientadora, Nadine Schubert, 2019.
99 p.

Dissertação (mestrado) - Universidade Federal de Santa Catarina, Centro de Ciências Físicas e Matemáticas, Programa de Pós-Graduação em Oceanografia, Florianópolis, 2019.

Inclui referências.

1. Oceanografia. 2. Espécies Invasoras. 3.Metabolismo. 4. Tolerância térmica. I. Horta, Paulo. II. Schubert, Nadine. III. Universidade Federal de Santa Catarina. Programa de Pós-Graduação em Oceanografia. IV. Título.

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Esta Dissertação foi julgada adequada para obtenção do Título de Mestre e aprovada em sua forma final pelo Programa de Oceanografia.

Florianópolis, 28 de março de 2019.

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Aos forasteiros que lutam dia a dia para
sobreviver em terras e águas estrangeiras.

# AGRADECIMENTOS

Este trabalho não teria sido possível sem a ajuda da equipe “coral sol” da UFSC: o Marcelo, a Bruna e a Grazielle. Obrigada pela paciência, as ideias e as longas jornadas compartilhadas no mesocosmos. Ao Lucas Battaglin que deu uma força também na manutenção do set-up e ajudou na coleta dos bichos.

A Reserva Biológica do Arvoredo (ReBio) e ao Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), especialmente a Adriana Carvalhal Fonseca pelo apoio no campo.

Ao EPAGRI pelos dados de temperatura e irradiância.

A Professora Bárbara Segal e o Thiago Cesar Lima Silveira, pelas ideias e contribuições para o trabalho.

Ao técnico Paulo Manso pelo apoio no sistema de mesocosmos, e ao Vini, a Fernanda, a Jaqueline, o Tiziano e o Hetor, que ajudaram na manutenção do mesmo.

Ao Walter Rich pelas correções de inglês para o artigo.

Ao projeto PELD-ILOC, pela bolsa e ao FINEP/Rede CLIMA pelo financiamento para a realização da pesquisa.

Aos professores do programa de pós-graduação de Oceanografia da UFSC.

Aos membros do Laboratório de ficologia, tanto professores quanto alunos, obrigada pela paciência para me ensinar como usar e como não usar cada coisa dentro do laboratório. Ao Secretario da botânica, o Fernando, pelas milhões de folhas impressas, incluso esta dissertação.

Aos professores Leo e Zé, por acompanhar meu progresso, e aceitar ser membros suplentes da banca.

Ao meu orientador o professor Paulo Horta, por estar sempre disposto a me escutar, pela boa energia e pela perspectiva que tem sobre a ciência e o mundo, pelas ideias que foram importantes para o desenvolvimento deste trabalho, e por me ajudar a conseguir a bolsa e ajudar com as embarcações para os campos.

A minha co-orientadora/orientadora: Nadine Schubert por me guiar em cada passo deste mestrado, pelas contribuições acadêmicas, por me ensinar a ser cientista, mas também pela amizade, pela atenção e paciência que teve com todas as minhas inseguranças e, sobretudo, pelo apoio e incentivo nos momentos mais difíceis durante este período. Obrigada por me ensinar tanto!.

Às amizades da turma e do caminho: A Gabi ,o Junior, a Dani, a Ruth, a Marduck, à bruxinha Fanny, a Mirta, ao Vicente e a Pris por me acolher nos primeiros dias em Florianópolis, por me ajudar com os documentos de ingresso e me motivar.

Al Manuel, mi compañerito de maestría y del camino, gracias por toda la paciencia, el cariño y el aguante. Por todas las conversaciones sobre nuestros proyectos de tesis y de la vida, durante, lunas, salidas de campo, sushis y vinos. Siempre ahí, enseñándome, aprendiendo, inspirándome y queriéndome 11.

A la familia del Manu, que fue una familia para mi acá en Brasil, Gracias a Georgina y Néstor por adoptarme y por la paciencia que tuvieron y tienen conmigo.

A minha família e amigos por acreditar em mim.

Aos bichinhos que ajudaram pra eu não pirar durante o mestrado: o bru, o peri, lola, sancho, huaynita y sobretodo a lupi miau.

I left my soul there, down by the sea
I lost control here, living free”
Moorcheba

# RESUMO

O impacto das espécies invasoras vem aumentando nas últimas décadas devido à globalização, ameaçando a biodiversidade marinha. *Tubastraea* spp. (coral sol) têm se espalhado pelo mundo, mostrando um rápido aumento na abundância e/ou na ocupação espacial e efeitos adversos nos ecossistemas receptores em algumas regiões. Especialmente no Brasil eles se tornaram grandes invasores, estendendo-se descontinuamente por mais de 3000 km ao longo da costa brasileira. No entanto, apesar do aumento nos esforços de pesquisa sobre ecologia/biologia do coral sol na última década, informações sobre a tolerância ambiental e as interações com espécies nativas ainda são escassas. Neste contexto, a temperatura pode ser um fator importante, pois afeta fortemente as interações entre as espécies, principalmente através de sua influência na fisiologia do organismo. Assim, no presente estudo, nós avaliamos os efeitos da temperatura sobre o invasor *T. coccinea* e o zoantídeo nativo *Palythoa caribaeorum*, bem como suas interações, através de um experimento de mesocosmos de três semanas, expondo às espécies (individualmente e juntas) a uma faixa de temperatura de 16 a 31°C. Sendo acompanhado pela medição das principais características fisiológicas (metabolismo, crescimento, taxas de alimentação, comportamento competitivo) que fundamentam o desempenho das espécies e, portanto, a força competitiva. Os resultados mostraram que na Ilha do Arvoredo, Brasil, sendo o limite de distribuição sul de ambas as espécies, (1) *P. caribaeorum* exibiu uma maior tolerância térmica que *T. coccinea*, (2) os ataques físicos de *T. coccinea* não afetaram ao *P. caribaeorum,* mas os custos metabólicos no coral sol aumentaram, enquanto desencadeou um crescimento no zoantídeo levando ao eventual “Overgrowth” do coral do sol, e (3) que a temperatura interagiu sinergicamente com a presença do competidor em ambas as espécies em seu limite superior térmico (31°C). Nossos resultados sugerem que a invasão bem-sucedida de *T. coccinea* está associada principalmente a características de história de vida-*r*, e não à força competitiva ou à tolerância ambiental e, portanto, algumas comunidades que abrigam competidores nativos específicos podem ser mais resistentes à invasão do coral sol.

**Palavras-chave**: Espécies invasoras. Metabolismo. Interações competitivas. *Palythoa caribaeorum*. Tolerância térmica. *Tubastraea coccinea*.

# ABSTRACT

The impact of invasive species has been increasing in recent decades due to globalization, threatening marine biodiversity. *Tubastraea* spp. (sun coral) have been spreading worldwide, showing rapid increases in abundance and/or spatial occupancy and adverse effects on recipient ecosystems in some regions. Especially in Brazil they have become major invaders, extending discontinuously for more than 3000 km along the Brazilian coast. Yet, despite increased research efforts on sun coral ecology/biology over the last decade, information about the species' environmental tolerance and interactions with native species is still scarce. In this context, environmental temperature may be an important driver, as it strongly affects species interactions, primarily through its influence on organismal physiology. Thus, in the present study we assessed the effects of temperature on the invasive *T. coccinea* and the native zoanthid *Palythoa caribaeorum*, as well as their interactions, via a three-week mesocosm experiment, exposing the species (individually and grafted together) to a temperature range of 16-31ºC. This was accompanied by measuring key physiological traits (metabolism, growth, feeding rates, competitive behavior) that underlie species performance, and hence, competitive strength. The results showed that at Arvoredo Island, Brazil, currently the southern distribution limit of both species, (1) *P. caribaeorum* exhibited a wider thermal tolerance than *T. coccinea*, (2) *T. coccinea*'s physical attacks did not affect *P. caribaeorum*, but induced increased metabolic costs in the former, while triggering increased growth in the latter, leading to eventual overgrowth of the sun coral, and (3) that temperature interacted synergistically with the presence of the competitor in both species at their upper thermal limit (31ºC). These findings suggest that *T. coccinea*'s successful invasion is mainly associated with *r*-selected life history traits, rather than competitive strength or environmental tolerance, and thus, some communities harboring specific native competitors may be more resistant to sun coral invasion.

**Keywords**: Invasive species, Metabolism, *Palythoa caribaeorum*, species interactions, thermal tolerance, *Tubastraea coccinea*

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## SUMÁRIO

# 1. INTRODUÇÃO

As espécies invasoras são consideradas a maior ameaça á biodiversidade marinha do mundo porque podem alterar as funções dos ecossistemas e a composição das comunidades, causando problemas ecológicos e econômicos (e.g., GROSHOLZ, 2002; BAX et al., 2003), impactos que têm sido aumentados nos últimos anos devido á globalização, comercio e turismo (Carlton, 2009; Hewitt et al., 2009). O sucesso das espécies invasoras em se estabelecer e se espalhar depende de vários fatores, e tem muita controvérsia sobre quais deles são os mais importantes. Geralmente, assume-se que o sucesso na invasão está negativamente correlacionado com a diversidade das espécies nativas, já que a diversidade fortaleça as interações entre espécies e consequentemente crie uma resistência biótica, através do uso de recursos (ex. diminui o espaço disponível) ou aumente a probabilidade da presença de um competidor dominante, mesmo que isso pareça ser depende da escala (STACHOWICZ et al., 1999, 2002; LEVINE, 2000; BYERS E NOONBURG, 2003; KIMBRO et al., 2013). Por exemplo, em escalas pequenas, sugere-se que fatores abióticos, a presença de competidores específicos ou a disponibilidade de recursos exibem uma influência maior do que a diversidade nativa em resistir às invasões (STACHOWICZ E BYRNES, 2006; DUNSTAN E JOHNSON, 2007). Portanto, o sucesso ou fracasso das invasões biológicas depende das interações entre espécies invasoras e as características biológicas e físicas do ambiente receptor, potencializando o sucesso quando o rendimento dos competidores é ameaçado e potencializando o fracasso quando o desempenho da espécie invasora é afetado negativamente (LEJEUSNE et al., 2014; KENWORTHY et al. 2018). O sucesso das espécies invasoras tem sido amplamente estudado (ver Bruno et al., 2005; KIMBRO et al., 2013; PAPACOSTAS et al., 2017), porém poucos estudos têm integrado estas interações com variáveis abióticas (KORDAS et al., 2011; BURNSIDE et al., 2014; KELLEY, 2014). Assim, informações sobre os efeitos abióticos versus bióticos no sucesso da invasão ainda são escassos. Entre os fatores abióticos, a temperatura tem mostrado de alterar os resultados das interações competitivas, pois afeta diretamente a fisiologia dos indivíduos e por tanto, o seu rendimento, incluindo a capacidade de se defender e de ministrar recursos (ver KORDAS et al., 2011; REUMAN et al., 2014). Tais casos foram documentados, por exemplo, em corais escleractíneos, onde o resultado competitivo variou com a temperatura, sugerindo também potenciais mudanças sazonais (COPE, 1981; JOHNSTON et al., 1981; LOGAN, 1984; CHORNESKY, 1989; FINE E LOYA, 2003). Por outro lado, estar em competição pode afetar a tolerância das espécies às mudanças ambientais e/ou sua aptidão, já que as interações estão geralmente associadas a custos metabólicos, implicando o redirecionamento de energia para mecanismos competitivos e deixando de lado outras demandas, como crescimento, reprodução e a tolerância ao estresse, conforme reportado para diferentes organismos recifais (RINKEVICH E LOYA, 1985; ROMANO, 1990; TANNER, 1995, 1997; LEONG E PAWLIK, 2010).

O coral sol pertence aos corais não-simbióticos escleractíneos do gênero *Tubastraea*. Estes corais originários do Indo-Pacifico, são considerados cosmopolitas, sendo amplamente distribuídos pelo mundo, com registro no Caribe, Asia, Africa, Australasia, Pacifico, Norte América, América central, América do sul e o Golfo de México (CREED et al., 2017a). Apesar de não ser considerado invasor em todas essas regiões, recebeu o status de "invasor" na base de dados "Global Invasive Species Database" (www.iucngisd.org/gisd/search.php) por seu rápido aumento na abundância e pelos efeitos adversos em alguns ecossistemas receptores (como no Golfo do México e Brasil). Pouca o nenhuma informação esta disponível sobre a origem desta espécie, mas devido a sua natureza invasora, o esforço de pesquisa por estudar sua biologia e ecologia tem aumentado, especialmente no Golfo do México e ao longo da costa brasileira. No México, foi descrita em 2011 (FENNER, 2001), onde foi registrada predominantemente em substratos artificiais, como plataformas de petróleo e navios naufragados. Nos ambientes naturais de recifes foi observada em baixa abundância e restrita a habitats críticos, tendo aparentemente pouco efeito nas comunidades nativas (SAMMARCO et al., 2014, 2015), embora estudos de laboratório e de campo tenham mostrado efeitos adversos em algumas espécies (HENNESSEY E SAMMARCO, 2014; SAMMARCO et al., 2015). Em contraste, no Brasil (primeiro registro no final dos anos 80) *T. coccinea* tornou-se um invasor prejudicial para os ecossistemas com uma extensão descontínua de mais de 3.000 km ao longo da costa brasileira (revisado em CREED et al., 2017a) sendo reportados efeitos negativos nas espécies e comunidades nativas (por exemplo, CREED, 2006; LAGES et al., 2011; MANTELATTO, 2012; SANTOS et al., 2013; MIZRAHI et al., 2017; SILVA et al., 2017; MIRANDA et al., 2018a, b), justificando a fundação do “Projeto Sol-Coral” para controle e manejo da invasão (CREED et al., 2017b).

O estabelecimento e disseminação de *T. coccinea* ao longo da costa brasileira e a ameaça associada às comunidades locais e serviços ecossistêmicos relacionados resultaram no aumento dos esforços de pesquisa e manejo dessa espécie no Brasil na última década, contribuindo para o conhecimento atual sobre aspectos relacionados à biologia, ecologia e invasão de *T. coccínea*. Compreensivelmente assim, os estudos têm sido focados no monitoramento da abundância e disseminação das espécies ao longo da costa brasileira (revisado em SILVA et al., 2014; BATISTA et al., 2017; CREED et al., 2017a), bem como alguns aspectos biológicos (ou seja, crescimento, reprodução; CAPEL et al. 2014; DE PAULA et al., 2014; MIZRAHI et al., 2014a, b; CAPEL et al., 2017) e ecológicos (ou seja, preferências de substrato, efeitos sobre composição da comunidade local e biodiversidade, CREED E DE PAULA 2007, LAGES et al., 2011, MANGELLI E CREED, 2012, MIZRAHI et al., 2014b, ARAUJO, 2016, MIZRAHI et al., 2017, MIRANDA et al, 2018a). No entanto, até agora, a tolerância ambiental da espécie tem sido pouco explorada como um potencial mecanismo para explicar o sucesso de sua invasão biológica (MIZRAHI, 2008; BATISTA et al., 2017; LUZ et al., 2018). Além disso, ainda se sabe pouco sobre a interação de *T. coccínea* com espécies nativas, porém, seu impacto negativo sobre o coral escleractíneo endêmico *Mussismilia hispida* está bem documentado (CREED, 2006; DE PAULA, 2007; LAGES et al., 2012; SANTOS et al., 2013). Esse resultado competitivo tem sido relacionado aos ataques físicos por *T. coccínea*, empregando filamentos mesentéricos, um mecanismo comum e agressivo encontrado nos corais escleractíneos (LANG E CHORNESKY, 1990), e ataques químicos (LAGES et al., 2012; Santos et al., 2013). No entanto, apesar de ter sucesso em algumas interações competitivas, descobriu-se também que *T. coccínea* pode perder ou não induzir nenhuma resposta quando competindo com outros organismos de recife (Fig. 1; Table A1) . Nesse contexto, recentes observações de campo sugerem que o coral sol pode ter um efeito adverso, induzindo necrose no tecido do zoantídeo *P. caribaeorum* Duchassaing & Michelotti, 1860, uma espécie bentônica dominante ao longo da costa brasileira (Fig. 2) levantando a questão sobre uma potencial substituição deste zoantídeo pelo invasor *T. coccínea* (LUZ E KITAHARA, 2017).

*Palythoa caribaeorum* é conhecido como um competidor agressivo, que usa o sobrecrecimento como a principal estratégia de competição (SUCHANEK E GREEN, 1981) sendo bem-sucedido na maioria de interações competitivas (Fig.1; Table A1). Além disso, contra outras espécies invasoras no Brasil, como os corais moles e bivalves, o zoantídeo mostrou uma forte resistência biótica (MENDONÇA-NETO E DA GAMA, 2009; MANTELATTO et al., 2018). Devido a sua ampla distribuição latitudinal ao longo da costa brasileira, muitas vezes co-ocorre com *T. coccínea* (Fig. 2), mas até agora não tem estudos detalhados sobre suas interações competitivas e os efeitos ambientais que podem ter sobre eles. Por conseguinte, no presente estudo, nós apontamos a estimar as interações competitivas e o resultado entre *T. coccínea* e o nativo zoantídeo *P. caribaeorum,* os custos metabólicos, bem como os efeitos que a temperatura exerce sobre o desempenho das espécies e suas interações, em um experimento de mesocosmos de três semanas.

Utilizamos uma abordagem experimental, pois isso permitiu avaliar a importância de diferentes fatores nas interações bióticas, devido ao maior controle sobre as condições ambientais e descrições mais precisas do comportamento competitivo do que possível durante os tempos limitados de mergulho. Além da coleta de dados observacionais sobre as interações entre as duas espécies, determinaram-se os efeitos dessas interações e da temperatura no desempenho fisiológico das espécies, monitorando a atividade de pólipos de *T. coccínea* e desempenho dos simbiontes de *P. caribaeorum,* assim como as taxas de alimentação ao longo do experimento e as taxas metabólicas, calcificação e/ou taxas de crescimento. Esta abordagem fisiológica permitiu definir a faixa de tolerância térmica e plasticidade da espécie, bem como avaliar os custos metabólicos das interações competitivas, o que tem implicações na aptidão da espécie em longo prazo (abundância, distribuição). Além disso, usamos observações de campo sobre as interações das espécies para corroborar nossos resultados experimentais.

# 2. OBJETIVOS

## 1.1 Objetivo geral

Investigar os efeitos da temperatura e da interação com o zoantídeo nativo *Palythoa caribaeorum* no rendimento do coral invasor *Tubastraea coccinea.*

## 1.2 Objetivos específicos

- Avaliar e comparar as respostas fisiológicas de *Tubastraea coccinea* e de *Palythoa caribaeorum* expostos a diferentes temperaturas.
    - Determinar as taxas de respiração e calcificação do coral sol (*Tubastraea coccínea)*
    - Determinar as taxas fotossintéticas e de respiração do zoantídeo *Palythoa caribaeorum*
    - Comparar a tolerância térmica das duas espécies.

- Caracterizar as interações entre as duas espécies a diferentes temperaturas.
    - Identificar os mecanismos de interação das duas espécies
    - Avaliar os efeitos da presença de *P. caribaeorum* no rendimento do coral sol em diferentes temperaturas.
    - Avaliar os efeitos da presença do coral sol no rendimento de *P. caribaeorum* em diferentes temperaturas.

- Estimar os custos metabólicos das interações competitivas nas duas espécies

# 3. HIPOTESES

$H0_1$: A variação da temperatura não terá efeitos no rendimento do coral sol

$H0_2$: O coral sol e o zoantídeo não apresentam interações competitivas

$H0_3$: A presença do zoantídeo/Coral sol não vai ter efeito no rendimento da outra espécie.

$H0_4$: A interação não será afetada pela temperatura

# 4. CAPITULO 1: ARTIGO

## UNRAVELING INTERACTIONS: DO TEMPERATURE AND COMPETITION WITH NATIVE SPECIES AFFECT THE PERFORMANCE OF THE NON-INDIGENOUS SUN CORAL, *TUBASTRAEA COCCINEA* LESSON 1829?

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### Abstract

The impact of invasive species has been increasing in recent decades due to globalization, threatening marine biodiversity. *Tubastraea* spp. (sun coral) have been spreading worldwide, showing rapid increases in abundance and/or spatial occupancy and adverse effects on recipient ecosystems in some regions. Especially in Brazil they have become major invaders, extending discontinuously for more than 3000 km along the Brazilian coast. Yet, despite increased research efforts on sun coral ecology/biology over the last decade, information about the species' environmental tolerance and interactions with native species is still scarce. In this context, environmental temperature may be an important driver, as it strongly affects species interactions, primarily through its influence on organismal physiology. Thus, in the present study we assessed the effects of temperature on the invasive *T. coccinea* and the native zoanthid *Palythoa caribaeorum,* as well as their interactions, via a three-week mesocosm experiment, exposing the species (individually and grafted together) to a temperature range of 16-31ºC. This was accompanied by measuring key physiological traits (metabolism, growth, feeding rates, competitive behavior) that underlie species performance, and hence, competitive strength. The results showed that at Arvoredo Island, Brazil, currently the southern distribution limit of both species, (1) *P. caribaeorum* exhibited a wider thermal tolerance than *T. coccinea*, (2) *T. coccinea*’s physical attacks did not affect *P. caribaeorum*, but induced increased metabolic costs in the former, while triggering increased growth in the latter, leading to eventual overgrowth of the sun coral, and (3) that temperature interacted synergistically with the presence of the competitor in both species at their upper thermal limit (31ºC). These findings suggest that *T. coccinea*’s successful invasion is mainly associated with *r*-selected life history traits, rather than competitive strength or environmental tolerance, and thus, some communities harboring specific native competitors may be more resistant to sun coral invasion.

**Keywords**: invasive species, metabolism, *Palythoa*, species interactions, thermal tolerance, *Tubastraea.*

## 1. **Introduction**

Marine invasive species are a major threat to biodiversity worldwide, altering ecosystem function and community composition and hence, causing ecological and economic problems (e.g., GROSHOLZ, 2002; BAX et al., 2003), impacts that are increasing in recent years due to the globalization of the world’s economies, trade and tourism (CARLTON, 2009; HEWITT et al., 2009). The success of invasive species in establishing and spreading depends on several factors and there is much controversy about which factors are more important. Generally, it is assumed that invasion success is negatively correlated with native species diversity, since increasing biodiversity strengthens species interactions and hence, biotic resistance, through complementary use of resources (i.e., decrease of available space) or increased probability of the presence of a dominant competitor, even though this seems to be scale-dependent (e.g., STACHOWICZ et al., 1999, 2002; LEVINE, 2000; BYERS and NOONBURG, 2003; KIMBRO et al., 2013). For example, at small scales, abiotic factors, the presence of specific competitors or resource availability have been suggested to exhibit a greater influence than native diversity in resisting invasions (STACHOWICZ and BYRNES, 2006; Dunstan and Johnson, 2007). Thus, complex interactions between the invading species and the biological, as well as physical characteristics of the recipient environment are involved in the establishment and spread of invasive species. Abiotic conditions can booster bioinvasions by reducing the performance of native competitors, but can also weaken them when the performance of the invasive species is negatively affected (e.g., LEJEUSNE et al., 2014; KENWORTHY et al., 2018).

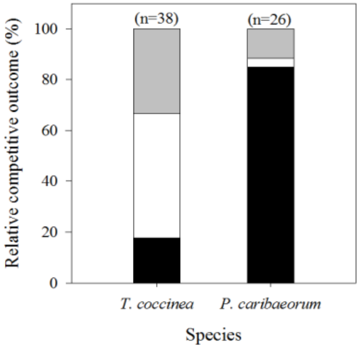
While the significant effects of biotic interactions on the success of marine invasive species have been widely studied (see Bruno et al., 2005; KIMBRO et al., 2013; PAPACOSTAS et al., 2017), few studies have integrated these interactions with abiotic variables (e.g., KORDAS et al., 2011; BURNSIDE et al., 2014; KELLEY, 2014). Thus, our understanding of the relative importance of abiotic versus biotic effects on invasion success is still quite lacking. Among abiotic factors, temperature has been shown to alter the outcomes of competitive interactions, as it directly affects the physiology of individuals and hence, their performance, including their ability to defend themselves and to exploit or provide resources (see KORDAS et al., 2011; REUMAN et al., 2014). Such cases have been documented for example in scleractinian corals, where the competitive outcome was shown to vary with temperature, suggesting also potential seasonal changes (COPE, 1981; JOHNSTON et al., 1981; LOGAN, 1984; CHORNESKY, 1989; FINE and LOYA, 2003). On the other hand, biological interactions can affect the species' tolerance to environmental changes and/or their fitness, as they are usually associated with metabolic costs, implying re-allocation of energy towards competitive mechanisms and away from other traits, e.g., growth, reproduction and stress tolerance, as reported for different reef organisms (RINKEVICH and LOYA, 1985; ROMANO, 1990; TANNER, 1995, 1997; LEONG and PAWLIK, 2010).

The sun coral *Tubastraea coccinea*, a non-symbiotic scleractinian, has been recorded in many regions worldwide, such as Caribbean, Asia, Africa, Australasia, Pacific, North America, Central America, South America and Gulf of Mexico (reviewed in CREED et al., 2017a). Even though not considered as invasive in all of these regions, its rapid increases in abundance and/or spatial occupancy, with adverse effects on recipient ecosystems (i.e., Gulf of Mexico, Brazil), earned it the "invasive" status in the Global Invasive Species Database (www.iucngisd.org/gisd/search.php).

Little to none information is available on this species from its native area, but due to its invasive nature, research efforts to study the biology and ecology of this species have been increasing, especially in the Gulf of Mexico and along the Brazilian coast. In the former, where it was first recorded in 2001 (FENNER, 2001), this species has been found to occur predominantly on artificial substrates, such as oil platforms and ship wrecks. Here, it has been reported in low abundances and restricted mostly to cryptic habitats in the natural reef environments, thus having seemingly little effect on native communities (SAMMARCO et al., 2014, 2015), though laboratory and field studies have shown adverse effects on some native species (HENNESSEY and SAMMARCO, 2014; SAMMARCO et al., 2015). In contrast, in Brazil (first record in the late 1980s) *T. coccinea* has become a major harmful invader, with a current discontinuous extension of more than 3000 km along the Brazilian coast (reviewed in CREED et al., 2017a) and reported negative effects on native species and communities (e.g., CREED, 2006; LAGES et al., 2011; MANTELATTO, 2012; SANTOS et al., 2013; MIZRAHI et al., 2017; SILVA et al., 2017; MIRANDA et al., 2018a, b), warranting the foundation of the "Sun-Coral Project" for control and management of the invasion (CREED et al., 2017b).

The establishment and spread of *T. coccinea* along the Brazilian coast and the associated threat to local communities and related ecosystem services have resulted in increased research and management efforts on this species in Brazil over the last decade, contributing greatly to our current knowledge on many aspects related to the biology, ecology and the invasive process of this species. Understandably, studies have been focused on monitoring the abundance and spread of the specie's along the Brazilian coast (reviewed in SILVA et al., 2014; BATISTA et al., 2017; CREED et al., 2017a), as well as on some of its biological (i.e., growth, reproduction; CAPEL et al., 2014; DE PAULA et al., 2014; MIZRAHI et al., 2014a, b; CAPEL et al., 2017) and ecological aspects (i.e., substrate preferences, effects on local community composition and biodiversity; CREED and DE PAULA, 2007; LAGES et al., 2011; MANGELLI and CREED, 2012; MIZRAHI et al., 2014b; ARAUJO, 2016; MIZRAHI et al., 2017; MIRANDA et al., 2018a). However, so far the specie's environmental tolerance has been little explored as a potential mechanism explaining its invasive success (MIZRAHI, 2008; BATISTA et al., 2017; LUZ et al., 2018). Also, little is still known about the interaction of *T. coccinea* with native species, though, its negative impact on the endemic scleractinian coral *Mussismilia hispida* is well documented (CREED, 2006; DE PAULA, 2007; LAGES et al., 2012; SANTOS et al., 2013). This competitive outcome has been related to physical attacks by *T. coccinea*, employing mesenterial filaments, a common aggressive mechanism found in scleractinian corals (LANG and CHORNESKY, 1990), and chemical warfare (LAGES et al., 2012; SANTOS et al., 2013). Yet, despite coming out as winner in some competitive interactions, *T. coccinea* has also been found to lose against a wide array of reef organisms or to show and induce no response when competing with others (Fig. 1; Table A1). In this context, recent field observations suggest that the sun coral may also have an adverse effect, by inducing tissue necrosis, on the zoanthid *Palythoa caribaeorum* DUCHASSAING & MICHELOTTI, 1860, a dominant benthic species along the South Atlantic coast (Fig. 2), raising the question about a potential replacement of this wide-distributed zoanthid by the invasive *T. coccinea* (LUZ and KITAHARA, 2017).

**Figure 1**. Overview of reported outcomes of *T. coccinea* and *P. caribaeorum* when competing with other species (black- wins, white- no response in either competitor, grey- loses). Numbers in parentheses indicate number of species with which interaction were documented (see Table in Appendix A for detailed information**).**



Source: See Table in Appendix A for references.

*Palythoa caribaeorum* is known as a strong competitor, using overgrowth as main competitive strategy (SUCHANEK and GREEN,

1981) and coming out as winner in most competitive interactions (Fig. 1; Table A1). Also, against other invasive species, such as soft corals and bivalves, the zoanthid has been shown to offer strong biotic resistance (MENDONÇA-NETO and DA GAMA, 2009; MANTELATTO et al., 2018). Due to its wide latitudinal distribution along the Brazilian coast, it often co-occurs with *T. coccinea* (Fig. 2), but so far no detailed study has been performed about their competitive interactions and potential outcome or the effect environmental factors may have on those.

Thus, in the present study we aimed to assess the competitive interactions and outcome between *T. coccinea* and the native zoanthid *P. caribaeorum*, the associated metabolic costs, as well as the effects temperature exerts over species' performance and their interactions in a three-week mesocosm experiment. We used an experimental approach, as this allowed assessing the importance of different factors in the biotic interactions due to greater control over environmental conditions, more frequent data collection, and more precise descriptions of the competitive behavior than is possible during limited dive times. Besides observational data collection on the interactions between the two species, the effects of these interactions and temperature had on each species' physiological performance was determined, by monitoring polyp activity and symbiont performance of *T. coccinea* and *P. caribaeorum*, respectively, as well as measuring feeding rates, metabolic rates, and calcification and/or growth rates throughout the experiment. This physiological approach allowed defining each species' thermal tolerance range and plasticity, as well as assessing the metabolic costs of the competitive interactions, which has implications on each species' fitness in the long-term (fitness, abundance, distribution). In addition, we used field observations of species interactions to corroborate our experimental findings.

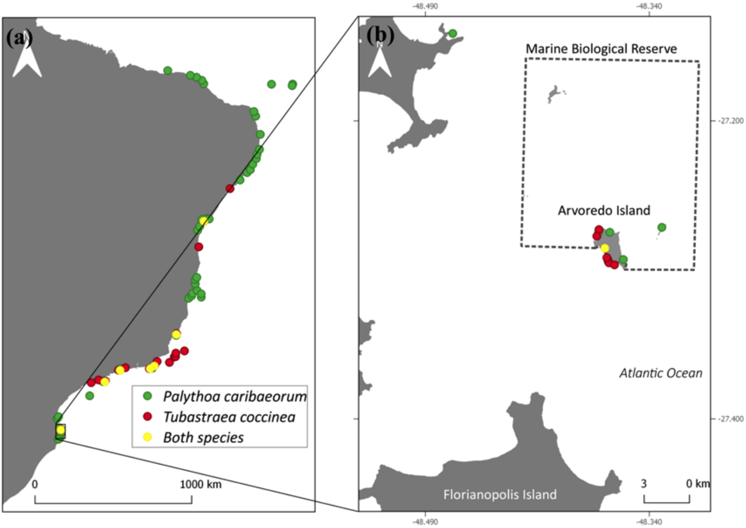
## 2. Materials and methods

### *2.1 Sampling site, collection and maintenance*

The Marine Biological Reserve of Arvoredo (ReBio), located approximately 11 km north of the Santa Catarina Island, South Brazil, represents the current southern distribution limit of the sun coral *Tubastraea coccinea* and the zoanthid *Palythoa caribaeorum* (Fig. 2;

CREED et al., 2017a; DURANTE et al., 2018). The invasive sun coral was recorded here for the first time in 2012 (CAPEL, 2012) and afterwards, several more isolated foci have been registered in the area (MAArE, 2017).

**Figure 2** Occurrence of *T. coccinea* and/or *P. caribaeorum* (a) along the Brazilian coast and (b) in the Marine Biological Reserve of Arvoredo

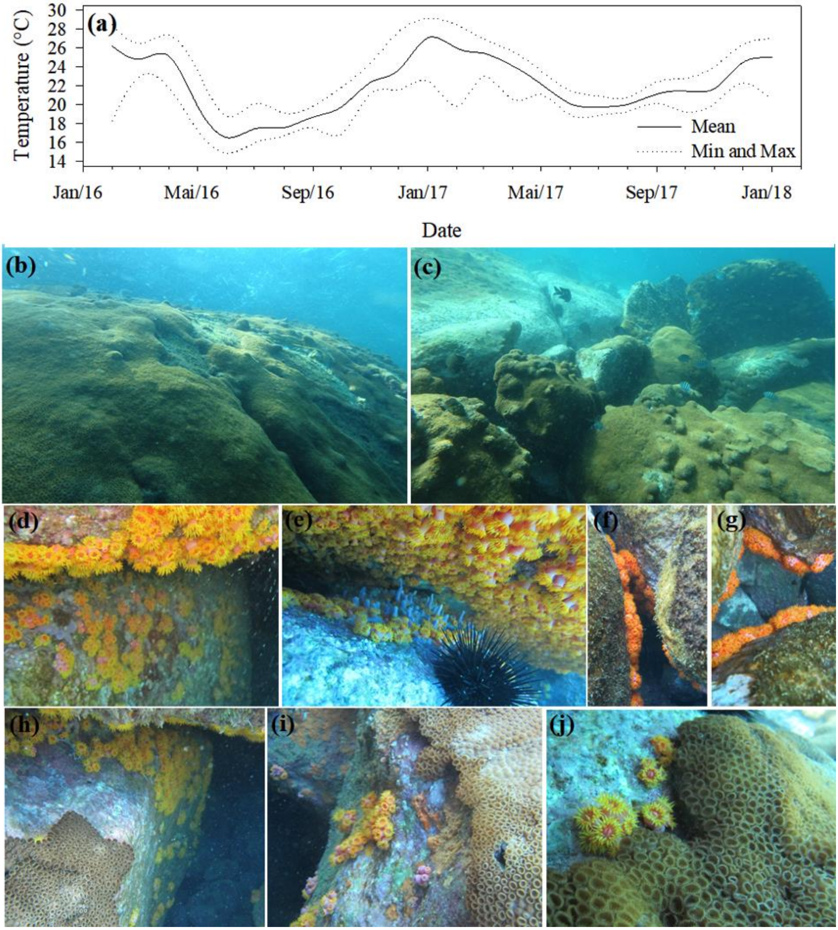


Source: Map elaborated by the author (2019), according to (Oliveira, 2014; Creed et al., 2017a; Durante et al., 2018).

The region exhibits two seasonal patterns, related to the dynamic of water masses: (a) spring/summer, with high stratification in the water column, phenomena of upwelling and subsidence, and a maximum seawater temperature recorded at the sampling site (~5 m depth) of ~29°C; and (b) autumn/winter, with a homogenous water column, advection of sub-Antarctic waters, and minimum water temperatures of 15-16°C (Fig. 3a; SARTI AND SEGAL, 2018). The light availability also varies seasonally, with depths of the euphotic zone ranging from 10-60 m in summer, corresponding to a $K_d$ of 0.08-0.46 $m^{-1}$, and 10-30 m in winter ($K_d$=0.16-0.46 $m^{-1}$) (MAArE, 2017).

Samples were collected at Arvoredo Island (Rancho Norte; 27.27°S 48.37°W), where the sheet-like *P. caribaeorum* covers extended areas of the rocky substrate (mean cover of 23% at Rancho Norte; Oliveira, 2014), while *T. coccinea* is found in caves, crevices and on vertical walls (Fig. 3b-j). For the experiment, 60 colonies of *T. coccinea* (~20 polyps per colony) and 60 pieces of *P. caribaeorum* were collected in March 2018 (late austral summer) by SCUBA diving at 5-7 m depth, using hammer and chisel. From large *P. caribaeorum* mats, single samples were obtained by separating pieces of marginal lobes of the colonies and dividing them into smaller pieces (~8-12 cm2). After collection, the samples were maintained in coolers with aeration and transported to the mesocosm facility at the Federal University of Santa Catarina (UFSC). To recover from handling and to pre-acclimate to the tank conditions, the samples of both species were maintained separately in a closed, temperature-controlled mesocosm system under natural light conditions (adjusted to light levels at collection depth, ~30% of incident light) for a two-week period at 22°C (temperature measured at collection site during sampling). Afterwards, the temperature was gradually increased or decreased (0.5°C per day) in a staggered manner, until reaching the intended target temperature at the same time, which was when the experiment was started.

**Figure 3** Arvoredo Island (Rancho Norte). (a) Seawater mean, maximum and minimum temperature variation 2016-2018. (b, c) Rocky shores are dominated by *P. caribaeorum*, while *T. coccinea* is found in caves, crevices and vertical walls (d-g), and both species are found in direct contact at the entry of the caves or crevices (h-j).



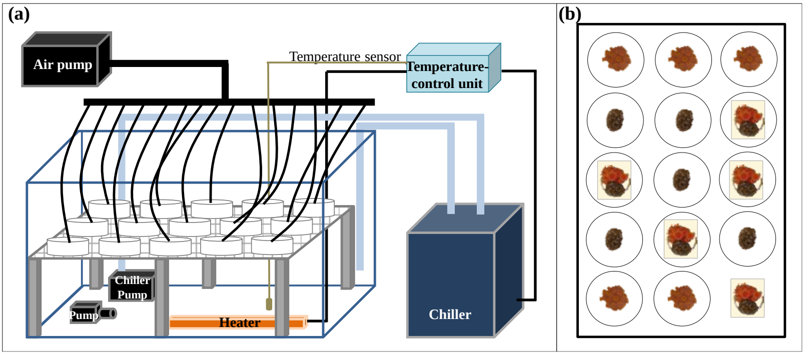
Source:(a) SARTI and SEGAL (2018) (b-j) photography by the author (2019)

### *2.2 Experimental set-up*

The experimental set-up consisted of six large tanks, filled with freshwater, that were used as water baths for smaller containers holding the samples (n=15 per tank). Each of the tanks represented a temperature treatment (16, 19, 22, 25, 28, 31°C) (Fig. 4a). A custom made temperature-control unit, connected to a chiller and an aquarium heater (300-500 W) was connected to each large tank, to maintain a constant temperature. For each temperature condition, five containers (V=400 mL each) per species, maintained individually, and another five containers with both species grafted together, were used (Fig. 4b). For the latter, individual colonies of *T. coccinea* were fixed with epoxy on PVC sheets and a fragment of *P. caribaeorum* was fastened securely on the sheet with a cut off semi-circle of a small PVC pipe, ensuring an interface of at least 2-3 cm of linear contact between the two species. Each small container was set-up with aeration, provided by an air pump that was connected to the tanks by PVC tubes, ending in a valve, to which a multi hose connector was attached, allowing for aeration to each individual container by small hoses (Fig. 4a). The organisms were fed every two days with newly hatched nauplii larvae of brine shrimp (*Artemia*). The brine shrimps remained in the containers with the samples overnight, to ensure both species had eaten their fill, and the next day the water was exchanged.

During the three-week experiment, the performance of *P. caribaeorum* and *T. coccinea* was monitored daily by chlorophyll *a* fluorescence measurements and every two days by determining polyp activity during feeding, respectively. Potential species interactions were monitored visually every day and documented photographically. In addition, feeding rates of both species were determined once a week during the experiment and at the beginning and the end of the experiment, incubations of *T. coccinea*, to measure respiratory and calcification rates, and of *P. caribaeorum*, for photosynthesis and respiration measurements, were performed for every temperature treatment, as well as for the samples that had been in contact with the other species. After the incubations, the samples of *P. caribaeorum* were flash-frozen in liquid nitrogen and stored at -80°C for subsequent determination of symbiont density and pigment concentration.

**Figure 4** Scheme of the experimental mesocosm set-up. (a) Experimental unit for one temperature treatment and (b) top view of the tank, showing the samples in their individual containers



Source: Elaborated by the author (2019)

### *2.3 Polyp activity of* T. coccinea

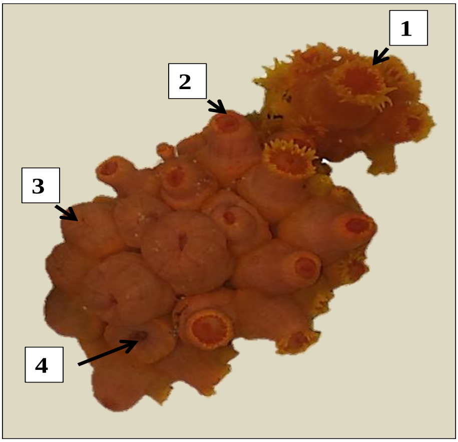
Polyp activity was recorded every other day at night, 2 h after *Artemia* nauplii were supplied to each container, and calculated according to Torrents et al. (2008), with slight modifications. For each colony, the percentage of four identified expansion stages of the polyps were recorded: polyp and tentacles totally expanded (state 1), polyp in emerged state without expanded tentacles (state 2), polyp in half-emerged state without expanded tentacles (state 3), and totally retracted polyp (state 4; Fig. 5). Using these data, the polyp activity per colony in (%) was calculated with the formula:

$$\frac{(\text{state } 1 \text{ x } 1) + (\text{state } 2 \text{ x } 0.5) + (\text{state } 3 \text{ x } 0.25) + (\text{State } 4 \text{ x } 0) \;\ast\; 100}{\text{number of polyps of the colony}} = \text{\% polyp activity per colony}$$

Thereby, all polyp expansion states were represented and weighted, offering a good insight into colony polyp activity.

**Figure 5** Different polyp states of *T. coccinea*, used to monitor coral performance through polyp activity: 1- polyp and tentacles totally expanded, 2-

polyp in emerged state, without expanded tentacles, 3- polyp in half-emerged state without expanded tentacles, 4- totally retracted polyp.



Source: Elaborated by the author (2019).

### *2.4 Chlorophyll* a *fluorescence measurements in* P. caribaeorum

The chlorophyll *a* fluorescence was used as a non-intrusive methodology to monitor the physiological state of the symbiotic *P. caribaeorum*. The maximum quantum yield of photosystem II ($F_v/F_m$; GENTY et al., 1989) of the experimental organisms was measured daily at dusk, using a pulse amplitude modulation fluorometer (Diving-PAM, Walz, Germany). As daily measured $F_v/F_m$ at dusk varies with the irradiance the organisms received during the day, mean daily irradiance data for the experimental time period were obtained from the Santa Catarina's Agricultural Research and Outreach division (EPAGRI) and matched with the respective $F_v/F_m$ data.

To assess any negative small-scale effects in *P. caribaeorum* in the contact zone with *T. coccinea* (e.g., tissue lesions, necrosis), at the end of the experiment fluorescence measurements with a pulse amplitude modulation fluorometer (Junior-PAM, Walz, Germany) were performed during dusk on *P. caribaeorum* samples that had been in contact with *T. coccinea*. Using the small fiber optic (∅1.5 mm), $F_v/F_m$ was measured directly in the contact zone between the two species and compared to measurements at 1.5 cm from the contact zone of the respective *P. caribaeorum* fragment, used as control.

### *2.5 Species´ metabolic rates*

At the end of the experiment, samples of both species were incubated, to measure photosynthesis and/or calcification and respiration. The individuals were incubated in filtered seawater (0.45 µm) at their respective treatment temperature in acrylic chambers (V=150 mL) with internal circulation, provided by a magnetic stirrer. The chambers were submerged in a water bath with a heater, to maintain stable temperature conditions during incubation. In the case of *T. coccinea*, the incubations were implemented in the dark for two hours, in order to determine simultaneously respiration and calcification rates. In preliminary tests, *T. coccinea* had been incubated for different time periods and 2 h was found to be an adequate length of the incubation, ensuring a good signal-to-noise ratio for oxygen and calcification measurements. The oxygen concentration was measured before and after the incubations with an oxymeter (YSI 5000-115, Yellow Springs, USA). For determination of calcification rates, control water samples were taken at the beginning of the incubations, and afterwards, two sub-samples (12 ml each) of the incubation water from each chamber were taken, poisoned with 20 µl of $HgCl_2$ and sealed without bubbles in borosilicate Winkler tubes. Both respiration and calcification were normalized to active polyp area (see below).

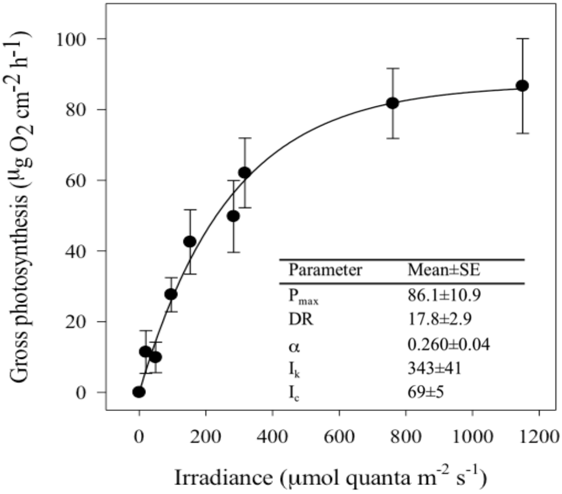
In the case of *P. caribaeorum,* the incubations, to determine maximum photosynthetic rates, were carried out for 30 min at a saturating irradiance of 500 µmol quanta $m^{-2}$ s-$^{1}$, an intensity chosen based on the irradiance at the onset of saturated photosynthesis ($I_k$~340 µmol quanta $m^{-2}$ $s^{-1}$). The $I_k$ was obtained from photosynthesis-irradiance curves, measured at the beginning of the experiment (Fig. 6). Afterwards, the samples were incubated for 15 min in the dark to measure postilluminatory respiratory rates that allowed calculation of gross photosynthesis. The photosynthetic and respiratory rates were normalized to surface area (see below) and their ratio was calculated (P/R; 12 h gross photosynthesis/24 h respiration).

For both species, the temperature coefficient ($Q_{10}$, indicator for changes in metabolic rate with a 10ºC temperature increase) was calculated to estimate and compare the sensitivity of species’ respiration to increased temperature, according to Atkin et al. (2005):

$$Q_{10}=\left(\frac{R_1}{R_2}\right)^{\left(\frac{10}{T_2-T_1}\right)}$$

Where $R_1$ is the metabolic rate measured at a lower temperature ($T_1$) and $R_2$ is the respiratory rate measured at a higher temperature ($T_2$).

**Figure 6** Photosynthesis-Irradiance curve of *Palythoa caribaeorum*. To determine the saturating light intensity to be used for incubations of measurements of maximum photosynthetic rates, samples of *P. caribaeorum* were incubated in sealed temperature-controlled acrylic chambers at 22ºC (n=5). Oxygen concentration in the seawater was measured at the beginning and end of the incubations, at which the samples were exposed to a series of increasing light intensities, as well as to darkness at the beginning (dark respiration, DR) and end of the light exposures (postilluminatory or light respiration). Gross photosynthetic rates were calculated by adding respiration (average between dark and light respiration) to net photosynthesis. The highest gross photosynthetic rate was considered as $P_{max}$ and the photosynthetic efficiency (α) was estimated from the initial slope of the light-response curve by linear least-square regression analysis. The irradiance at the onset of saturated photosynthesis ($I_k$) was obtained from the ratio $P_{max}/\alpha$ and the compensation irradiance ($I_c$), where photosynthesis equals respiration was calculated through the ratio DR/α.Pmax and DR - maximum gross photosynthetic rate and dark respiration, in µg $O_2$ cm-$^2$ h$^{-1}$; α- photosynthetic efficiency, in (µg $O_2$ cm$^{-2}$ h$^{-1}$) (µmol quanta m$^{-2}$ s-$^1$)$^{-1}$; $I_k$ and $I_c$ - saturating and compensatory light intensity, in µmol quanta m-$^2$ s-$^1$).



Source: Elaborated by the author (2019).

### *2.6 Calcification*

The calcification rates were estimated using the alkalinity anomaly technique, based on the ratio of two equivalents of total alkalinity (TA) per mol of $CaCO_3$ precipitation (SMITH and KINSEY, 1978). TA was determined using the Gran titration method (HANSSON and JAGNER, 1973; BRADSHAW et al., 1981). The samples were titrated with HCl 0.01 M and the pH and temperature was recorded, using a pH meter (Metrohm, Switzlerland). The data of the obtained titration curve were uploaded to a web-based alkalinity calculator (https://or.water.usgs.gov/alk/index.html),), to obtain the TA values of the samples. Alkalinity values were corrected, using Certified Reference Materials (CRMs, Batch No. 129) supplied by A. Dickson (Scripps Institution of Oceanography, La Jolla, CA, USA).

### *2.7 Symbiont and pigment extraction*

The frozen tissue of *P. caribaeorum* was grinded with liquid $N_2$, filtered seawater was added to a final volume of 50 mL and the samples were centrifuged at 3000 rpm for 5 min. The supernatant was discarded and the remaining pellet, containing the symbiotic cells, was resuspended to a final volume of 10 mL with filtered seawater and sub-samples were taken for subsequent cell density and chlorophyll determinations. A subsample of 1 mL of each sample was taken from the resuspended tissue pellet, fixed with Lugol solution and subsequently, the symbiont cells were counted, using a Neubauer hemocytometer, and normalized to *P. caribaeorum* surface area. Three subsamples (1 mL each) were taken for pigment extraction. The photosynthetic pigments were extracted overnight in darkness at 4°C, using acetone: dimethyl sulfoxide (20:1 V: V; IGLESIAS-PRIETO et al., 1992) and extracts were measured spectrophotometrically. The concentrations of chlorophyll *a* and *c* were calculated using the equation of Jeffrey and Humphrey (1975) and normalized to *P. caribaeorum* surface area.

### *2.8 Surface area and active polyp area determination*

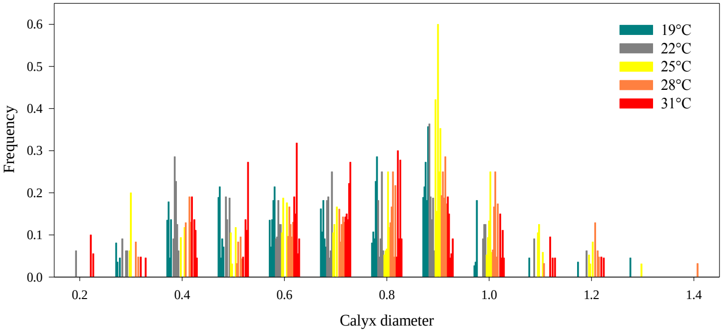
Normalization of measured response parameters of *P. caribaeorum* was performed by projected surface area, which was estimated by image processing (ImageJ) of photographs taken of the samples. For *T. coccinea*, instead of commonly used number of polyps, the active polyp area was used for normalization (GORI et al., 2015). Each colony's polyps were counted, their respective calyx diameters were measured with caliper and the areas calculated as circles (Area= $\pi r^2$). The sum of these areas represented the colony's active polyp area. This allowed accounting not only for differences in polyp number among *T. coccinea* colonies, but also for their highly variable sizes (Table 1, Fig.7), as polyp size can have an effect on coral metabolic and feeding rates (e.g., LASKER, 1981; SEBENS et al., 2016; SCHUBERT et al., 2017).

**Table 1** Number of polyps and mean calyx diameter per *T. coccinea* colony (min-max), and the resulting active polyp area (sum of calyx areas of all polyps of the colony)

| Treatment | # Polyps (colony$^{-1}$) | Calyx diameter (cm) | Active polyp area (cm$^2$) |
|---|---|---|---|
| 19°C | 37 | 0.645 (0.3-1.0) | 12.68 |
| | 28 | 0.675 (0.3-1.2) | 10.83 |
| | 22 | 0.809 (0.4-1.3) | 11.99 |
| | 22 | 0.681 (0.4-1.1) | 8.74 |
| | 14 | 0.764 (0.6-0.9) | 6.62 |
| 22°C | 11 | 0.718 (0.3-0.9) | 4.79 |
| | 21 | 0.610 (0.4-0.9) | 6.69 |
| | 22 | 0.692 (0.4-1.1) | 9.11 |
| | 16 | 0.756 (0.3-1.2) | 7.89 |
| | 16 | 0.631 (0.2-1.0) | 5.63 |
| 25°C | 19 | 0.841 (0.5-1.1) | 11.13 |
| | 32 | 0.772 (0.3-1.2) | 16.74 |
| | 15 | 0.787 (0.3-1.0) | 8.01 |
| | 12 | 0.892 (0.7-1.2) | 7.67 |
| | 17 | 0.747 (0.4-1.1) | 8.05 |
| 28°C | 31 | 0.816 (0.4-1.4) | 23.57 |
| | 12 | 0.750 (0.3-1.0) | 5.31 |
| | 16 | 0.856 (0.6-1.2) | 9.52 |
| | 21 | 0.720 (0.3-1.2) | 8.92 |
| | 23 | 0.754 (0.4-1.0) | 10.77 |
| 31°C | 21 | 0.705 (0.3-1.1) | 9.13 |
| | 20 | 0.740 (0.2-1.1) | 9.34 |
| | 22 | 0.676 (0.4-1.2) | 8.60 |
| | 18 | 0.694 (0.4-1.0) | 6.71 |
| | 22 | 0.692 (0.3-1.1) | 8.26 |

Source: Elaborated by the author (2019)

**Figure 7** Frequency of different calyx diameters within *T. coccinea* colonies used in the experiment



Source: Elaborated by the author

### *2.9 Feeding rates*

Both species were fed every other day, using a syringe to inject 30 mL of concentrated freshly hatched *Artemia* nauplii into each container (~1300 nauplii per container, 3 nauplii mL$^{-1}$), ensuring the same prey concentration for each container. Every eight days, the feeding rates were determined by collecting the seawater of each container the morning after the feeding and fixing the samples with formol. Also, blank control samples from containers without organism (n=3 per temperature) were taken and fixed with formol to determine the exact initial prey concentration and account for any temperature effect on nauplii concentration. Later on, *Artemia* nauplii were counted and the feeding rates were calculated as the decrease in prey concentration for a given amount of time. For comparative purposes between treatments (individual species *vs* both species in conjunction) the feeding rates determined for each container were expressed in percentage of the respective feeding rates at the beginning of the experiment.

### *2.10 Species' responses to the presence of the competitor*

Two types of *T. coccinea* reactions in response to direct tissue contact with *P. caribaeorum* were observed: 1) fully expanded *T. coccinea* polyps during day and night, extending over

*P. caribaeorum,* which in absence of competitor were observed only during feeding nighttime, and 2) extrusion of mesenterial filaments through the polyp wall of *T. coccinea* towards *P. caribaeorum,* mainly during nighttime. Thus, during the experiment, polyp behavior and the presence/absence of mesenterial filaments of *T. coccinea* were recorded daily (Table 2) and expressed as percentage of occurrence over the duration of the experiment.

*Palythoa caribaeorum*'s main competitive strategy is overtopping its competitor (*sensu* Suchanek and Green, 1981) hence; the growth during the experiment was measured as response parameter for competitive interaction with *T. coccinea*. The growth was determined from photos, taken from each *P. caribaeorum* sample at the beginning and end of the experiment, and calculated as relative growth rate ($\text{RGR}=(\ln \text{area}_{\text{final}}-\ln \text{area}_{\text{initial}})/\text{days}_{\text{experiment}}$; Hunt, 1990). In addition, in a preliminary experiment we observed a strong upward extension of *P. caribaeorum* tissue when in contact with *T. coccinea* (Fig. 8). Thus, also the height of *P. caribaeorum* fragments grafted with *T. coccinea* was measured and the upward extension during the experiment was calculated as the differences between initial and final height.

**Table 2** Observations of fully expanded polyps and mesenterial filaments of *T. coccinea* during the experiment. Data are given in relative values, considering the number of replicates per treatment (n=5).

| | Experimental day | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Temperature | **0** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** | **14** | **15** | **16** | **17** | **18** | **19** | **20** | **21** | **22** | **23** |
| **Fully expanded polyps**<br>19°C | | | | | | | | | | | | 0.4 | | 0.4 | 0.6 | 0.4 | | | | | | | | |
| 22°C | | | | | | | | | | | | 0.6 | | | 0.6 | | | | 0.6 | | | | | |
| 25°C | | | | | | | | | | | | 0.2 | | | 0.4 | | | | | | 0.2 | | | |
| 28°C | | | | | | | | | | | 0.4 | 0.2 | | | | | | | | | | | | |
| 31°C | | | | | | | | | | | | 0.2 | | | | | | | | | | | | |
| | | | | | | | | | | | | | | | | | | | | | | | | |
| **Mesenterial filaments**<br>19°C | | 0.2 | | | | | 0.2 | | | | | | | | | | | | | | | | | |
| 22°C | | | | | | | | | | | | | | | | | | | | | | | | |
| 25°C | | | | | | | | 0.2 | | | | | | | 0.2 | | | | | | | | | |
| 28°C | | | | | | | | | | | 0.2 | | | | | | | | | | | | | |
| 31°C | | | | | | | | 0.2 | | | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | | | | | | | | | | | |

Source: Elaborated by the author (2019),

**Figure 8** Upward extension of *P. caribaeorum* tissue in response to the contact with a *T. coccinea* colony, observed during a preliminary experiment.

Source: Photography by the author (2019).

### *2.11 Statistical analysis*

Data were tested *a priori* for normality, using the Shapiro-Wilk test. Analyses of variance (two-way ANOVA) and subsequent Student-Newman-Keuls posthoc, with temperature and the presence of the competitor as independent factors, were used for the determination of significant differences ($p<0.05$) in physiological parameters of *T. coccinea* and *P. caribaeorum* (photosynthesis, respiration, P/R, calcification, symbiont cell density). In the case of the other measured response parameters, normality was not satisfied and thus, data were analyzed for effects of temperature, presence of competitor and/or time (in case of feeding rates), using the Kruskal–Wallis test. The statistical analyses were conducted using Statistica 7.0.

## **3. Results**

### *3.1 Species' metabolic performance*

*Tubastraea coccinea* performance, monitored every other day through polyp activity, varied widely during the experiment (Fig. 9 a, b). At the lowest temperature (16ºC) the colonies showed zero activity and were dead after the 6th day of the experiment. The mean polyp activity throughout the experiment showed significant temperature effects (Table 3), with the lowest activity recorded at 19°C and a decline at 31°C (Fig. 10a). There was no significant effect due to the presence of *P. caribaeorum* (Table 3), though polyp activity generally tended to be higher when in contact with the zoanthid, except for the highest temperature treatments (31°C), where the pattern was inverse (Fig. 10a).

The respiratory response of *T. coccinea* showed a linear increase with temperature (Fig. 10b), yielding a $Q_{10}$ value of 2.51. The contact with *P. caribaeorum* led to respiratory rates 1.6-2.7 times higher compared to the respective treatment without the zoanthid (ANOVA, Newman-Keuls, $p<0.001$; Table 4), yet the resulting $Q_{10}$ value of 2.35 was quite similar to the one found in *T. coccinea* colonies in absence of *P. caribaeorum* (Fig. 10b). At the highest temperature, a slight but significant decrease in respiratory rates, compared to the respective 28°C-treatment (ANOVA, Newman-Keuls, $p=0.0304$), was found in *T. coccinea* colonies that had been in contact with *P. caribaeorum* (Fig. 10b).

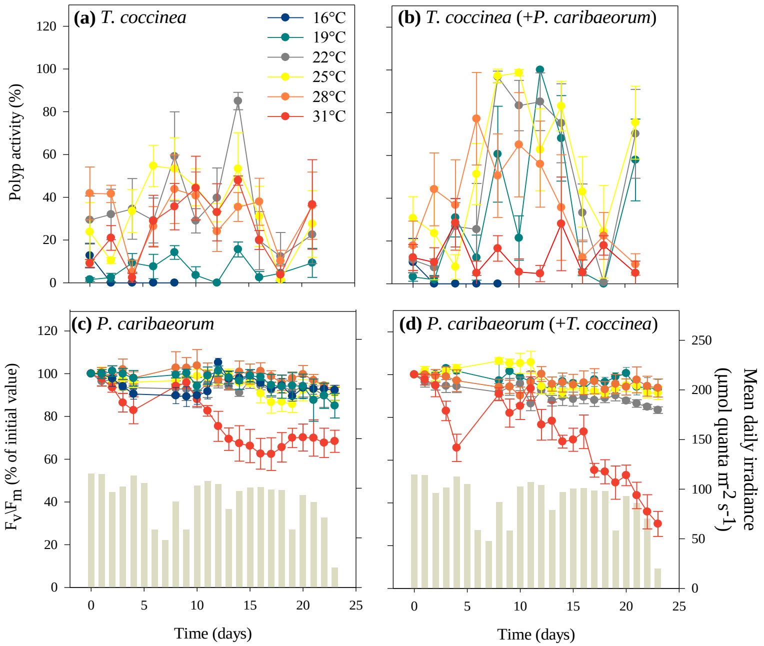
Besides respiration, also calcification of *T. coccinea* was significantly affected by temperature, as well as showing a synergistic interaction between temperature and the presence of *P. caribaeorum* (Table 4). In both, absence and presence of *P. caribaeorum*, net calcification was found only at temperatures ≤25° C, with the highest rates at 22°C (Fig. 10c). At higher temperatures, calcification was negative, indicating dissolution of calcium carbonate. Here, the contact with *P. caribaeorum* resulted in a significantly stronger negative effect of temperatures ≥28°C on calcification (ANOVA, Newman-Keuls, $p<0.001$), compared to colonies kept without of the zoanthid (Fig. 10c).

*Palythoa caribaeorum*'s photosynthetic performance, monitored daily through $F_v/F_m$ measurements, showed no differences or significant changes throughout the experiment in the temperature range of 16-28°C (Fig.9 c, d). On the other hand, there was a gradual decrease after the first few days of the experiment in organisms exposed to 31ºC that leveled off after about 12 days at values of ~0.41 in *P. caribaeorum* maintained individually, while showing a stronger and continuous decline in the organisms in contact with *T. coccinea*, exhibiting $F_v/F_m$ values as low as 0.19 at the end of the experiment (data not shown). Temperature, but not the presence of the sun coral, exhibited a significant effect on the final $F_v/F_m$ values (Table 3), with the lowest $F_v/F_m$ values at 31°C (30% and 68% of initial values in presence and absence of *T. coccinea*, respectively) (Fig. 11a).

Gross photosynthesis of *P. caribaeorum* did not show a significant effect due to the presence of *T. coccinea*, but exhibited a significant response to temperature (Table 4) that was reflected in an increase with temperature up to 28°C and a subsequent strong drop at 31°C (Fig. 11b). Similarly, respiration also increased significantly with temperature (Table 4), yielding a $Q_{10}$ value of 1.68, without a significant effect due to the presence of *T. coccinea* (Fig. 11c). Yet, the contact with the sun coral had a synergistic effect with temperature, resulting in a strong increase in respiration at the highest temperature, compared to individual *P. caribaeorum* exposed to the same treatment (Fig. 11c).

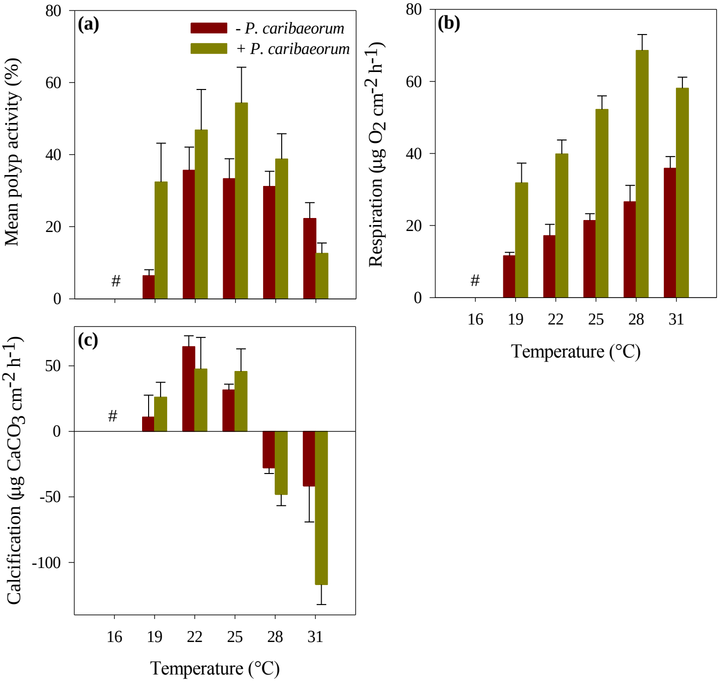
The above-described metabolic responses of *P. caribaeorum* caused a significant temperature effect in the ratio (P/R), without being affected by the presence of *T. coccinea* (Table 4). As expected, the lowest ratio were found at 31°C, even lower still in the presence of *T. coccinea* (Fig. 11d), though the differences were not significant (ANOVA, Newman-Keuls, $p=0.1263$).

**Figure 9** Daily performance of *T. coccinea*, monitored through polyp activity (a, b) and of *P. caribaeorum*, measured as $F_v/F_m$ (c, d) when exposed to different temperatures and the presence of the other species. Daily recorded polyp activity of *T. coccinea* during the experiment in (a) absence and (b) presence of *P. caribaeorum* and $F_v/F_m$ measured in *P. caribaeorum* in (c) absence and (d) presence of *T. coccinea*. Data show mean±SE (n=5).



Source: Elaborated by the author (2019)

**Figure 10** *Tubastraea coccinea*. Performance response to different temperature treatments and the presence of *P. caribaeorum*: (a) Mean polyp activity over the experimental period, (b) respiration, and (c) calcification rates at the end of the experiment ([#]*T. coccinea* in this treatment died after the first few days of the experiment). Data show mean±SE (n=5).



Source: Elaborated by the author (2019).

**Table 3** Summary of Kruskal-Wallis tests to examine differences in measured response parameters due to temperature and the presence of the competitor (significant p-values<0.05 are indicated in bold). Response parameters that were induced by the presence of the competitor were tested only for significant effects due to temperature. #The 16°C-treatment was not included in the statistical analyses, due to the missing treatment of *T. coccinea* and both species grafted together (*T. coccinea* colonies died after the first few days of the experiment).

| Response parameter | Temperature | | Presence of competitor | |
|---|---|---|---|---|
| | $X^2$ | p-value | $X^2$ | p-value |
| ***T. coccinea*#** | | | | |
| Mean polyp activity | 88.9 | **0.0008** | 0.036 | 0.8488 |
| Fully expanded polyps | 7.46 | 0.1137 | - | - |
| Mesenterial filaments | 3.07 | 0.5462 | - | - |
| | | | | |
| ***P. caribaeorum*#** | | | | |
| Final $F_v/F_m$ | 22.0 | **0.0002** | 0.333 | 0.5637 |
| Fine-scale $F_v/F_m$ | 0.94 | 0.9181 | - | - |
| Relative growth | 10.4 | **0.0347** | 4.25 | **0.0393** |
| Upward extension | 9.93 | **0.0416** | - | - |

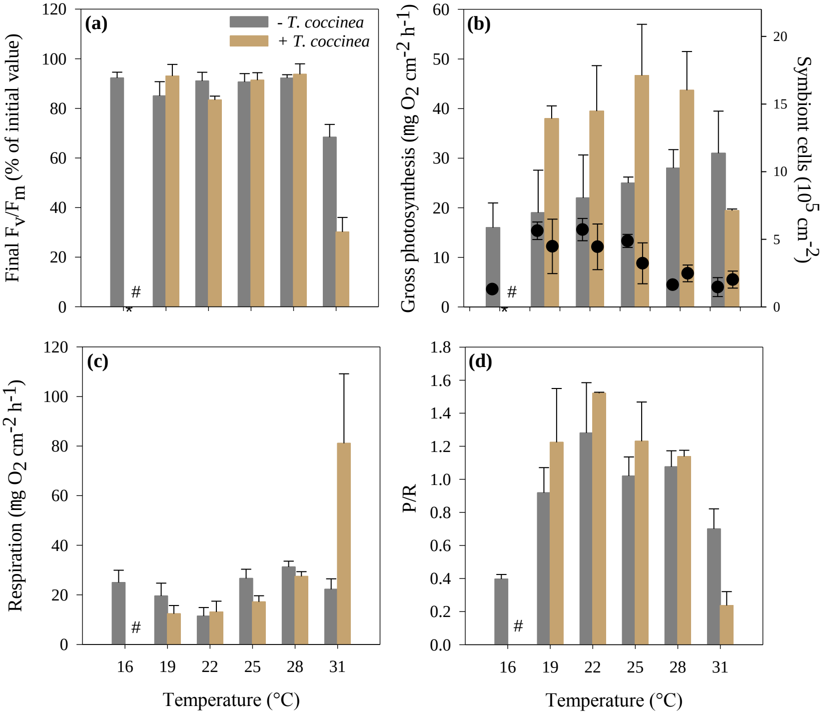
Source: Elaborated by the author (2019)

**Table 4** Summary of the results of two-way ANOVA to test for differences in measured response parameters (significant p-values <0.05 are indicated in bold). [#]The 16°C-treatment was not included in the statistical analyses, due to the missing treatment of *T. coccinea* and both species grafted together (*T. coccinea* colonies died after the first few days of the experiment).

| Response parameter | Temperature | | Presence of competitor | | Temperature x Presence of competitor | |
|---|---|---|---|---|---|---|
| | F | p-value | F | p-value | F | p-value |
| ***T. coccinea*[#]** | | | | | | |
| Calcification | 32.1 | **0.0001** | 3.39 | 0.0733 | 3.32 | **0.0199** |
| Respiration | 26.2 | **0.0001** | 165.9 | **0.0001** | 2.05 | 0.1069 |
| ***P. caribaeorum*[#]** | | | | | | |
| Gross PS | 3.20 | **0.0289** | 2.22 | 0.1479 | 1.11 | 0.3718 |
| Respiration | 7.25 | **0.0003** | 0.054 | 0.8186 | 2.83 | **0.0418** |
| P/R | 5.32 | **0.0041** | 0.29 | 0.5906 | 1.19 | 0.3454 |
| Symbiont cells | 4.31 | **0.0079** | 0.66 | 0.4240 | 1.18 | 0.3410 |

Source: Elaborated by the author (2019).

**Figure 11** *Palythoa caribaeorum*. Photosynthetic performance response to different temperature treatments and the presence of *T. coccinea*: (a) Final $F_v/F_m$, (b) gross photosynthesis, (c) respiration and (d) photosynthesis to respiration ratio (P/R) at the end of the experiment ($^{\#}$*T. coccinea* in this treatment died after the first few days of the experiment). Data show mean±SE (n=5).



Source: Elaborated by the author (2019).

### *3.2 Symbiont cell density and pigment content in* P. caribaeorum

Significant differences in symbiont cell density due to temperature were found, while the presence of *T. coccinea* did not induce any changes (Table 4). The effects of temperature were mainly due to significant lower symbiont cell numbers (ANOVA, Newman-Keuls, $p<0.05$) at 16° and temperatures ≥28°C (Fig. 11b). These changes were accompanied by significant lower total chlorophyll contents (Chl*a+c*) per surface area of *P. caribaeorum* due to temperature (ANOVA, $p<0.0001$), whereas the chlorophyll content per symbiont cell (Ci) did not show any changes to either, temperature or presence of *T. coccinea* (ANOVA, $p>0.05$) (Table 5).

**Table 5** *Palythoa caribaeorum* symbiont cell density and total chlorophyll contents (per $cm^2$ and symbiont cell- $C_i$) at different temperature and in the absence and presence of *T. coccinea*. Data represent mean±SE (n=5).

| Temp | ***P. caribaeorum*** | | | ***P. caribaeorum* (+ *T. coccinea*)** | | |
|---|---|---|---|---|---|---|
| | Cells ($10^5$ $cm^{-2}$) | Chl*a+c* (µg $cm^{-2}$) | $C_i$ (µg Chl*a+c* $10^5$ $cells^{-1}$) | Cells ($10^5$ $cm^{-2}$) | Chl*a+c* (µg $cm^{-2}$) | $C_i$ (µg Chl*a+c* $10^5$ $cells^{-1}$) |
| 16°C | 1.32 ± 0.14 | 10.50 ± 3.2 | 4.72 ± 3.7 | - | - | - |
| 19°C | 5.64 ± 0.65 | 18.60 ± 1.2 | 3.49 ± 0.6 | 4.48 ± 2.01 | 13.16 ± 0.6 | 3.94 ± 1.8 |
| 22°C | 5.72 ± 0.95 | 23.87 ± 5.2 | 4.03 ± 1.0 | 4.45 ± 1.69 | 10.22 ± 0.5 | 4.32 ± 1.9 |
| 25°C | 4.88 ± 0.56 | 21.70 ± 5.3 | 4.62 ± 1.2 | 3.23 ± 1.35 | 8.94 ± 1.2 | 3.90 ± 0.8 |
| 28°C | 1.64 ± 0.21 | 7.78 ± 1.5 | 5.02 ± 1.0 | 2.48 ± 0.71 | 4.78 ± 1.4 | 2.25 ± 0.7 |
| 31°C | 1.47 ± 0.81 | 5.96 ± 3.7 | 2.46 ± 1.7 | 2.02 ± 0.72 | 3.24 ± 0.6 | 0.91 ±0.18 |

Source: Elaborated by the author (2019).

### *3.3 Feeding rates*

Unsurprisingly, the feeding rates of the non-symbiotic *T. coccinea* were ~2-3 times higher compared to the symbiotic *P. caribaeorum* (Table 6). In the former species, neither temperature nor time affected feeding significantly, while in *P. caribaeorum* significant differences in feeding rates over time were found (Fig. 12a, b; Table 7). *Tubastraea coccinea* only survived the first few days of the experiment at the lowest temperature (16°C) and its feeding rates showed a tendency to decline over time at the next higher temperature (19°C; Fig. 12a). In contrast, *P. caribaeorum* tolerated the lowest temperature, but exhibited a significant drop in feeding rates toward the end of the experiment to 57% of the initial values (Fig. 12b). On the other hand, both species responded to the highest temperature (31°C), with a drop to 40% and 23% of initial feeding rates in *T. coccinea* and *P. caribaeorum*, respectively (Fig. 12a, b). The feeding rates of the treatment where both species were in direct contact with each other also changed significantly over time (Table 7), but showed slightly different response patterns, compared to the individual treatments. While in the individual treatments the feeding rates mostly decreased over time, here the feeding rates declined only at temperatures ≥28°C, reaching final values of 35% of initial values at 31°C (Fig. 12c). At 19°C and 22°C though there was a noticeable increase in feeding rates.

**Table 6** Feeding rates (nauplii polyp$^{-1}$ h$^{-1}$) at different temperatures, determined at different time intervals during the experiment (the ratio of Pc/Tc indicates the proportion of the number of polyps of *P. caribaeorum* to *T. coccinea*). Data represent mean±SE (n=5).

| Species | Treatment | Pc/Tc | Day 0 | Day 6 | Day 14 | Day 22 | Mean |
|---|---|---|---|---|---|---|---|
| *T. coccinea* | 16°C | | 1.81±0.53 | 0.84±0.23 | - | - | - |
| | 19°C | | 2.20±0.22 | 1.93±0.17 | 1.38±0.16 | 1.58±0.38 | **1.77±0.21** |
| | 22°C | | 3.13±0.56 | 2.70±0.46 | 2.96±0.45 | 2.83±0.60 | **2.91±0.11** |
| | 25°C | | 2.71±0.57 | 2.35±0.55 | 2.03±0.32 | 1.69±0.55 | **2.19±0.25** |
| | 28°C | | 2.11±0.41 | 1.75±0.25 | 2.14±0.35 | 1.95±0.35 | **1.99±0.10** |
| | 31°C | | 1.74±0.32 | 1.33±0.33 | 1.53±0.37 | 0.79±0.18 | **1.81±0.53** |
| *P. caribaeorum* | 16°C | | 1.40±0.10 | 1.55±0.11 | 0.70±0.14 | 0.73±0.16 | **1.10±0.26** |
| | 19°C | | 1.32±0.08 | 1.02±0.11 | 0.84±0.09 | 1.06±0.29 | **1.06±0.29** |
| | 22°C | | 1.12±0.19 | 0.86±0.08 | 0.96±0.16 | 1.07±0.20 | **1.00±0.07** |
| | 25°C | | 1.10±0.14 | 1.08±0.13 | 1.04±0.02 | 0.74±0.35 | **0.99±0.09** |
| | 28°C | | 0.68±0.16 | 0.72±0.15 | 0.79±0.12 | 0.53±0.18 | **0.68±0.06** |
| | 31°C | | 0.60±0.14 | 0.64±0.11 | 0.68±0.17 | 0.11±0.07 | **0.51±0.15** |
| *T. coccinea* +*P. caribaeorum* | 16°C | 2.6±0.3 | 1.16±0.22 | 0.81±0.21 | - | - | - |
| | 19°C | 5.7±1.5 | 1.14±0.16 | 0.91±0.14 | 0.93±0.07 | 1.30±0.05 | **1.07±0.11** |
| | 22°C | 4.4±1.0 | 1.14±0.07 | 0.81±0.11 | 1.13±0.12 | 1.23±0.10 | **1.08±0.11** |
| | 25°C | 4.7±0.5 | 1.20±0.21 | 0.92±0.09 | 0.83±0.12 | 1.53±0.20 | **1.12±0.18** |
| | 28°C | 5.5±0.7 | 0.86±0.08 | 1.09±0.18 | 1.10±0.09 | 0.65±0.09 | **0.92±0.13** |
| | 31°C | 3.6±0.7 | 0.77±0.12 | 0.78±0.23 | 0.84±0.12 | 0.16±0.25 | **0.64±0.19** |

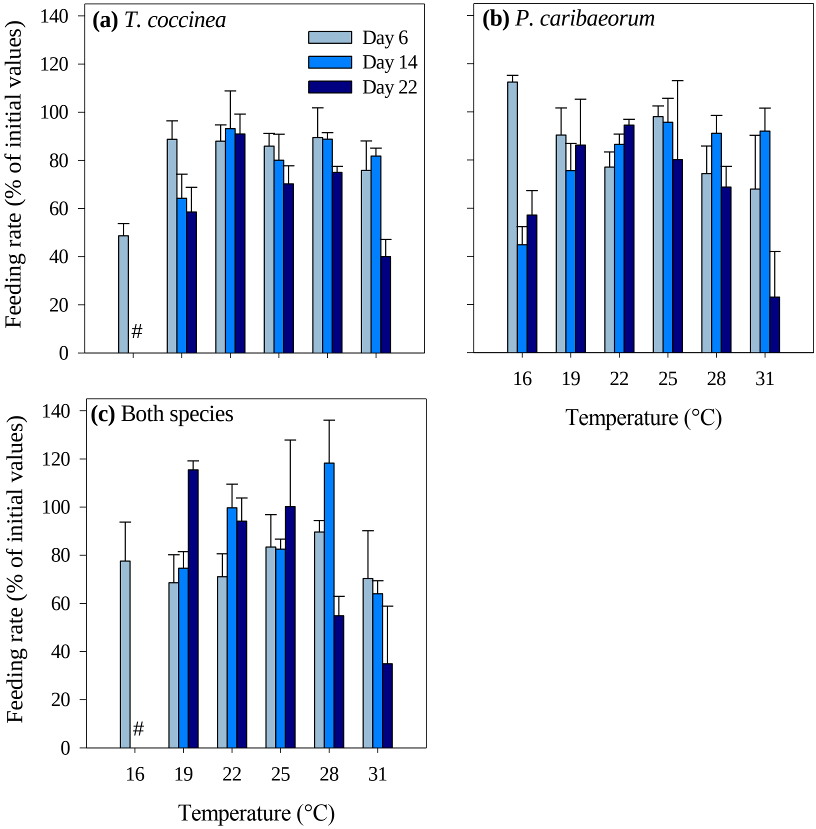
Source: Elaborated by the author (2019).

**Table 7** Summary of Kruskal-Wallis tests to examine for differences in feeding rates due to temperature and time (significant p-values <0.05 are indicated in bold). #The 16°C-treatment was not included in the statistical analyses, as *T. coccinea* colonies (individually and grafted with *P. caribaeorum*) died after the first few days of the experiment**.**

| Treatment | Temperature | | Time | |
|---|---|---|---|---|
| | $X^2$ | p-value | $X^2$ | p-value |
| *T. coccinea*[#] | 1.46 | 0.8335 | 0.495 | 0.9740 |
| *P. caribaeorum* | 4.84 | 0.4352 | 42.8 | **0.0001** |
| Both species[#] | 0.705 | 0.9507 | 41.2 | **0.0001** |

Source: Elaborated by the author (2019).

**Figure 12** Feeding rates of (a) *T. coccinea*, (b) *P. caribaeorum* and (c) both species grafted together, determined at different time intervals during the experiment ($^{\#}$*T. coccinea* in this treatment died after the first few days of the experiment). Data show mean±SE (n=5).



Source: Elaborated by the author (2019).

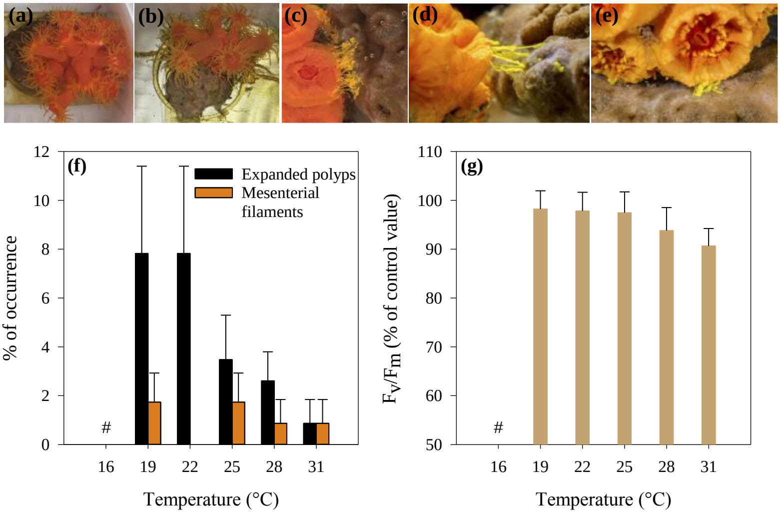
### *3.4 Species' responses to the presence of the competitor*

*Tubastraea coccinea* reacted to direct tissue contact with *P. caribaeorum* with fully expanded polyps, extending over *P. caribaeorum* (Fig. 13a, b) and with the extension of mesenterial filaments (Fig. 13c-e). The occurrence of fully expanded polyps was observed mainly between day 11 and 14 of the experiment (Table 2) and was highly variable between replicates, not yielding significant differences between temperatures (Table 3), even though there was a tendency of decreasing occurrence at higher temperature (Fig. 13f). Also, no significant differences between temperature treatments were observed in the formation of mesenterial filaments (Table 3), whose occurrence was generally lower compared to the fully extended polyps (Fig. 13f, Table 2).

The fine-scale $F_v/F_m$ measurements, directly in the contact zone between the two species, showed no significant response to temperature (Table 3), though there was a slight but significant decline at 31ºC, compared to the respective control values ($X^2$=6.00, p=0.0143), suggesting some localized tissue damage in *P. caribaeorum* at this temperature (Fig. 13g).

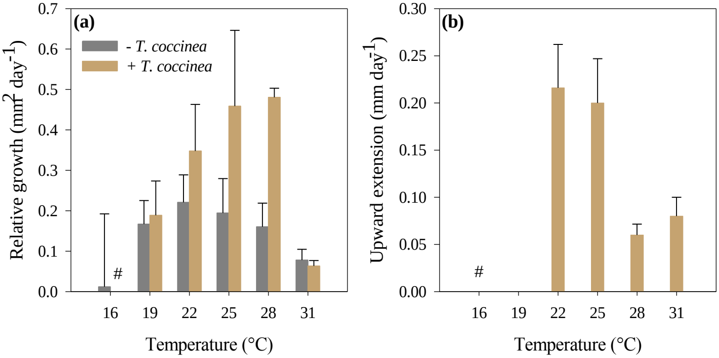
*Palythoa caribaeorum'*s relative growth rate responded significantly to temperature and the presence of *T. coccinea* (Table 3). The last induced a strong increase in growth that however, dropped strongly at 31ºC, both in absence and presence of the competitor (Fig. 14a). In addition, the tissue contact with *T. coccinea* induced an upward extension of *P. caribaeorum* that was significantly affected by temperature (Table 3), with the largest extension (0.5-0.54 cm during the experiment) at intermedium temperatures, but no extension at 19ºC and lower extension at ≥28ºC (Fig. 14b).

**Figure 13** Competitive interactions of *T. coccinea*, when grafted with *P. caribaeorum*: (a, b) fully expansion of polyps and (c-e) mesenterial filaments projected toward *P. caribaeorum*. (f) Percentage of occurrence of completely extruded polyps and mesenterial filaments and (g) small-scale $F_v/F_m$ measurements to detect potential tissue damage of *P. caribaeorum* in the contact zone due to attacks of *T. coccinea*, expressed in % of value at 1.5 cm distance from contact zone (${}^{\#}$*T. coccinea* in this treatment died after the first few days of the experiment, *significant difference to respective control value). Data show mean±SE (n=5).



Source: Elaborated by the author (2019).

**Figure 14** Growth of *P. caribaeorum*. (a) Relative vertical growth and (b) upward extension in response to tissue contact with *T. coccinea*, the latter of which was not observed in absence of the competitor ($^{\#}$*T. coccinea* in this treatment died after the first few days of the experiment). Data show mean±SE (n=5).



Source: Elaborated by the author (2019).

## 4. Discussion

This study shows that the invasive sun coral *T. coccinea* has a relatively narrow thermal tolerance window, indicating limited plasticity to respond to changes in temperature, contrary to its potential competitor, the native zoanthid *P. caribaeorum*, which has a broader thermal tolerance range. Further, experimental data and field observations indicate that the invasive species at its current southern distributional limit in Arvoredo may potentially lose when in competition with *P. caribaeorum*, an interaction that negatively impacts *T. coccinea*, by increasing metabolic demands, while not causing any negative effects in the zoanthid. Our data also show that temperature does not exert an influence over these interactions, unless it represents a stressful condition for the species (temperatures at their upper thermal limit), under which the presence of the competitor reinforces the impacts on physiological and growth performance synergistically in both species.

### *Temperature effects on the performance of the invasive sun coral* T. coccinea *and the native zoanthid* P. caribaeorum

*Tubastraea coccinea* is known as circumtropical species, with records from the Indo-Pacific, Eastern Pacific, the Caribbean, the southwestern Atlantic and the Red Sea (reviewed in CREED et al., 2017a). The species has a seemingly wide thermal tolerance, occurring in both tropical warm waters and temperate regions or even in colder upwelling regions (CAIRNS, 2000; DE PAULA and CREED, 2005; PAZ-GARCÍA et al., 2007; GLYNN et al., 2008; CARLOS et al., 2013). Our results indicate that its lower thermal threshold lies at temperatures ≤19°C, as physiological performance was low at 19°C and colony mortality was observed after a few days at 16°C, which also agrees with another experimental study on this species (BATISTA et al., 2017). The upper thermal limit of this species was found to be at temperatures ≥28°C, which corresponds to the summer maximum temperature of the region.

In contrast to the lower thermal limit, the high temperature response did not cause mortality of *T. coccinea* during the experiment, however, the corals were experiencing stress, as expressed by the increased respiratory rates and the complete cease of calcification and dissolution of the carbonate skeleton. This indicated severe consequences for coral growth and in the long-term most likely survival, which is consistent with recent findings of a strongly reduced survival of *T. coccinea* fragments at temperatures ≥27°C (LUZ et al., 2018).

The largely reduced performance of *T. coccinea* colonies at the specie’s lower and upper thermal tolerance limits was most likely related with the reduced polyp activity and consequently a decrease in feeding rates, and at the lower thermal limit also a decrease in oxygen consumption. These findings were not surprising, as these processes are known to be linked (i.e., polyp expansion ensuring food capture and increasing coral respiration and *vice versa*; FABRICIUS and KLUMPP, 1995; COMA et al., 1998, 2002; COMA and RIBES, 2003), and to be affected by abnormally low or high temperatures (PALARDY et al., 2005; FERRIER-PAGÉS et al., 2010; PREVIATI et al., 2010; GORI et al., 2015). Generally, under high-temperature stress it is assumed to be a trade-off between conserving energy by reducing polyp activity, at the cost of reducing energy intake through feeding, a strategy reported also in other non-symbiotic corals (SEBENS, 1987; COMA and RIBES, 2003; PREVIATI et al., 2010). On the other hand, reported declines or even cease of coral feeding under low-temperature stress (MAYER, 1915; EDMONDSON, 1928; PALARDY et al., 2005) has been explained by a slowing of polyp contraction or a loss of nematocyst function, allowing certain organisms to escape prior ingestion (JOHANNES and TEPLEY, 1974). The observed decrease in energy input through zooplankton uptake during the experiment was most likely accountable for the decline in calcification in this non-symbiotic coral (CROOK et al., 2013; NAUMANN et al., 2014). The observed reduction in calcification and hence, coral growth at low temperature was supported by differences in growth rates of *T. coccinea* found at field sites with varying temperature regimes. Growth rate estimates at two closely related tropical Brazilian sites showed that in Arraial do Cabo, a site influenced by upwelling (13.5-26.5°C), the growth rate was lower (3.31 $cm^2$ $year^{-1}$; MIZRAHI, 2008), compared to the growth reported for Ilha Grande (5.85 $cm^2$ $year^{-1}$; DE PAULA, 2007). In addition to the declining performance of adult colonies at low temperatures, settlement of *T. coccinea* larvae has also been reported to decline strongly at lower temperatures (MIZRAHI, 2008; BATISTA et al., 2017).

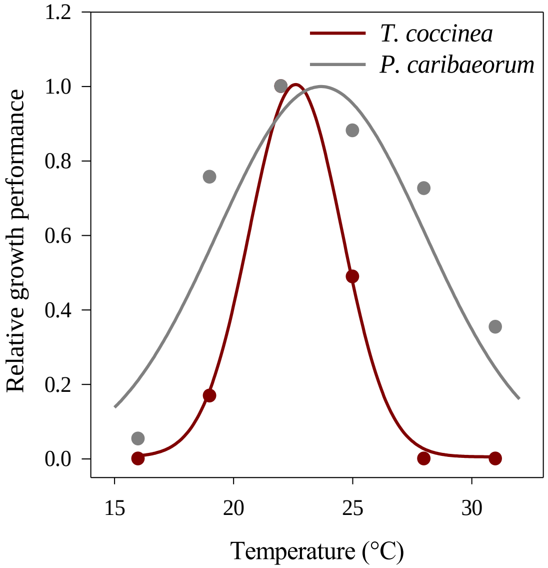
Conversely, the impact of temperatures ≥28°C on the specie’s performance was unexpected, as *T. coccinea* is widely distributed in tropical regions, where summer temperatures reach commonly ~30°C, and has also been reported on oil-platforms in tropical latitudes reaching as far as 10°S along the Brazilian coast (CREED et al., 2017a). The thermal optimum of the species determined in this study corresponded to the local condition during sample collection (Fig. 15), pointing towards local acclimation/adaptation and based on the narrow thermal window also an inability of *T. coccinea* to compensate metabolic rates for rapid changes in temperature.

*Palythoa caribaeorum* is found on almost the entire West Coast of the Atlantic, from Florida to Santa Catarina, Brazil (KEMP et al., 2006; BOUZON et al., 2012), indicating that this species has a wide thermal tolerance range (17-30°C). This agrees with our results, as the specie’s physiological and growth performance declined only in temperature treatments below and above this range, at 16°C and 31°C, respectively (Fig. 11, 15). The exposure to 16°C, which corresponds to the recorded local minimum winter temperature, resulted in lower symbiont cell density, while only slightly affecting their performance (see Fig. 11a, b), which however, together with a small increase in host respiration resulted in a drop in P/R to 0.4 (Fig. 11d), suggesting that autotrophic nutrition could not keep pace with the metabolic demands. This was accompanied by a strong decline in feeding rates, indicating that temperatures of ≤16°C might impair *P. caribaeorum* performance and consequently growth and survival in the long-term due to insufficient energy input from both autotrophic and heterotrophic nutrition, also supported by the almost complete cease in growth (Fig. 14, 15). This was consistent with previous ecological studies on the species in the region, showing that *P. caribaeorum* does not occur further south and suggesting that minimum winter temperature represents an important factor in limiting the distribution of this and congeneric species towards higher latitudes (REIMER et al., 2008; JÚNIOR, 2014; OLIVEIRA, 2014). More specifically, Júnior (2014) defined the distribution limit for this species to regions where temperatures below 16°C are not experienced for more than 17% of the time during winter months. The importance of the duration of exposure to low temperatures in its resistance is also indicated by the report of the little effect a cold wave event in Florida had on *P. caribaeorum,* where temperatures dropped below 16°C for five days (KEMP et al., 2011; LIRMAN et al., 2011).

Similarly to the low temperature range tested in this study, the exposure to the highest temperature (31ºC) significantly affected the performance of *P. caribaeorum*. Though, in addition to heterotrophic feeding, here principally symbiont cell density and their performance were impacted, as indicated by the strong drop in $F_v/F_m$ and gross photosynthesis, while there was no increase in host respiration. This was in concordance with an experimental study, showing that photosynthetic carbon fixation in *Palythoa* sp. was significantly impaired under ≥31°C (GRAHAM and SANDERS, 2015), which might be related to the impact on symbiont carbonic anhydrase activity at these temperatures (GRAHAM et al., 2015). Our findings are also consistent with experimental and field observations of severe *P. caribaeorum* bleaching at temperatures between 30ºC and 33.5°C (LASKER et al., 1984; LESSER et al., 1990; MIGOTTO, 1997; KEMP et al., 2006; BAKER et al., 2008; PRADA et al., 2010; GRAHAM and SANDERS, 2015; FUJIMURA and RIEGL, 2017).

The differences in thermal tolerance range between the invasive *T. coccinea* and the native *P. caribaeorum* (Fig. 15) were opposite of what would have been expected, based on the general assumption of broader environmental tolerances of invasive species, and particularly a higher physiological tolerance to increasing temperature of invasive compared to native species (LENZ et al., 2011; ZEREBECKI and SORTE, 2011; KELLEY, 2014; LEJEUSNE et al., 2014; KENWORTHY et al., 2018). The explanation may lie in the fact that invader traits that facilitate rapid colonization, such as expressed by *T. coccinea*, often come at a cost, e.g. competition-colonization tradeoffs, stress tolerance (reviewed in PAPACOSTAS et al., 2017). Certainly, our findings and previous studies suggest that the sun coral does not exhibit a high thermal stress tolerance and a rather limited plasticity to cope with changes in temperature, as indicated by its inability to compensate metabolic rates for changes in temperature ($Q_{10}$=2.51, compared to $Q_{10}$=1.68 of *P. caribaeorum*). Yet, high stress tolerance is not a necessary requirement for invasive success (see MCMAHON, 2002), though it may have implications for the specie's distributional limits, as well as its competitive strength along its distribution range.

**Figure 15** Thermal response curve of relative growth performance of the invasive *T. coccinea* and the native *P. caribaeorum* (calcification rates were used as proxy of growth for *T. coccinea*



Source: Elaborated by the author (2019).

### *Competitive interactions between the invasive sun coral* T. coccinea *and the native zoanthid* P. caribaeorum

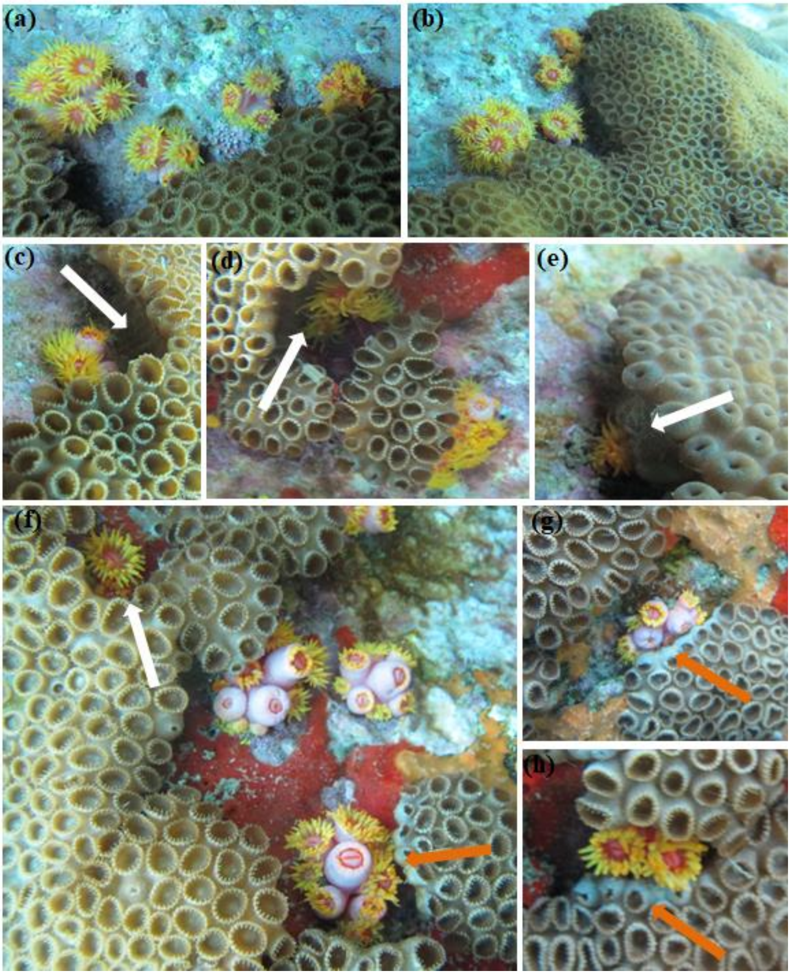
This study shows that *T. coccinea* and *P. caribaeorum* were competing with each other by deploying different strategies, aggressive physical attacks *versus* overgrowth, respectively. The invasive *T. coccinea,* known as an aggressive competitor, used mesenterial filaments to attack *P. caribaeorum,* a strategy reported to be quite effective when competing with other reef invertebrates, causing necrosis and death (SANTOS et al., 2013; HENNESSEY and SAMMARCO, 2014). In the case of *P. caribaeorum,* though deleterious effects were not visible and a small degree of tissue lesions and necrosis was detected by fine-scale measurements in the contact zone only at the highest temperature (Fig. 13g). This was consistent with the rather infrequently appearance of mesenterial filaments only during the first part of the experiment, as it has been shown that this strategy is used by corals discriminately, i.e. when there is a high probability of success, in order to minimize costs associated with this strategy (LANG, 1971, 1973; CONNELL, 1976; SHEPPARD, 1979; COPE, 1981; BAK et al., 1982; LOGAN, 1984; YAMAZATO and YEEMIN, 1986; ROMANO, 1990).

Another competitive strategy of *T. coccinea*, induced by the presence of *P. caribaeorum,* was the full expansion of polyps to cover large parts of the zoanthid. This interaction had also been previously observed in the species under laboratory conditions (SANTOS et al., 2013) and documented in the field, when the sun coral was competing with encrusting gorgonians and sponges (WITMAN, 1992). It appears to be a common defense mechanism of cup corals and octocorals against overgrowth via damage to competitors by tentacular contact (SEBENS, 1982; BRUNO and WITMAN, 1996). However, as for the mesenterial filaments, this was also induced rather occasionally, considering that expanding polyp over the entire day, instead of only during feeding time, associates with higher energetic costs (SEBENS, 1987). In addition to these physical attacks, *T. coccinea* possesses chemical defenses that cause tissue necrosis in scleractinian corals (LAGES et al., 2012; SANTOS et al., 2013). Yet, no signs of a potential chemical attack were observed in *P. caribaeorum*, which agrees with the conclusion of the latter authors that *T. coccinea* uses mainly physical defenses against competitors.

*Palythoa caribaeorum*, in contrast to *T. coccinea*, is known as a strong competitor deploying strategies that affects its competitor in an indirect manner, by overgrowing them without physical contact ("overtopping"; SUCHANEK and GREEN, 1981; Table A1), thereby interfering with the competitor's access to light and/or food and consequently causing their death (LANG, 1971, 1973; PORTER, 1974; BUSS, 1979; SUCHANEK and GREEN, 1981). Also, chemical defense can be expressed by the species, related to a powerful toxin (palytoxin), which can act as an allelochemical that inhibits the larval settlement and the growth of competitors (SUCHANEK and GREEN, 1981). Our experimental findings indicated that the "overtopping" strategy of *P. caribaeorum* was in progress, as shown by the induced upward extension of the zoanthid tissue, as well as its increased vertical growth when grafted with *T. coccinea* (Fig. 14), and thus, we can conclude that over longer term, *P. caribaeorum* would have overgrown the sun coral, which is fully consistent with field observations of the species' interactions at the collection site (Fig. 16).

The aforementioned observed competitive interactions, together with the determinations of the physiological performance of the competitors indicated that they were associated with energetic costs, at least in the case of *T. coccinea*. This was not surprising, as this species deployed physical attacks against *P. caribaeorum,* which usually increase metabolic demands, even though *T. coccinea* attempted to reduce these costs by ceasing the unsuccessful attacks almost completely after the first two weeks of the experiment (Table 3). Yet, the presence of the zoanthid still induced higher metabolic costs in the sun coral, as shown by the twice as high respiratory rates when in contact with *P. caribaeorum*, compared to being hold individually (Fig. 10b). This was most likely related to the observed strategy of full expansion of all polyps, as well as the augmented polyp activity of *T. coccinea* during feeding (Fig. 10a), competing with *P. caribaeorum* for the available food. Long-term, these increased energetic costs, generated by the competitive interactions, will most likely result in resource trade-offs, such as reduced growth and reproductive output, as documented also previously in other scleractinian corals (RINKEVICH and LOYA, 1985; ROMANO, 1990; CHADWICK, 1991; TANNER 1995, 1997). Similarly, trade-offs might also be present in *P. caribaeorum*, as even though the presence of *T. coccinea* did not have any effects on the specie's physiology, considering that its "overtopping" strategy implies highly increased growth rates, both vertically and horizontally, and thus, resources would have to be reallocated from other ecological functions, such as stress tolerance and reproduction. Therefore, it can be assumed that the competition between *T. coccinea* and *P. caribaeorum* will have ecological consequences for both species, potentially affecting their fitness and hence, abundance in the communities.

**Figure 16** Interactions between *T. coccinea* and *P. caribaeorum*, observed under natural settings in the Marine Biological Reserve of Arvoredo (white arrows: "overtopping" strategy of *P. caribaeorum* in progress; orange arrow: polyps leaning away, indicating an avoidance response).



Source: Photography by the author (2019).

### *Competitive interactions and the interplay with temperature*

Interactions between competitors are influenced by abiotic aspects of their external environment and changes can potentially alter the outcome of competitive interactions between corals and other reef invertebrates (e.g., LANG, 1971, 1973; JOHNSTON et al., 1981; ALINO et al., 1992; FINE and LOYA, 2003). The competitive interactions of *T. coccinea* and *P. caribaeorum* studied here over a 15°C-temperature range did not vary significantly with temperature, with exception for the upper thermal tolerance limit of the species at ≥28 and ≥31°C, respectively. Under these conditions, the presence of the competitor reinforced synergistically the negative effects of temperature, resulting in a more dramatic reduction of calcification in *T. coccinea*. In the case of *P. caribaeorum*, the competitive interaction with *T. coccinea* intensified the high-temperature impact on the autotrophic energy input through increased reduction of symbiont performance and increased host respiration. This, in turn, translated in a strong reduction of the zoanthid’s growth rates, thus reducing its competitive ability to overgrow its competitor. Hence, the performance and competitive ability of both species was strongly affected under these conditions; however, more studies over long-term under natural setting, as well as assessments of specie’s capacity for recovery after a stress condition will be needed to determine if this would have an influence on the competitive outcome. Nevertheless, alterations of competitive interactions due to changes in temperature have been known to occur in scleractinian corals (JOHNSTON et al., 1981; FINE and LOYA, 2003) and thus, it was suggested that competitive outcomes might change with season (JOHNSTON et al., 1981; COPE, 1981; LOGAN, 1984; CHORNESKY, 1989). Information on seasonal variation in the performance of *T. coccinea* is missing, but considering for example the seasonal influence on growth rate in *P. caribaeorum* (BASTIDAS and BONE, 1996; RABELO et al., 2013), the possibility of competitive stand-off (*sensu* CONNELL, 1976) with *T. coccinea* or even a competitive reversal of the outcome, depending on season, is feasible.

In addition, our findings of an effect due to the presence of *T. coccinea* on *P. caribaeorum*’s performance and signs of tissue lesion at 31°C, as well as the more deleterious effect observed in *T. coccinea* performance under temperatures that represent stressful conditions for the species, suggests that there may have been some additional interactions between the two species, undetectable under non-stress conditions. Considering that the two species are known to deploy chemical defenses against competitors (SUCHANEK and GREEN, 1981; LAGES et al., 2012; SANTOS et al., 2013), it is conceivable that they were also engaged in chemical warfare, with both species able to withstand the attacks, but that this resistance was affected under stress conditions.

### *Ecological implications*

The Marine Biological Reserve of Arvoredo represents the current southernmost distribution limit of the invasive sun coral *T. coccinea* in the Atlantic (CREED et al., 2017a). Here, the species is found restricted to vertical surfaces, overhangs, caves and crevices, habitats usually not occupied by other species (see Fig. 3d-i), which is consistent with reports from other Brazilian locations and the Gulf of Mexico (DE PAULA and CREED, 2005; FERREIRA et al., 2009; MANGELLI and CREED, 2012; SAMMARCO et al., 2014, 2015) This exploitation of space unsuitable for most resident species, such as the light-dependent symbiotic zoanthid *P. caribaeorum* that occupies the horizontal surfaces (Fig. 3b, c), agrees with a suggestion put forward by Miranda et al. (2018a). These authors suggested that the invasive success of *T. coccinea* can be explained by the niche theory, more specifically through resource partitioning, in this case space. Its restriction to these habitats is also an indication for the low ability of the sun coral to compete with the native cnidarian- and sponge-dominated community at Arvoredo Island (Fig. 17; BOUZON et al., 2012; PICOLOTTO, 2017). According to our experimental findings, *T. coccinea* appears to be unable to prevent overgrowth by *P. caribaeorum*, as even deploying polyp expansion to elevate its feeding structure above the substrate, a seemingly successful strategy when competing with other colonial organisms (WITMAN, 1992), does not appear to be effective. This might be related with the “overtopping” strategy of *P. caribaeorum*, consisting in an elevation of the zoanthid tissue above the substrate and the competitor (~0.65 cm per month recorded here) before moving forward, thus avoiding any physical contact. So, it can be assumed that if the height of the zoanthid tissue exceeds the height of the *T. coccinea* polyps, overgrowth will take place. Indeed, our field observations of the species’ interactions, show that at Arvoredo Island *P. caribaeorum* arches just above (“overtopping”, Fig. 16c-e) or in other cases expands around the margins of the nearby *T. coccinea* colonies ("peripheral encircling", Fig. 16d, f), without obvious soft-tissue injuries, a strategy also reported in competitive interactions among scleractinian corals (LANG, 1973; LANG and CHORNESKY, 1990). It is also consistent with the general assumption that coral taxa that are good competitors in direct contact competition, such as *T. coccinea*, tend to lose in "overtopping" competition (LANG and CHORNESKY, 1990). These findings, however, contradict recently published observations at Búzios Island, Brazil, where *T. coccinea* was suggested to cause necrosis in *P. caribaeorum* (LUZ and KITHARA, 2017). We can only speculate about the reason(s) behind this discrepancy, but it might be related to differences in environmental conditions between the sites that, as discussed above, can influence competitive outcomes, or differences in relative competitive abilities among geographically separated populations. Regarding the former, Sammarco et al. (2015) found that the competitive outcomes between *T. coccinea* and several sponge species were highly variable among offshore platforms exposed to different environmental conditions, indicating that the environment may influence the interactions. Concerning the latter hypothesis, differences among localities have been found in the success of deploying mesenterial filaments by scleractinian corals against opponents (LANG and CHORNESKY, 1990) and also in the expression of palytoxin in *P. caribaeorum*, with toxic and non-toxic populations found in the same region (SOARES et al., 2006; MELO et al., 2012). Thus, it is conceivable that the competitive outcome of the interaction of these two species, as found here at their southernmost distribution limit, may be different in other locations.

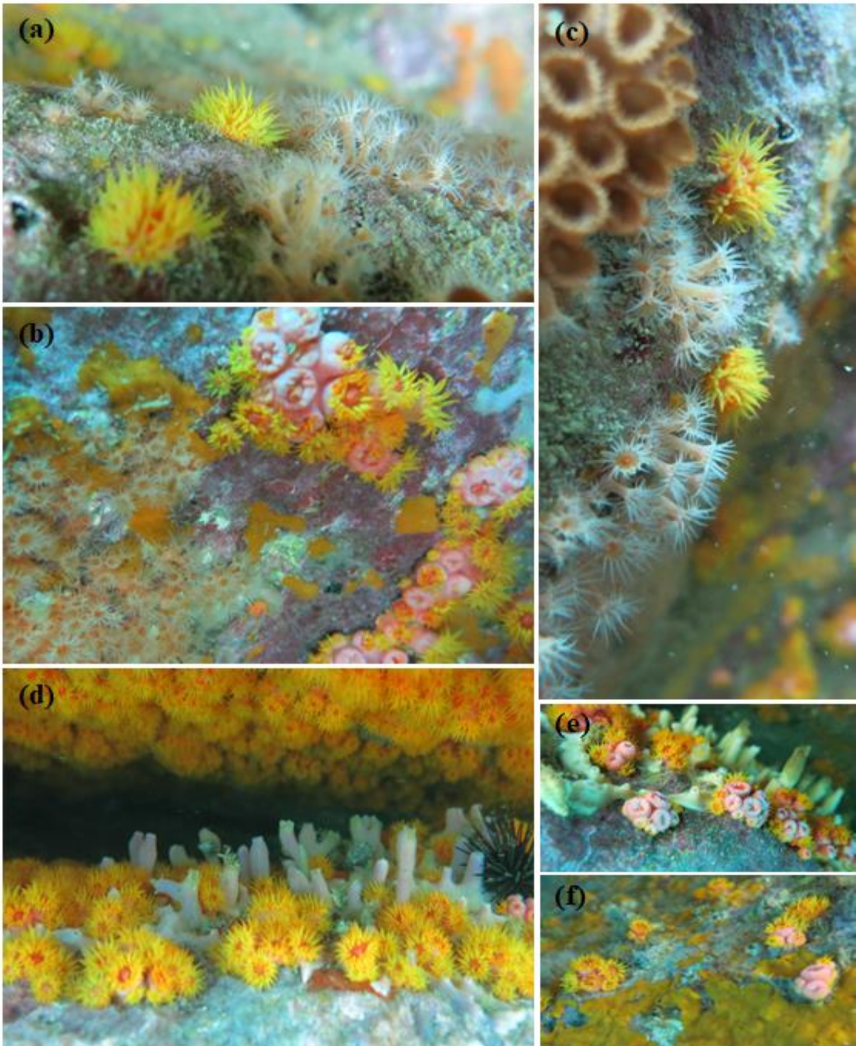
Generally, the successful establishment of non-indigenous species in marine benthic communities is mediated by specific traits (reviewed in PAPACOSTAS et al., 2017), including life history traits such as rapid growth rates, early maturation and high reproductive output, all of them expressed by *T. coccinea* (FENNER and BANKS, 2004; VERMEIJ, 2005, 2006; GLYNN et al., 2008; DE PAULA et al., 2014). However, our study shows that other traits, such as strong competitive ability and those that confer a high plasticity and hence, tolerance to environmental changes, seemed to be less developed.

Information on environmental tolerance of *T. coccinea* is scarce and focused so far solely on specie's thermal responses, but the reported strong impacts of high and low temperatures on adult and larval survival (MIZRAHI, 2008; BATISTA, et al. 2017; LUZ et al., 2018) support our findings of limited plasticity (see Fig. 15) and hence, tolerance to cope with environmental changes. Also, despite coming out as winner in interactions with some cnidarian and sponge species (Table 1), there are several works that support our conclusion on the low to intermedium competitive strength of this species: Cnidarian- (dominated by *Carijoa riisei*, zoanthids, hydroids) and sponge-dominated environments seem to represent obstacles for the successful establishment of the sun coral, as they provide resistance against its spreading (MIZRAHI et al., 2017) and often outcompete *T. coccinea* (VERMEIJ, 2005; DE PAULA, 2007; MEURER et al., 2010; LAGES et al., 2012; HENNESSEY and SAMMARCO, 2014; SILVA et al., 2017). Therefore, the specie's invasive success in the Gulf of Mexico and along the Brazilian coast is associated mainly to *r*-selected life-history traits (rapid growth, early maturation, high reproductive output) (DE PAULA et al., 2014; SAMMARCO et al., 2014; MIRANDA et al. 2018a), rather than strong competitive ability or environmental tolerance. Hence, some regions might present a higher biotic resistance under certain conditions (e.g., Arvoredo Island), resulting in a less severe impact of this invader, due to specific native competitors, such as zoanthids, sponges or the snowflake coral *Carijoa riisei*, able to outcompete *T. coccinea* or inducing high mortality and inhibiting the settlement of its larvae (MIZRAHI et al., 2017; see Table-Annex A). However, it is important to keep in mind that despite some communities being potentially more resistant to the invasion, at a larger scale the generally lower species richness and a higher level of endemism of Brazilian coral reefs, in contrast to the more diverse Gulf of Mexico, where *T. coccinea* does not represent a threat to natural reefs (SAMMARCO et al., 2014, 2015), may facilitate the successful establishment of this invader, as invasion resistance decreases with community diversity (e.g., STACHOWICZ et al., 1999, 2002; LEVINE, 2000). This assumption is supported by the already reported negative impacts of this invader on native scleractinian species, their recruitment and reef ecological processes, and/or through facilitation of the establishment of other invasive species (CREED, 2006; LAGES, et al. 2011; MANTELATTO, 2012; SANTOS et al., 2013; MIRANDA et al., 2018a, b; VINAGRE et al., 2018).

Regarding a potential spread from its current distribution limit in Arvoredo, Santa Catarina, further south towards higher latitudes, our data suggests that the probability is very low: Firstly, because of the specie's high susceptibility to low temperatures, with 100% mortality at 16°C, and secondly, the invader's quite limited plasticity to respond to sudden changes in temperature and high susceptibility to temperatures

≥28°C. The latter may limit the specie's southward extension in the context that the region of Santa Catarina exhibits a trend of increased frequency and intensity of heat waves (GOUVÊA et al., 2017), which will have strong negative impacts on the invader's fitness and hence, survival and spread. Our conclusions, based on the specie's thermal response, however, are not consistent with the predicted potential distribution of *T. coccinea* along the southwest Atlantic coast. These models suggest that also further south from Santa Catarina the habitat is suitable for this species (RIUL et al., 2013; CARLOS-JÚNIOR et al., 2015, 2016). However, it should be pointed out that the models differed in the environmental variables used, as for example temperature was included by Riul et al. (2013), but excluded by Carlos-Júnior et al. (2015, 2016) due to its poor contribution to model gain. Thus, gathering more information about the performance and environmental tolerance of *T. coccinea* under different conditions is needed, as well as on biotic interactions with a broad array of dominant native species that can influence the suitability of a habitat for the invader, to achieve more accurate models of future *T. coccinea* distribution.

**Figure 17** *Tubastraea coccinea* at Rancho Norte (Arvoredo Island) found in association with other benthic invertebrates, such as the zoanthid *Parazoanthus* sp. (a-c) and sponges (d-f).



Source: Photography by the author (2019).

## 2 CONCLUSÃO

Este estudo mostra que a espécie invasora coral sol *Tubastraea coccínea,* encontrada na Reserva Biológica Marinha do Arvoredo (ReBio), tem uma janela de tolerância térmica relativamente estreita, indicando plasticidade limitada para responder a mudanças de temperatura, contrariamente ao seu potencial concorrente, o zoantídeo nativo *Palythoa caribaeorum,* que possui uma faixa de tolerância térmica mais ampla. Além disso, dados experimentais e observações de campo indicam que a espécie invasora no seu atual limite de distribuição no sul do Arvoredo pode potencialmente perder quando em competição com *P. caribaeorum,* uma interação que afeta negativamente a *T. coccinea,* aumentando as demandas metabólicas, sem causar nenhum efeito negativo no zoantídeo. Nossos dados também mostram que a temperatura não exerce influência sobre essas interações, a menos que represente uma condição estressante para as espécies (temperaturas em seu limite térmico superior), sob as quais a presença do competidor reforça os impactos sobre o desempenho fisiológico e de crescimento a ambas as espécies.

## CONISDERAÇÕES FINAIS

Devido aos poucos trabalhos encontrados sobre o coral sol é necessário reunir mais informações sobre o desempenho e a tolerância ambiental de *T. coccinea* sob diferentes condições, bem como sobre as interações bióticas com uma ampla gama de espécies nativas dominantes que podem influenciar a adequação de um habitat para o invasor, para alcançar modelos precisos da futura distribuição de *T. coccinea.*

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# APÊNDICE A – - APPENDIX A

**Table 1.** Summary of reported experimentally and naturally observed competitive outcomes between the invasive sun coral *Tubastraea coccinea*, the zoanthid *Palythoa caribaeorum* and other reef invertebrates. Types of interactions are indicated by superscript letters (mf- mesenterial filaments, c- chemical defense, lm- causes *T. coccinea* larval mortality, ls- inhibits *T. coccinea* larval settlement, o- overgrowth, ot- overtopping, *- on offshore platforms, $^{\#}$- invasive species).

| | | | Competitive outcome | | | |
|---|---|---|---|---|---|---|
| Order | Interacting species | Location | Win | No response | Loss | Ref |
| ***T. coccinea*** | | | | | | |
| Scleractinia | *Mussismilia hispida* | Brazil | $X^{mf,c}$ | | | 4-Jan |
| | *Tubastraea micranthus*$^{\#}$ | Gulf of Mexico | | X | | 5 |
| Alcyonacea | *Carijoa riisei* | Brazil, Colombia | | X | $X^{lm, ls}$ | 6, 7 |
| Corallimorpharia | *Ricordea florida* | Gulf of Mexico | $X^{mf}$ | | | 5 |
| Zoantharia | *Palythoa caribaeorum* | Brazil | X | | | 8 |
| | *Parazoanthus* sp. | Brazil | | | $X^{ls}$ | 6 |
| Actinaria | *Phymanthus crucifer* | Gulf of Mexico | $X^{mf}$ | X | X | 5 |
| | *Condylactis gigantea* | Gulf of Mexico | | X | | 5 |
| Bryozoa | *Virididentula dentata* | Brazil | | | $X^{ls}$ | 6 |
| Sponge | *Desmapsamma anchorata* | Brazil | | | $X^{o}$ | 2, 4, 9 |
| | *Scopalina reutzleri* | Brazil | | | $X^{lm}$ | 6 |
| | *Dragmacidon reticulatum* | Brazil | | | $X^{lm, ls}$ | 6 |
| | *Ulosa* sp. | Curaçao | | | X | 10 |
| | *Dictyonella funicularis** | Gulf of Mexico | X | | X | 11 |
| | *Haliclona vansoesti** | Gulf of Mexico | X | | X | 11 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | *Mycale carmigropila** | Gulf of Mexico | X | | | 11 |
| | *Xestospongia carbonaria** | Gulf of Mexico | X | | X | 11 |
| | *Phorbas amaranthus** | Gulf of Mexico | X | | | 11 |
| | Various species (22) | Brazil | | X | X | 12 |

***P. caribaeorum***

| | | | | | | |
|---|---|---|---|---|---|---|
| Scleractinia | *Acropora* spp. | Caribbean | X$^{ot}$ | | | 13 |
| | *Agaricia agaricites* | Caribbean | X$^{ot}$ | | | 13, 14 |
| | *Dichocenia stokesii* | Caribbean | X$^{ot}$ | | | 13 |
| | *Diploria* spp. | Caribbean | X$^{ot}$ | | | 13 |
| | *Eusmilia fastigata* | Caribbean | X$^{ot}$ | | | 13 |
| | *Favia fragum* | Caribbean | X$^{ot}$ | | | 13 |
| | *Isophyllia sinuosa* | Caribbean | X$^{ot}$ | | | 13 |
| | *Meandrina meandrites* | Caribbean | X$^{ot}$ | | | 13 |
| | *Montastraea cavernosa* | Caribbean | X$^{ot}$ | | | 13, 15 |
| | *Orbicella annularis* | Caribbean | X$^{ot}$ | | | 13 |
| | *Mycetophyllia* spp. | Caribbean | X$^{ot}$ | | | 13 |
| | *Porites* spp. | Caribbean | X$^{ot}$ | | | 13, 14 |
| | *Siderastraea* spp. | Caribbean | X$^{ot}$ | | | 13 |
| | *Stephanocoenia michelini* | Caribbean | X$^{ot}$ | | | 13 |
| Alcyonacea | *Carijoa riisei* | Brazil | X$^{ot}$ | | | 16 |
| | *Pseudopterogorgia* sp. | Caribbean | X$^{ot}$ | | | 13 |
| | *Plexaurella* sp. | Caribbean | X$^{ot}$ | | | 13 |
| | *Erythropodium caribaeorum* | Caribbean | | | X | 13, 14 |
| Hydrozoa | *Millepora* spp. | Caribbean | X$^{ot}$ | | | 13, 14 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Zoantharia | *Zoanthus* spp. | Caribbean, Brazil | X$^{ot}$ | X | | 13, 14, 17, 18 |
| | *Protopalythoa variabilis* | Brazil | X$^{ot}$ | | | 18 |
| Actiniaria | *Bunodosoma caissarum* | Brazil | | | X | 19 |
| Sponge | *Cliona tenuis* | Caribbean | X$^{ot}$ | | | 20 |
| | *Haliclona* sp. | Caribbean | X$^{ot}$ | | | 13 |
| Tunicata | *Trididemnum solidum* | Caribbean | | | X | 21 |
| Bivalve | *Isognomon bicolor*$^{\#}$ | Brazil | X$^{ot}$ | | | 22 |

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