

# Invasive sun corals and warming pose independent threats to the brain coral *Mussismilia hispida* in the Southwestern Atlantic

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**ABSTRACT:** Sun corals *Tubastraea tagusensis* have invaded reef habitats along the tropical-sub-tropical Western Atlantic, negatively impacting native habitat-forming species, including the most abundant scleractinian in Southeastern Brazil, the brain coral *Mussismilia hispida*. We combined field and laboratory experiments to closely evaluate temperature effects on the interaction between these corals. Field experiments undertaken during winter and late summer-fall aimed to test species interactions under current temperature regimes. When in contact with sun corals, all brain corals necrosed (8 to 12 % colony surface mo<sup>-1</sup>). Their growth rates were also lower compared to stand-alone control colonies (−0.17 vs. 1.23 cm<sup>2</sup> mo<sup>-1</sup>). Necrosis was never observed in sun corals, and average growth rates (0.36 cm<sup>2</sup> mo<sup>-1</sup>) did not differ between interacting and isolated colonies. No season effects were detected for any of the coral traits examined. Negative effects of sun corals were further investigated in the laboratory both at current winter (23°C) and summer average temperatures (26°C), as well as extreme low (20°C) and high (29°C) temperature conditions that might persist under a climate-change scenario. Results suggest that species interactions may remain unaffected by climate change. Temperature effects were important but independent of whether brain corals were held isolated or in contact with sun corals. Interestingly, brain corals performed better at 20°C, with most colonies remaining undamaged over 95 d. Sea-temperature increase and the sun coral invasion may thus be viewed as independent drivers potentially impacting brain coral populations and their associated assemblages.

**KEY WORDS:** Biological invasions · Global warming · Interference competition · Chemical ecology · Southeastern Brazil · Rocky reefs

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## 1. INTRODUCTION

Sun corals *Tubastraea* spp. have been recognized as alien and invasive species in the South Atlantic Ocean (e.g. Ferreira 2003, De Paula & Creed 2004, Fenner & Banks 2004). Native to the Indo-Pacific Ocean, they were first reported in Southeast Brazil in

the late 1980s, colonizing oil and gas platforms in the Campos Basin (Castro & Pires 2001). More recently, they have expanded to numerous sites along the Brazilian coast, spanning from north to south the states of Ceará (de Oliveira Soares et al. 2018), Bahia (Sampaio et al. 2012, Creed et al. 2017), Rio de Janeiro (De Paula & Creed 2005, Creed et al. 2017), São Paulo

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(Mantelatto et al. 2011, Creed et al. 2017) and Santa Catarina (Lopes 2009, Creed et al. 2017). The 'invasive' status of sun corals (Global Invasive Species Database, [www.invasivespecies.net](http://www.invasivespecies.net)) is largely due to a unique combination of reproductive and larval traits. Sun coral colonies mature fast (Glynn et al. 2008) and show remarkable regeneration capacity (Luz et al. 2018). Adult colonies also have the ability to reproduce sexually and asexually (Campbell 1983), including fragmentation (Luz et al. 2018) and the release of asexually derived larvae (Capel et al. 2017). Planula larvae can metamorphose into planktonic polyps allowing an extended pelagic phase and thus increasing their dispersal potential (Mizrahi et al. 2014a). Because artificial substrates are often colonized first (Creed & De Paula 2007), harbors, marinas and other coastal facilities built along coastlines may constitute stepping stones holding large reproducing coral populations, while floating oil platforms and commercial vessels may greatly enhance the connectivity among such populations and deliver propagule pressure on as yet uninvaded reefs.

Once established, the biological interactions of sun corals with pre-established assemblages may lead to reduced reef biodiversity and profound alterations of whole-ecosystem functioning. There is evidence of their competitive dominance over native corals (Creed 2006, dos Santos et al. 2013, Miranda et al. 2016) and their capacity to inhibit recruitment of other species through negative allelopathic interactions (Lages et al. 2006, 2011). Moreover, sun corals can cope with substantial environmental change (Lenz et al. 2011) and lack any known natural predators in the Southwest Atlantic (Lages et al. 2010). Combined, all these characteristics may have contributed to the present-day generalized dominance of sun corals at sites where first colonization dates back a decade or more. At some sites from northern São Paulo to southern Rio de Janeiro states, sun corals almost saturate space at patches several tens to a few hundreds of meters long, especially on vertical walls (e.g. Creed 2006, Creed & De Paula 2007, Lages et al. 2011, 2012, Silva et al. 2019). In addition to the exclusion of several fouling species, ultimately reducing reef species richness (Mizrahi et al. 2017), sun corals reengineer reef space and may indirectly cause the near collapse of important components of mobile invertebrate assemblages (Silva et al. 2019).

Still, there is at present no information on the potential effects of climate change on the invasive dynamics of sun corals along the southwestern Atlantic. Understanding the outcomes of species interactions under alternative climate scenarios in this region

is important to predicting how stable sun coral populations will be in their current invasive range and to anticipating any range shifts, chiefly towards southern, presently warm-temperate regions. We tackle this issue by examining competitive interactions between the yellow sun coral *Tubastraea tagusensis* Wells, 1982 and the most abundant native scleractinian in Southeastern Brazil, the brain coral *Mussismilia hispida* (Verrill, 1902) (a species endemic to Brazilian coastal waters; Oigman-Pszczol et al. 2004), under different temperature conditions. Understanding the interaction effects on the endemic brain coral is particularly important because this species may be already threatened (Mazzei et al. 2017). Previous studies showed that sun corals may cause tissue necrosis on *M. hispida*, suggesting a competitive advantage for the alien species (Creed 2006, Miranda et al. 2016), and predicted widespread, strong declines of the native species *M. hispida* as a result of the broad environmental overlap between brain corals and the sun coral *Tubastraea coccinea* (as estimated by species distribution modelling; Riul et al. 2013). Yet, experimental evidence for the outcomes of sun vs. brain coral interactions at different thermal regimes is still lacking.

In this study, we carried out field experiments to examine the interactions between *T. tagusensis* and *M. hispida*, during summer-fall and winter, to test any seasonal trends of the outcome of coral-coral interactions, and then extended the approach in the laboratory to obtain independent evidence of interactions not only at present-day thermal conditions but also at far ranging extremes (warm and cold) that may frequently endure for long periods by 2100 (IPCC 2013, Brazilian Panel on Climate Change [PBMCI] 2014). Historical averages of sea surface temperature ([www.seatemperature.org](http://www.seatemperature.org)) in the native geographic area of *T. tagusensis* (Galapagos) largely overlap the ones observed at the area we conducted this study (Ilhabela, SP, Brazil; Fig. 1), where both this sun coral species and the brain coral *M. hispida* are abundant. Nevertheless, Ilhabela is close to the southern range limit of brain corals, which extends northwards up to Maranhão (northern Brazil, Zilberberg et al. 2014), where average temperatures are much higher (Fig. 1). Even when the species are locally coexistent, the thermal niche of sun corals *Tubastraea* spp., as a whole, should also differ to some extent from that of the brain coral *M. hispida* because *Tubastraea* spp. do not host symbiont zooxanthellae and tend to be distributed in reef habitats with lower light intensity, over vertical and negative surface orientations (Mizrahi et al. 2014b) and at

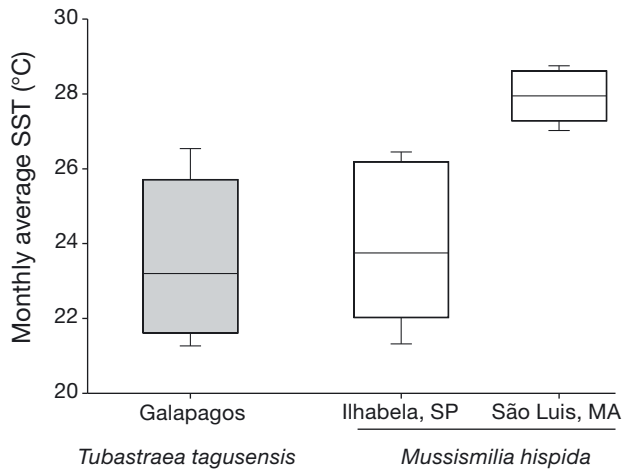


Fig. 1. Box-and-whisker plots, showing 10<sup>th</sup>, 50<sup>th</sup> and 90<sup>th</sup> percentiles, of monthly sea-surface temperature averages (covering a period of >100 yr; [www.seatemperature.org](http://www.seatemperature.org)) of sun coral *Tubastraea tagusensis* and brain coral *Mussismilia hispida* in native areas. *T. tagusensis* were originally restricted to Galapagos (left), and *M. hispida*, while endemic to the Brazilian coast, are distributed from São Paulo State, close to our study area (Ilhabela), to Maranhão State (São Luis, right)

greater depth, where temperature may be considerably lower. Thus, we predicted that the outcome of competitive interactions between *M. hispida* and *T. tagusensis* would be less detrimental for the former species in a warming scenario.

## 2. MATERIALS AND METHODS

### 2.1. Seasonal interactions in nature

#### 2.1.1. Fieldwork

Coral performance was assessed at Búzios Island, 25 km off the coast of São Paulo state, Brazil, during the summer-fall (from 26 January to 5 May) and winter (from 13 June to 19 September) of 2017, over 98 d each season. We compared coral performance when colonies were held isolated or in heterospecific pairs. Through SCUBA diving, small *Tubastraea tagusensis* (T;  $33.1 \pm 17.4$  cm<sup>2</sup>) and *Mussismilia hispida* (M;  $70.6 \pm 45.8$  cm<sup>2</sup>) colonies were removed using hammer and chisel and then randomly fixed with epoxy cement (Tubolit®) to nearby new sites at the same depth (7 to 10 m) and substrate orientation (nearly horizontal), identified with numbered plastic tags. The whole experiment was conducted within an area of nearly 150 m<sup>2</sup>. Five treatments were applied to each coral species: single colonies were either (1) transplanted and held isolated (Tt, Mt), or (2) trans-

planted to the side of a heterospecific colony, allowing physical contact by moving either *T. tagusensis* (MTt) or (3) *M. hispida* (TMt), or (4) not transplanted but otherwise in contact with the epoxy cement to control for any possible effects of this material on coral performance (Te, Me), or (5) control colonies, naturally found isolated and left untouched (Tc, Mc). Sample size in each treatment was 7. In all cases, the rock surface around colonies (ca. 5 cm) was scraped off to minimize any effects of other sessile organisms on corals. All experimental colonies were photographed every 10 to 20 d, depending on weather conditions, comprising 8 sampling dates for the summer-fall season and 7 dates for the winter season. Images were then processed to estimate rates of colony growth (as increments of basal area; cm<sup>2</sup> mo<sup>-1</sup>) and tissue necrosis (percent mo<sup>-1</sup>), using the software ImageJ 1.50b (Schneider et al. 2012) (<http://imagej.nih.gov/ij/index.html>), as well as to spot the first appearance of turf filamentous algae over the damaged coral surface. Temperature was recorded every 2 h over the 2 sampling seasons with i-button® loggers.

#### 2.1.2. Statistical analyses

For each focal replicate colony of either *T. tagusensis* or *M. hispida*, estimates of percent tissue necrosis and growth were obtained by regressing these variables against time (thus providing monthly rates of change). Two-way factorial GLMs were used to test any contrasts of necrosis and growth rates according to 'treatment' (as explained above) and 'season' (summer-fall vs. winter), both considered fixed factors. Growth data for both species were heteroscedastic and remained so after log-transformation. GLMs were still used in these cases because the sampling size was sufficiently large and the analysis is balanced (Underwood 1996). After obtaining omnibus mean-square error estimates for overall treatment effects, we proceeded to planned comparisons testing for (1) artifact epoxy effects (control vs. cemented colonies), (2) artifact transplant effects (cemented colonies vs. cemented colonies transplanted elsewhere), (3) overall effects of species contact interactions (stand-alone vs. interacting colonies), and (4) status-specific effects of contact interactions (interacting transplanted vs. interacting non-transplanted colonies). Necrosis was only observed in interacting brain corals, and therefore contrasts were restricted to Test 4, for both seasons. In this case, the SNK procedure was used for *post-hoc* pairwise comparisons. The proportion of damaged colo-

nies overgrown by turf algae was compared between seasons using a 2-tailed z-test.

## 2.2. Interactions under average present-day and extreme future temperature conditions in the laboratory

### 2.2.1. Laboratory work

Small colonies of the sun coral *T. tagusensis* (maximum diameter  $3.7 \pm 0.5$  cm) and the brain coral *M. hispida* (maximum diameter  $5.0 \pm 1.2$  cm) were collected in November 2016 at Búzios Island and brought to the Centre for Marine Biology, University of São Paulo (CEBIMar - USP). All attached organisms were removed with tweezers, then coral colonies were acclimated for 2 mo in indoor 500 l tanks, provided running seawater pumped from a near-shore inlet, with no temperature control (average daily minimum and maximum temperature:  $22.1 \pm 1.9^\circ\text{C}$  and  $26.6 \pm 2.8^\circ\text{C}$ ).

We examined the performance of individual brain coral colonies over 4 mo (from 1 Feb to 8 May 2017), either alone or in heterospecific pairs (allowing physical contact between colonies), across different temperature regimes based on historical monthly averages and annual warming rates calculated by Valentin et al. (2013), and temperature extreme events (both warming and cooling) expected in our study region by 2100 (IPCC 2013, PBMC 2014). To maintain temperature regimes as close as possible to target ranges, we set the room temperature to  $25^\circ\text{C}$ , while maintaining a natural photoperiod (12 h light: 12 h dark), and used chillers or heaters to adjust the temperature to treatment specifications in four 150 l reservoir tanks that supplied experimental units. We were able to set conditions closely matching the (1) average current winter temperature (treatment 'C';  $23.3 \pm 2.5^\circ\text{C}$ ), (2) the average current summer temperature (treatment 'H';  $26.3 \pm 1.8^\circ\text{C}$ ), and the temperature compatible to (3) winter cold fronts (treatment 'C-';  $20.3 \pm 1.8^\circ\text{C}$ ), and (4) summer heat waves (treatment 'H+';  $29.3 \pm 2.5^\circ\text{C}$ ), which are expected to be more prolonged and frequent in the future.

A water pump constantly replenished reservoir tanks with filtered sea water (through a sequence of 100, 50 and 10  $\mu\text{m}$  meshes), and the water flow set to individual experimental tanks (1 l circular units; diameter: 14 cm, height: 7.5 cm) was approximately  $1.0 \text{ ml s}^{-1}$ , allowing the water to be renewed 3 to 4 times each hour and the temperature to remain close to that of the source reservoir tank. For each temper-

ature regime, 5 circular replicate tanks were used for 2 different treatments: *M. hispida* alone and *M. hispida* interacting with *T. tagusensis*. All coral colonies were randomly distributed in experimental treatment combinations, and all tanks occupied random and shifting positions over the working space. Every other day, corals were fed living plankton ( $>150 \mu\text{m}$ ) *ad libitum* and inspected for tissue necrosis or death (devoid of any living tissue).

### 2.2.2. Statistical analyses

Survival analysis was used to examine damage rate, based on the time when necrosis was first observed for any given colony, across factors 'temperature' (C-, C, H, H+) and 'species interaction' (stand-alone vs. interacting colonies). In some cases, healthy colonies died over the next 2 d without intermediate tissue loss, and therefore damage rates combine necrosis and deaths. The Kaplan-Meier analysis (Kaplan & Meier 1958) was applied to obtain survival probabilities (i.e. the percentage of healthy colonies) of coral colonies from different experimental treatments over time. The Cox proportional-hazards regression (Fox & Weisberg 2011) was used to model and test the significance of the experimental factors on coral survival. This method assumes that the hazard of an event at a given time can be modeled by the product of a baseline hazard function and a regression function of tested covariates (Sinnott & Cai 2016). Analyses were performed in R v.3.2 using the functions *survfit* and *coxph* from the 'Survival' package (R Core Team 2014).

## 3. RESULTS

### 3.1. Seasonal interactions in nature

*In situ* temperature regimes were strikingly different between the 2 sampled seasons. During the summer-fall period, temperatures varied more uniformly around a median value of  $25.0^\circ\text{C}$ , while during winter, the temperature distribution was clearly left-skewed, with a median value at  $20.7^\circ\text{C}$  and repeated observations near extreme low values (Fig. 2). These are in general lower values than historical averages. During the warmer season, daily averages never reached the 29 to  $30^\circ\text{C}$  range at which native corals in the region start bleaching (Migotto 1997), and, notably, at the end of the cooler season, temperature ranged between

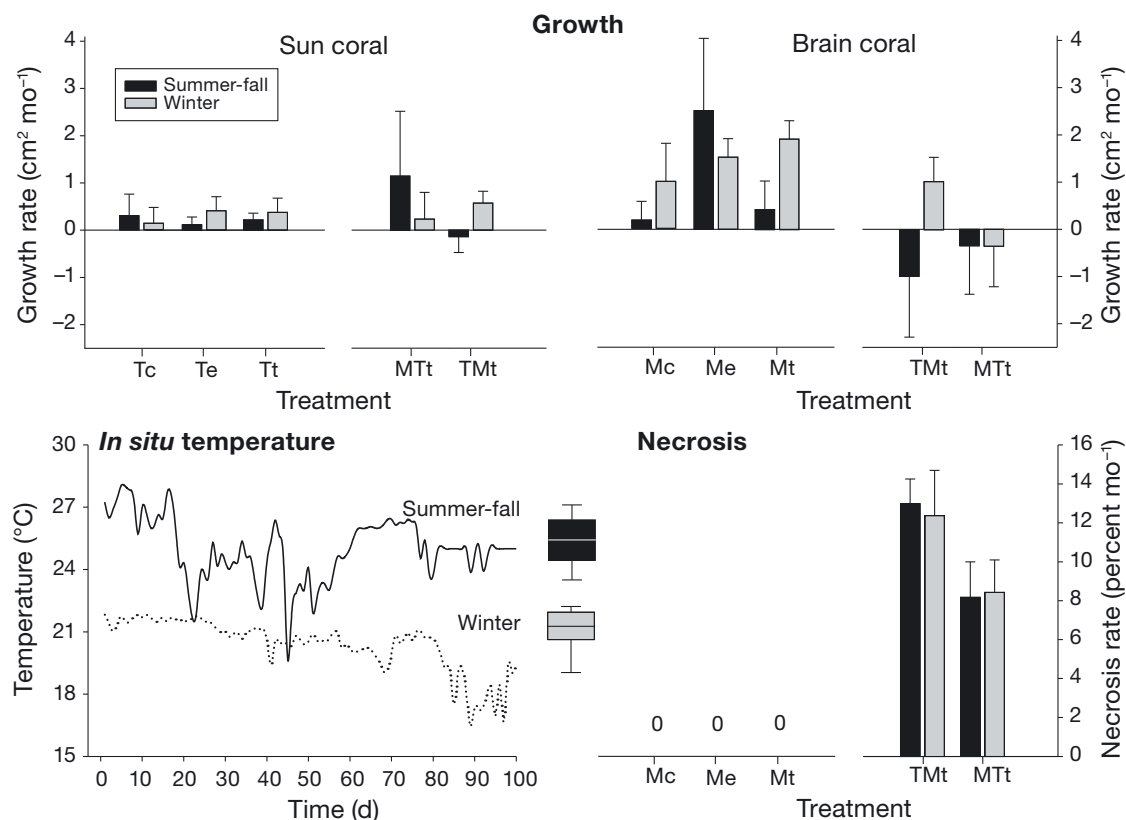


Fig. 2. Results of the field experiment testing the outcomes of species interactions for both the invasive sun coral *Tubastraea tagusensis* (T) and the native brain coral *Mussismilia hispida* (M) in 2 different seasons. Treatments in which colonies were held isolated served both as controls (lowercase c), and procedural controls for possible effects of epoxy cement (lowercase e) and transplanting (lowercase t), as well as a baseline for colony performance without interspecific contact interactions. TMt and MTt stand for interacting treatments in which the transplanted colonies were *M. hispida* and *T. tagusensis*, respectively. Error bars stand for +1 SE. Boxplot specifications representing the thermal conditions at the sampled seasons were the same as in Fig. 1

16 and 18°C for half a month. Despite the great difference between temperature regimes during the sampled seasons, there were no seasonal effects on any of the coral traits examined in this study, including the outcome of species interactions (Table 1, Fig. 2).

Necrosis was never observed in sun corals *Tubastraea tagusensis*, and differences in growth rates among treatments, which included isolated and interacting colonies, were not significant (Table 1). Yet, responses were clearly more variable for the pool of the 2 interacting treatments (coefficient of

Table 1. Summary results of 2-way GLMs testing seasonal effects of interspecific contact interactions (treatment) on sun coral *Tubastraea tagusensis* and brain coral *Mussismilia hispida* in the field (Ilha de Búzios, SP, Brazil). Response variables were growth (basal area) and the apparent area of tissue necrosis; the latter was never observed in the sun coral. The p-values of significant sources of variation are in **bold**. C stands for the Cochran statistic testing for variance heterogeneity

	Growth (mm <sup>2</sup> mo <sup>-1</sup> )					Necrosis (% mo <sup>-1</sup> )		
	df	Sun coral		Brain coral		df	Brain coral	
		<i>F</i>	p	<i>F</i>	p		<i>F</i>	p
Treatment	4	0.23	0.920	2.61	<b>0.044</b>	1	5.79	<b>0.024</b>
Season	1	0.00	0.987	2.26	0.138	1	0.01	0.919
T × S	4	0.77	0.552	1.37	0.256	1	0.06	0.811
Res	60					24		
		ln-transformed		ln-transformed			Raw data	
		<i>C</i> = 0.8056; p < 0.01		<i>C</i> = 0.3568; p < 0.01			<i>C</i> = 0.4144; p > 0.05	



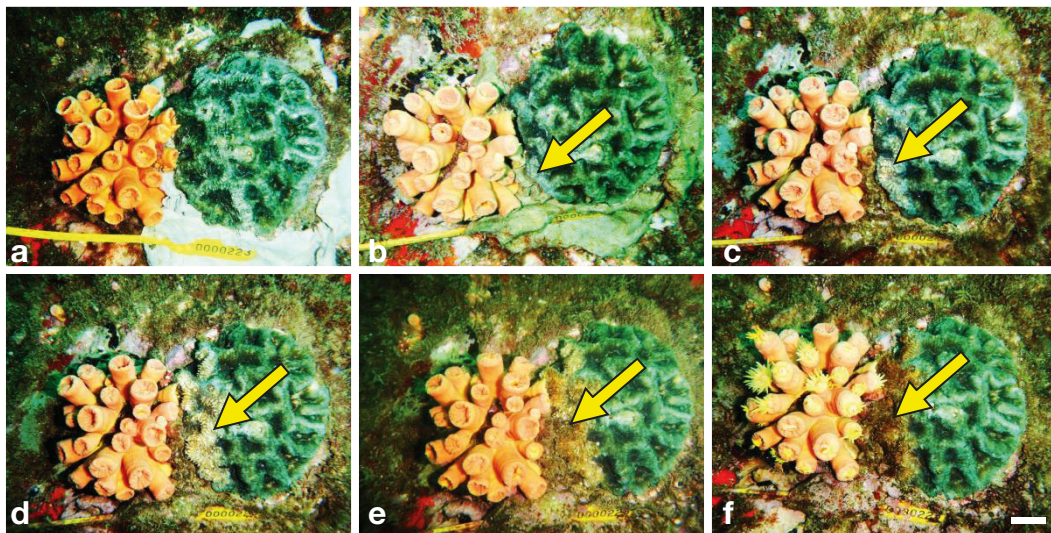


Fig. 3. Temporal change of a transplanted brain coral colony in contact with a pre-established sun coral colony during winter. Yellow arrows point to necrosed brain coral tissue from (c) onwards. Note a conspicuous cover of filamentous green algae over dead coral areas in panels e–f. (a) Day 0, (b) Day 13, (c) Day 29, (d) Day 43, (e) Day 56, (f) Day 77. Scale bar = 2.5 cm

variation [CV] = 48.4%) compared to the pool of stand-alone treatments (CV = 39.2%; Fig. 2), but the responses were still around the overall growth rate estimate ( $0.36 \pm 0.16 \text{ cm}^2 \text{ mo}^{-1}$ ). Although low, growth estimates differed significantly from zero ( $t = 2.25$ ;  $p < 0.05$ ).

In contrast, contact interactions with sun corals greatly affected growth rates and tissue necrosis in brain corals *Mussismilia hispida* (Table 1, Fig. 2). The growth rate estimate for overall stand-alone treatments (Mc, Me and Mt) was  $1.26 \pm 4.6 \text{ cm}^2 \text{ mo}^{-1}$  (Fig. 2), and planned comparisons evidenced no artifact effects of contact with epoxy cement (Mc vs. Me;  $F = 2.75$ ,  $p = 0.102$ ) nor any artifacts owing to the transplantation procedure itself (Me vs. Mt;  $F = 0.96$ ,  $p = 0.329$ ). Growth rates, however, greatly decreased when colonies were held in contact with the sun coral ( $-0.17 \pm 6.21 \text{ cm}^2 \text{ mo}^{-1}$ ; Fig. 2), with the respective planned contrast indicating this is a significant difference (Mc-Me-Mt vs. MTt-TMt;  $F = 6.55$ ,  $p = 0.013$ ). There was no apparent relevance of whether the transplanted species was *M. hispida* or *T. tagusensis* (TMt vs. MTt;  $F = 1.62$ ,  $p = 0.208$ ; Fig. 2). Growth responses were generally more variable for *M. hispida* compared to *T. tagusensis*, with no substantial differences for stand-alone brain corals (CV = 55.8%) and interacting individuals (CV = 56.4%). Tissue necrosis was never detected for isolated brain coral colonies but was observed for all individuals in contact with sun corals. In contrast to growth rates, necrosis rate depended on the transplanted coral

species (Table 1). Brain corals transplanted to the vicinity of a sun coral colony suffered higher necrosis rates than brain corals in contact with a transplanted sun coral colony (12 and 8% tissue loss each month, respectively; Fig. 2). After necrosis, bare coral skeleton was frequently overgrown by filamentous turf algae at some point during the experiment (Fig. 3). However, the proportion of damaged colonies covered by algal turf was higher during winter-fall (0.93) compared to summer (0.57;  $z = 2.18$ ,  $p = 0.015$ ).

### 3.2. Interactions at average and extreme temperature conditions in the laboratory

Survival analyses indicated that damage rate on brain corals depended on both the temperature regime and whether or not colonies were held alone or in contact interaction with sun corals (Table 2, Fig. 4). Only main effects were detected, without interactions between the 2 factors. Hence, the initial

Table 2. Survival analysis results on *Mussismilia hispida* damage rates. The interaction between factors 'temperature' and 'coral interaction' was not significant ( $p > 0.05$ )

	<i>Mussismilia hispida</i> necrosis		
	Hazard rate	z	p
Temperature	1.8113	3.556	<b>0.0004</b>
Coral interaction	4.1023	3.453	<b>0.0006</b>

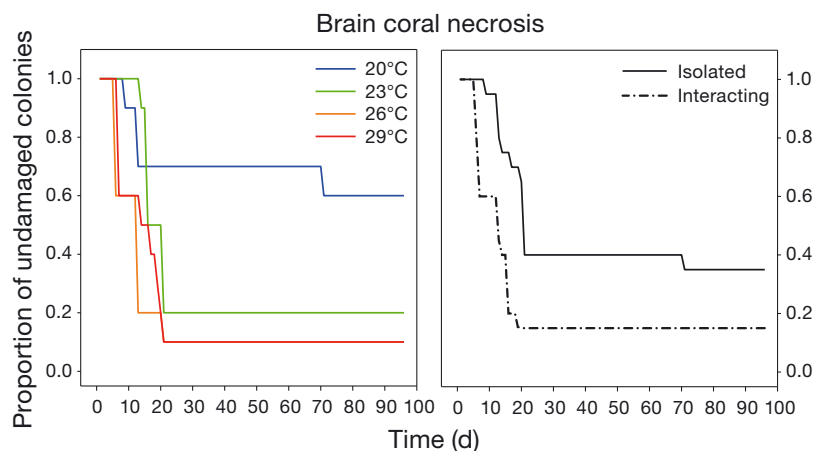


Fig. 4. Result of survival analysis showing the decay of the proportion of undamaged brain coral colonies according to temperature and whether or not colonies were placed in contact with a sun coral colony

prediction that damage rates through contact interactions would be reduced at higher temperatures finds no support. In fact, regardless of the interaction status, brain corals performed better at the coldest temperature regime (20°C; Fig. 4), compatible to the unusual cold season we sampled in the field and a more likely scenario during future cold fronts. Of the 10 colonies held in this treatment, 6 remained undamaged until the end of the experiment (95 d), of which 3 were isolated and 3 were interacting individuals. Brain coral performance at all the other temperature treatments was similar, with undamaged colonies making up only 10 to 20% of initial stocks by Day 20. The overall effect of contact interactions is clear (Table 2); decay curves never crossed over time, and at the end of the experiment, the proportion of undamaged colonies was 35% for isolated individuals and only 15% for colonies maintained in contact with the sun coral (Fig. 4).

#### 4. DISCUSSION

Competition for space is often cited as a major mechanism influencing the structure of hard-bottom benthic ecosystems (Menge 1976, Lubchenco 1980), including coral reefs (Lang & Chornesky 1990, Karlsson 1999). Negative interspecific interactions between corals are frequent, and competing individuals often experience reduced growth rates (Sammarco et al. 1983, Tanner 1997) or damage through direct interference (Lapid et al. 2004, Hennessey & Sammarco 2014). When in equilibrium, coral interactions combined with environmental change may actually promote whole-reef diversity, either through reci-

procal interaction outcomes between species with similar competition capacity or through disturbance-mediated declines of superior competitors, which provide the opportunity for the establishment of several different species that would be otherwise absent (Connell 1976, Porter et al. 1981, Connell et al. 2004). Our results, however, indicate that contact interactions between sun and native brain corals, presently the most important scleractinians along the subtropical southwest Atlantic, may further contribute to the impoverishment of reef systems owing to the dominance of invasive sun corals *Tubastraea* spp.

In this non-equilibrium state, species traits challenge the traditional view (Connell 1976) that high growth rates are characteristic of strong competitors and that the capacity to deter neighboring heterospecifics, either through extra-coelenteric digestion (Lang 1973) or negative allelopathy (Sammarco et al. 1983), is a defensive response of weak competitors. Here, we showed that stand-alone *Mussismilia hispida* colonies are capable of much higher growth rates than isolated *Tubastraea tagusensis* colonies, and that negative contact effects are restricted to those of *T. tagusensis* on *M. hispida*, never the other way around. Still, we regard sun corals as the competitively superior species because effects on brain corals are not limited to tissue necrosis (and thus defense), extending to growth potential. Regardless of season, overall growth rates of brain corals turned negative ( $-0.16 \text{ cm}^2 \text{ mo}^{-1}$ ) and necrosis ranged between 8 and 12% when in contact with sun corals. Although varying in a relatively narrow range, necrosis estimates should be interpreted carefully because the identity of the transplanted species mattered. Since the overall abundance of sun corals is increasing everywhere in the region, and because sun corals strongly inhibit the settlement of other fouling organisms nearby (both sessile and encrusting; Lages et al. 2010), potential necrosis rates upon contact are probably closer to the lower estimate (ca. 8%), obtained for contact interactions in which *T. tagusensis* was the transplanted species. That is, physical contact should take place mostly after a sun coral settler has grown to touch a pre-established brain coral. Even at an 8% rate, tissue necrosis and reduced growth combined would lead to death of *M. hispida* colonies in <1 yr, regardless of season,

assuming that the estimated rates will hold until total tissue necrosis. Of course, these results are only applicable to small brain coral colonies within the size used in this study. Other things being equal, larger colonies would suffer less tissue damage, as observed for *M. hispida* interacting with macroalgae (Ferrari et al. 2012) and zoanthids (Cruz et al. 2016).

It is interesting to note, however, that growth rates of interacting colonies of both brain and sun corals are highly variable, in the case of the latter species contrasting with the markedly uniform growth rate observed for stand-alone treatments. Such plastic responses introduce some degree of uncertainty in the long-term effects of heterospecific contact interactions. There is considerable debate on whether adaptive evolution is restrained (through genotype 'shielding') or facilitated (through genetic 'assimilation' of adaptive phenotypes) by trait plasticity (Price et al. 2003, Ghalambor et al. 2007), but relative consensus that genetic variation may underlie faster directional selection towards the 'optimal' phenotype upon environmental change (e.g. Rainey & Travisano 1998, Barrett & Schluter 2008). Contact interactions between sun and brain corals constitute a novel situation for both species, and, thus, whether or not there is room for adaptive evolution to a favorable phenotype (i.e. resistant to contact with heterospecific corals) becomes a relevant question. Present-day average outcomes suggest a very negative scenario for brain corals, but strong genetic structure along the Southwest Atlantic (Peluso et al. 2018), coupled with the highly variable growth response of interacting individuals, suggests there is potential for selection of more resistant genotypes. In contrast, prevailing asexual reproduction with high proportion of clones and lack of genetic structure along the invaded region (Capel et al. 2017) suggests there is virtually no room for genetically based improvements of the competitive ability of sun corals in the future. As such, we speculate that brain corals may be eventually better defended against sun coral contact interactions in the long-term. Brain coral colonies capable of maintaining control-like growth rates, as observed for some individuals in winter for the TMT treatment, may have some extra time to spawn before tissue necrosis advances to a critical extent and therefore have lesser negative indirect impacts on propagule production and recruitment.

The lack of detectable seasonal effects suggests that present-day temperature variation is insufficient to modulate the outcome of interactions between sun and brain corals. Namely, departures from eventual temperature optima for these 2 species would not

underlie, nowadays, any apparent arms-race in the capacity of sun corals to directly damage neighbor brain corals or the ability of the latter to recover. Interestingly, overgrowth of necrosed *Mussismilia* tissues by filamentous algae was very common and could have played an indirect but important role on the mediation of direct coral interactions. McCook et al. (2001) reviewed the experimental work examining the interaction between corals and the algae overgrowing them and found that the few studies allowing a proper test for cause-effect relationships provided different conclusions. There is general agreement that algae do not cause tissue damage or bleaching in the first place, but rather use inert coral surface opportunistically. Once established, however, most studies did report negative effects of algae on their host corals (shading, abrasion or smothering causing reduced growth, reproductive output or even death), but some work revealed neutral effects. For instance, mixed-species algal turf, preventing the proliferation of a harmful red filamentous alga, causes no measurable effects on massive *Porites* spp. (Jompa & McCook 2003), even along a gradient of terrestrial inputs that could have increased turf dominance and competitive superiority (McCook 2001). In our study region, the concentration of nutrients in the water column is usually markedly low (Flores et al. 2015), but higher nutrient concentration owing to vertical mixing during the passage of cold fronts may increase primary production in wintertime (Ciotti et al. 2010). The seasonal trend of primary production could explain why nearly all damaged brain coral colonies were overgrown by filamentous algal turfs in winter, but only 57 % were overgrown during summer-fall. Considering the evidence to date, we would thus expect a much worse performance of damaged colonies in winter compared to summer-fall, but no seasonal effects were detected. As such, our result is aligned to the fewer studies suggesting null effects of overgrowing algal turfs. At this stage, it is difficult to identify the mechanisms cancelling out any stresses that overgrowing algae may impose to corals at the edge between necrosed and living tissues, but it is possible that filamentous turf growing at the contact zone between corals (as experimental nylon mesh screens; dos Santos et al. 2013) may actually protect *M. hispida* from further aggression. Further experimental work is needed to tease apart the effects of these and other possible mechanisms controlling the performance of interacting brain corals in the field.

In contrast with the field results, laboratory trials testing effects at average and extreme conditions showed that temperature may play an important role



in the damage caused to brain corals, independently of contact interactions. We hypothesized that hetero-specific interactions would be less detrimental to brain corals in warmer conditions, because brain corals are found over a wide latitudinal range, expanding to warmer-water ecoregions, but over a short depth range, restricted to well-lit shallow reef habitats where the temperature is higher. The results, however, do not support this prediction. In fact, regardless of whether or not individuals were held in contact with a heterospecific, brain coral colonies did worse at temperatures above 25°C, similarly to the congener *Mussismilia harttii*, which suffers tissue necrosis at temperatures between 26.5 and 35.0°C (Winter et al. 2016). Interestingly, at the coolest temperature treatment, ~20°C, 60% of *M. hispida* colonies remained undamaged at the end of the experiment, even when in contact with the sun coral ( $n = 3$ ). While this result suggests that brain corals would be particularly resistant over prolonged periods of cool water, extrapolations to natural conditions should be addressed with caution, since all interacting brain colonies necrosed in the field, with no exception, during both summer-fall and winter. Clearly, other environmental variables not controlled in the laboratory mediate the outcomes of interspecific coral interactions in nature. Still, it is noteworthy that at Arraial do Cabo, RJ, an area prone to extensive upwelling, sun coral colonies and recruits become less abundant at sites where the average temperature is <20°C (Batista et al. 2017). Since thermal conditions are favorable and competition with sun corals relieved, brain corals may thus thrive at similar upwelling spots. In contrast, the ongoing warming of most coastlines along the Southwest Atlantic will likely impact brain corals the most (as indicated by bleaching; Dias & Gondim 2016), chiefly because they tend to colonize warmer reef habitats (shallow and horizontal). Unlike sun corals, *M. hispida* relies on the primary production of zooxanthellae, which are very susceptible to warming (Hoegh-Guldberg 1999). Prolonged warming to ca. 1°C over maximum average summer temperature typically causes the photo-inhibition of zooxanthellae, their death and ultimately coral bleaching (Hughes et al. 2003), and this might have caused the exceedingly high damage rate observed for brain corals in the 29°C treatment. Tissue necrosis and bleaching would therefore contribute to decrease brain-coral populations. It is not still well understood how warming will affect the development of sun coral patches spreading to near-surface habitat. More specific work should be carried out to investigate whether sun corals perform better

during extreme warming events and are thus capable of displacing brain corals even in the shallowest, best-illuminated reef habitats.

The brain coral *M. hispida* is not only the most important native scleractinian in the study region but also a host for >130 different invertebrates, comprising mobile, fouling and endolithic species, some of those using this biogenic habitat as a nursery ground (Nogueira 2003). Severe declines of brain coral populations may negatively impact not only biological diversity but also ecosystem functioning, because the replacement of autotrophic brain corals by heterotrophic sun corals may profoundly alter food webs (Mantelatto 2011). Also, the invertebrate fauna associated to invasive sun corals is overall less abundant compared to the assemblages hosted by the native natural fouling communities they replace, especially micro-crustaceans that virtually collapsed in saturated sun coral patches, with likely negative effects on invertivore reef fishes (Silva et al. 2019). At reef habitats where the invasion history is still recent, heavy sun coral colonization is almost restricted to preferred vertical surfaces (Mizrahi et al. 2014b), and therefore brain corals are relatively safe because they tend to concentrate at flat horizontal surfaces where light conditions are more adequate. However, sun corals may also occasionally settle (Mizrahi et al. 2014b) and thus spread to horizontal reef substrates as their abundance increases, with contact interactions putting the native coral species at risk. Any efforts to protect *M. hispida* populations would thus target flat reef habitat, when the density of sun coral colonies is still low and removals are feasible. Laboratory rearing of recruits and their transplantation to favorable habitat may also be viewed as a complementary procedure to protect brain corals because we observed no effects of moving colonies from one place to another, and also no effects of contact with epoxy cement, compared to control colonies in the same area. Therefore, assisted recovery of degraded reefs (Rinkevich 2014, Rodgers et al. 2017) is likely an appropriate restoration strategy, especially if transplant individuals are still young brain coral colonies with growth rates that exceed the ones observed for invasive sun corals.

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