

Antagonism between invasive pest corals *Tubastraea* spp. and the native reef-builder *Mussismilia hispida* in the southwest Atlantic



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ABSTRACT

The biological invasion of the scleractinian corals *Tubastraea coccinea* and *Tubastraea tagusensis* into the Atlantic has resulted in their juxtaposition with native reef corals. We used microcosm and field experiments to investigate and separate the effects of chemical vs. physical mechanisms potentially responsible for observed antagonistic interactions between the invasive corals and the endemic (southwest Atlantic) reef-building coral *Mussismilia hispida*. In the short term microcosm experiment *M. hispida* extruded a substantial amount of mesenterial filaments in an aggressive response to proximity to both invasive species within a few hours. However, in the field only the native coral suffered necrosis, which was visible after only four days. The use of physical barriers to separate chemical and physical effects demonstrated that antagonistic effects were far greater in the absence of a physical barrier than in the partial or complete barrier treatments, so although there is evidence that these invasive corals may produce allelochemicals against possible competitors we demonstrated that the main mechanism *Tubastraea* spp uses to exclude the native coral species is principally a rapid physical response.

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1. Introduction

Biological invasions can affect the integrity of natural communities, influence species interactions and alter food webs and nutrient cycles (Carlton and Geller, 1993; Crooks, 1998; Grosholz and Ruiz, 1996; Lafferty and Kuris, 1996; Lodge, 1993; Vitousek, 1990). Moreover, invaders can compete with native species and change the rules of existence for all species by altering ecosystem processes (Vitousek, 1990). Since some invasive species may cause extinction of native species, increasing introductions will lead inevitably to further reductions in global biodiversity (Lodge, 1993).

The scleractinian corals *Tubastraea coccinea* Lesson 1829 and *Tubastraea tagusensis* Wells 1882 originate from the Indo Pacific region and were first reported off the Brazilian coast in the 1980's, encrusting oil and gas platforms in the Campos Basin, state of Rio de Janeiro (Castro and Pires, 2001). In the 1990's *Tubastraea* spp. were observed on the tropical rocky shores of southeast Brazil (De Paula and Creed, 2004) at Ilha Grande Bay, where most subsequent studies of this biological invasion have been concentrated (Creed et al., 2008). Ilha Grande Bay has eleven conservation areas and the region is known for its high marine biological diversity and ecological significance compared to adjacent regions (Creed et al., 2007). The biological invasion represents a serious threat to the local marine biodiversity because the invasion of

these congeners is thought to be harmful to native species through negative competitive interactions (Creed, 2006) and also modifies whole benthic communities (Lages et al., 2011).

The scleractinian *Mussismilia hispida* Verrill 1902 (Mussidae) is not only a member of a genus endemic to Brazil but also one of the most widely distributed coral species along the Brazilian coast (Laborel, 1969; Oigman-Pszczol and Creed, 2004). Species Distribution Modeling has recently shown that this native species and the invasive *Tubastraea* spp. have similar ecosystem requirements and overlapping distributions (Riul et al., 2013). Field observations have shown that in 100% of *M. hispida*-*Tubastraea* spp. contacts *M. hispida* exhibited tissue necrosis when found in proximity (≤ 5 cm) to the invasive corals, but the effect was not reciprocal; it has been suggested that the invasive corals can reduce or exclude the native species (Creed, 2006). Furthermore, manipulative experiments have investigated the competitive potential of *Tubastraea* spp. and the results demonstrated inhibition of certain calcareous algae and tissue necrosis on *M. hispida*, when transplanted close to the invasive species (De Paula, 2007).

Competition for space is an important determinant of the distribution, abundance and diversity of sessile invertebrates (Jackson, 1979; Jackson and Buss, 1975), since the space for settlement and growth of scleractinian corals can be a highly limiting resource in marine hard-substrate environments (Connell et al., 2004; Foster et al., 2008). Corals may compete indirectly via overtopping, whereby one colony overshadows another or directly, contacting and damaging the soft tissues of opponents (Connell, 1973). Scleractinian corals have evolved mechanisms to compete directly with neighboring animals for space, including:

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1) extracoelenteric digestion, whereby the mesenterial filaments normally used for feeding serve as aggressive organs and digest the tissues of adjacent corals (Lang, 1973); 2) sweeper tentacles which are elongate tentacles with nematocysts that develop from normal feeding tentacles (Hidaka and Yamazato, 1984); 3) sweeper polyps (Peach and Hoegh-Guldberg, 1999). When corals of different species are placed into direct contact, the mesenterial filaments can be deployed within hours and then digest tissues on the opposing coral (Lang, 1971, 1973). On some corals, sweeper tentacles may develop after damage by mesenterial filaments (Bak et al., 1982; Chornesky, 1983; Wellington, 1980) or after contact and recognition of other corals (Chornesky, 1983). The morphogenesis of sweeper tentacles occurs over several weeks following the initiation of contact with certain cnidarian competitors (Chornesky, 1983).

As well as physical mechanisms, chemical defenses against predators and competitors (allelopathy) are commonly reported in the marine environment and may be employed by invasive species to colonize, expand and invade (Fleury et al., 2008; Lages et al., 2005; Pereira, 2004). Several types of bioactive compounds have been detected in scleractinians (Fusetani et al., 1986; Koh, 1997), some of which likely function as allelochemicals. Lages et al. (2010) suggested that *T. coccinea* and *T. tagusensis* have chemical defenses that may inhibit potential predators and competitors. Furthermore Koh and Sweatman (2000) demonstrated that the extracts of *Tubastraea faulkneri* were toxic to eleven heterospecific sympatric coral larvae, so a chemical mechanism may also be in play.

Elucidating the mechanisms behind the apparent competitive superiority of the invasive corals over the native species will contribute to our understanding of the invasion process and provide important information regarding both management of coral invasion and likely implications for the maintenance of native biodiversity. As the relative importance of chemical versus physical mechanisms is unknown, the aim of this study was to identify the competitive mechanisms used by corals through manipulative microcosm and field assays.

2. Material and methods

2.1. Study area

Microcosm and field experiments were carried out at Ilha Grande, Angra dos Reis (Rio de Janeiro State, Brazil) between March and May 2011. The microcosm experiment was installed at the Sun Coral Project Visitors Center and the field experiment was conducted on nearby rocky reefs at Ilha dos Macacos (23°04'36"S; 44°13'47"W). This site was chosen because it presents relatively high densities of all three corals (C.B. Lima, personal communication).

2.2. Microcosm experiment

To investigate the competitive mechanisms behind the interaction of *Tubastraea* species and *M. hispida*, an experiment using paired species was established in an aquarium system, using a total of 36 transparent plastic aquaria of 16.7 L capacity. The aquaria were aerated by an air compressor which was connected to the aquaria through silicone hoses. A physical barrier – nylon plankton net material, 30 µm mesh size – that allowed the flow of water and soluble toxins but prevented the passage of physical structures (Bruno and Witman, 1996) was positioned in the middle of the aquaria to separate the pairs of colonies. Colonies (diameter ≈ 5 cm) of *T. coccinea*, *T. tagusensis* and *M. hispida* were fixed on the porous side of ceramic plates with marine epoxy (Tubolit) 0.5 cm apart. Each aquarium contained a pair of colonies and the experiment was divided into 6 treatments: complete barrier or partial barrier (with small (0.6 cm) holes at the contact area allowing physical contact but maintaining part of the barrier as an artifact control), in three combinations: 1) *M. hispida* colonies with *T. coccinea*; 2) *M. hispida* with *T. tagusensis*; 3) *M. hispida* with *M. hispida* (control).

Each treatment was replicated six times. Water was changed every other day. Water temperature varied from 21 to 32 °C during the experiment and shading (50%) incident light was used to mimic natural light levels. The experiment was monitored every 6 h during the first 24 h and once every 12 h subsequently with photographic records taken of the organisms behavior and possible competitive interactions between the invasive and native corals. The experiment was terminated after 60 h.

The occurrence of mesenterial filaments was classified as: absent, projected (projection of mesenterial filaments laterally), superficial (mesenterial filaments evident all over the colony), superficial and projected (both forms simultaneously). We used the G-test for goodness of fit for more than two classes (Sokal and Rohlf, 2003) to test for significant differences from the null hypothesis of 100% absence of mesenterial filaments. In order to quantify directionality in the projected mesenterial filaments, photographs of the native coral colonies were divided into four quarters through the colony center with the aid of Adobe Photoshop CS2 software using the position closest to the competitor as reference. The extent (%) of each portion perimeter with presence of projected mesenterial filaments was estimated using the Image Tool 3.0 software. Significant differences between the mesenterial filaments proportions from each treatment were tested using ANOVA (Zar, 1999); where ANOVA assumptions were violated, we used the G-test for goodness of fit for more than two classes (Sokal and Rohlf, 2003).

2.3. Field experiment

A total of 54 ceramic plates (15 × 15 cm) served as experimental units. Each unit had a u-shaped steel rod inserted through two holes onto which the nylon barrier (30 µm mesh) was attached rather like a table-tennis net. Pairs of corals (diameter ≈ 5 cm) were cemented on the porous side the experimental units with marine epoxy (Tubolit) and left to harden for 2 h in aquaria before being fixed onto cement blocks previously placed on the rocky shore at 2–3 m depth with cable ties. Four different experimental units were randomly (position) fixed to each cement block (Fig. 1A). The experiment was divided into nine treatments: 1) complete physical barrier; 2) partial physical barrier with small holes at the contact area (allowing physical contact but maintaining part of the barrier as a partial artifact control); and 3) absence of barrier, in each of the following combinations: 1) *M. hispida* with *T. coccinea*; 2) *M. hispida* with *T. tagusensis*; 3) *M. hispida* with *M. hispida* (control). Each treatment had six replicates.

The experiment was run for 40 days with observations carried out on day 1, 4, 13, 25, 33 and 40 using SCUBA diving and underwater photography. Necrosis of *M. hispida* was estimated as % of total coral colony area. To analyze how necrosis expanded over time, photographs of the colonies were divided into 3 distance bands (0–1, 1–2 and 2–3 cm) and % necrosis of the total coral area estimated from ten randomly placed points in each band. Both analyses were carried out with the aid of the Coral Point Count with Excel extensions software (CPCe 4.0). To compare differences in necrosis at different distances we used ANOVA (Zar, 1999).

3. Results

3.1. Microcosm experiment

In the microcosms *M. hispida* rapidly reacted to the presence *T. tagusensis* and *T. coccinea* behind partial or complete barriers by extruding white mesenterial filaments (Fig. 1B, C) within the first six to twelve hours (Fig. 2A, B) in contrast to the controls (*M. hispida*–*M. hispida*) which did not produce mesenterial filaments in response to their intraspecific neighbors during this time. *T. tagusensis* and *T. coccinea* produced very few mesenterial filaments though they did expand to cover parts of the native coral with an expanded polyp (Fig. 1B). During the first 24 h the partial barrier induced a stronger reaction by the native coral than the full barrier for both invasive species

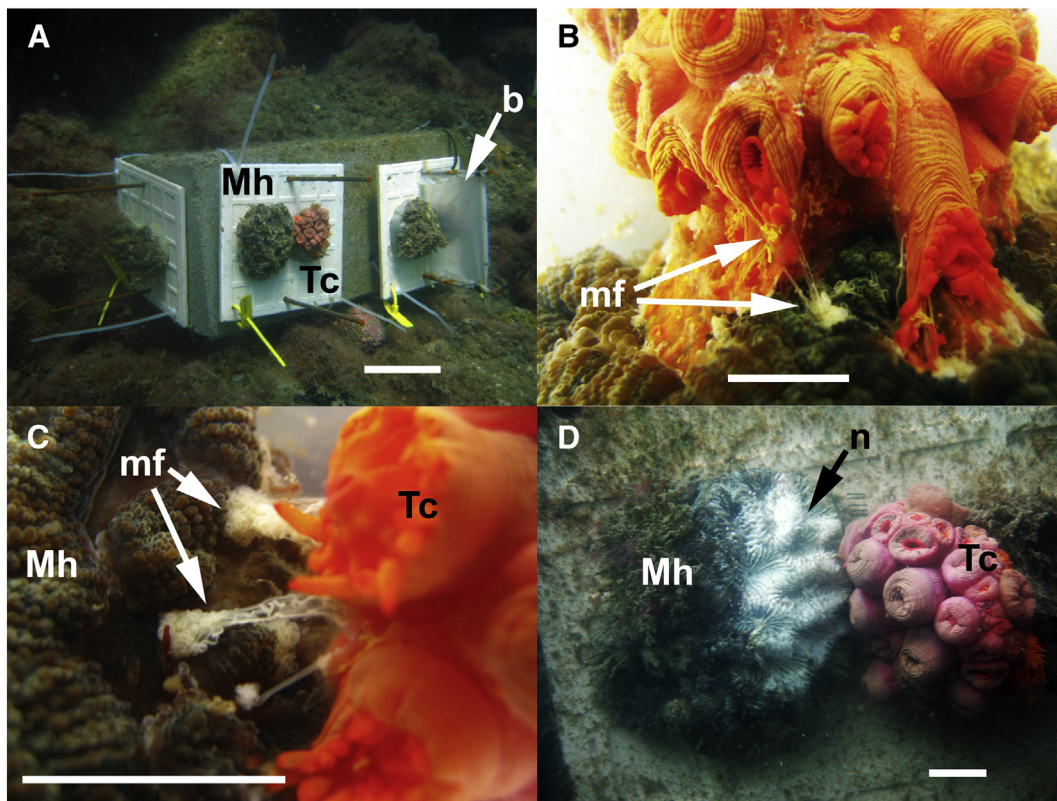


Fig. 1. Experiments investigating antagonistic interactions of the native coral *Mussismilia hispida* with the invasive species *Tubastraea coccinea*. A Experimental units (plates) on concrete block (field experiment), B mesenterial filaments produced by both native and invasive coral (microcosm), C detail of mesenterial filaments (microcosm), D necrosed area on native coral (field experiment). Scale bars A = 10 cm; B–D = 1 cm; Mh = *Mussismilia hispida*, Tc = *Tubastraea coccinea*, mf = mesenterial filaments, b = barrier.

(Fig. 2A–D). The reaction to *T. tagusensis* was slightly quicker and stronger (Fig. 2A–D) than to *T. coccinea* which was slightly more sustained (Fig. 2D–F) when compared to its congener. For example, after 12 h *M. hispida* had significantly different proportions of mesenterial filaments (G-test) in treatments where *Tubastraea* was present (*T. coccinea* complete barrier $G = 30.4$, $df = 3$, $p < 0.001$; *T. coccinea* partial barrier $G = 69.3$, $df = 3$, $p < 0.001$; *T. tagusensis* complete barrier $G = 69.3$, $df = 3$, $p < 0.001$; *T. tagusensis* partial barrier $G = 59.7$, $df = 3$, $p < 0.001$) than controls (*M. hispida* control, complete barrier $G = 0$, $df = 3$, $p > 0.995$; *M. hispida* control, partial barrier $G = 69.3$, $df = 3$, $p < 0.001$). There was a tendency for mesenterial filaments to reduce over time (Fig. 2).

The only part of the *M. hispida* colonies' perimeters that revealed projected mesenterial filaments was the part on the side closest to the barrier (and thus to the *Tubastraea* spp.) (100%), indicating that the projection of mesenterial filaments toward the barrier was a unidirectional response to the presence of the *Tubastraea* spp. along a perceived gradient. Considering only the projection of mesenterial filaments from the closest quarter's perimeter (Fig. 3) it became still more clear that the native coral responded more quickly and more strongly to *T. tagusensis* than *T. coccinea* initially (Fig. 3A–B); due to heterogeneity inherent in such studies ANOVA could not be carried out (Zar, 1999) but the null hypothesis that all treatments had equal proportions of projected mesenterial filaments was rejected by a G-test ($G = 16.6$, $df = 5$, $p < 0.01$). Furthermore, treatments with *Tubastraea* spp. and partial barriers showed more sustained production of mesenterial filaments than full barriers over time. No mesenterial filaments were projected from controls during 60 h (Fig. 3).

3.2. Field experiment

During the 40 day experimental period no necrosis was observed on *T. tagusensis* or *T. coccinea*; in contrast during this period all the stages of

necrosis were observed on *M. hispida*, from coenosarc discoloration to colonization of newly exposed skeleton by epibionts (Fig. 1D). No difference was observed on day 1. By the fourth day it was already possible to observe tissue discoloration and necrosis of parts of the native coral when in proximity to *T. coccinea* behind a complete barrier, *T. coccinea* with no barrier, *T. tagusensis* behind a partial barrier and *T. tagusensis* with no barrier (the strongest reaction at this time – Fig. 4A). Over the next 36 days the area of necrosis became more pronounced in treatments without barriers when compared with treatments with partial or complete barriers to physical contact for both invasive species (Fig. 4B–E). On day 40 the null hypothesis that all treatments had equal proportions of necrosis was rejected by a G-test ($G = 307.5$, $df = 8$, $p < 0.001$).

As well as total area necrosed being greater in the treatments where there was no physical barrier between *M. hispida* and both *Tubastraea* spp., necrosis was spatially concentrated in tissues closest to the invasive corals (Figs. 1D; 5). For example after 40 days the treatment with *T. coccinea* and no barrier showed significantly greater necrosis in *M. hispida* at 0–1 cm and 1–2 cm than at 2–3 cm distance (ANOVA between distances $p = 0.006$; Tukey test; Fig. 5E). In contrast, in the treatment with *T. tagusensis* and no barrier there was no significant difference between the three distances (ANOVA between distances $p = 0.321$; Fig. 5E), suggesting that with *T. tagusensis* the expansion of necrosis had reached distances of over 3 cm from the contact area.

4. Discussion

M. hispida reacted rapidly and antagonistically toward the invasive corals *T. coccinea* and *T. tagusensis* when placed in close proximity. Fast reactions of this type have also been reported in another coral species, such as *Platygyra daedalea*, which extruded the same structures after a few hours of initial contact with a massive coral *Favites complanata* in a laboratory assay (Lapid et al., 2004). As the release of mesenterial

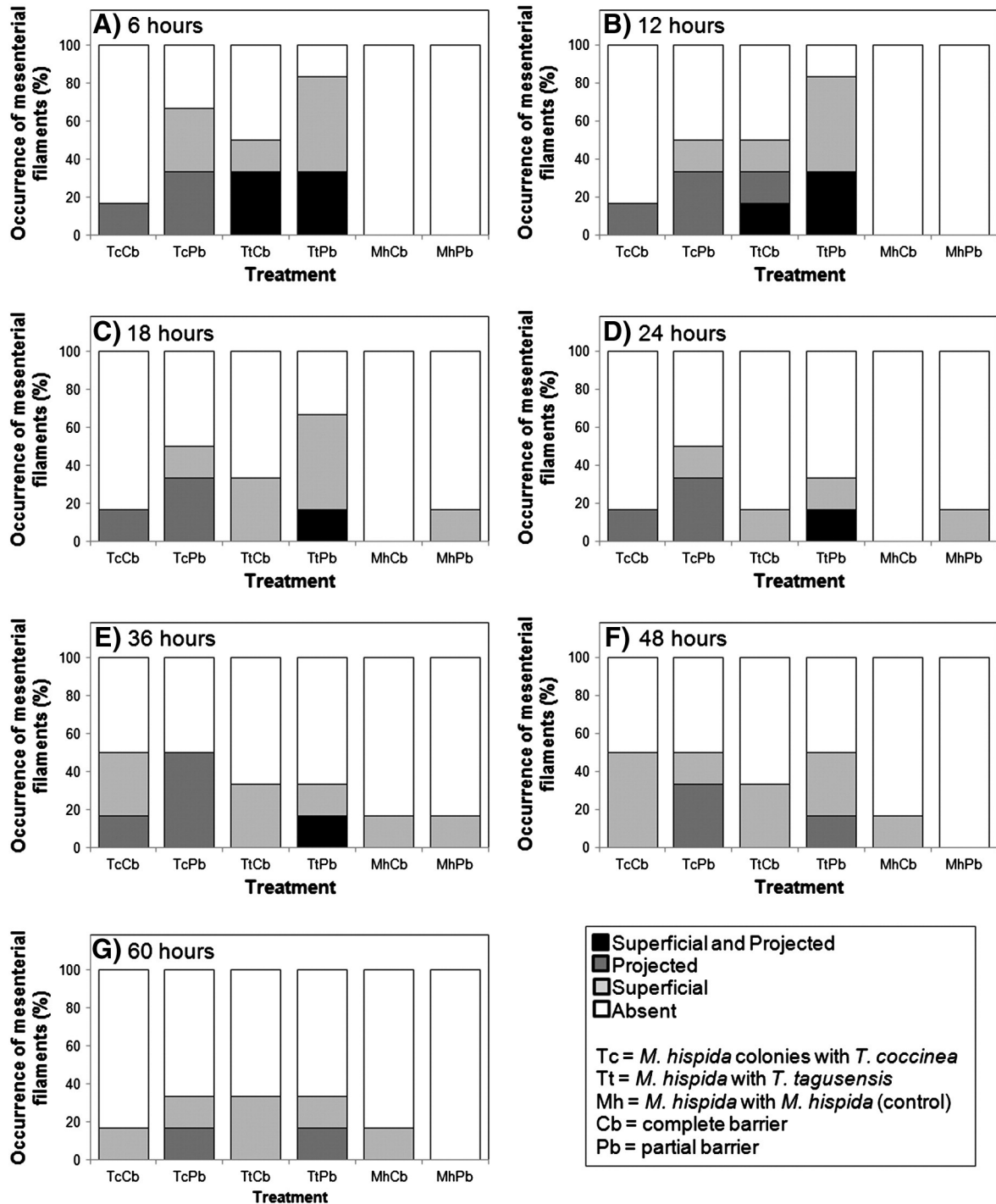
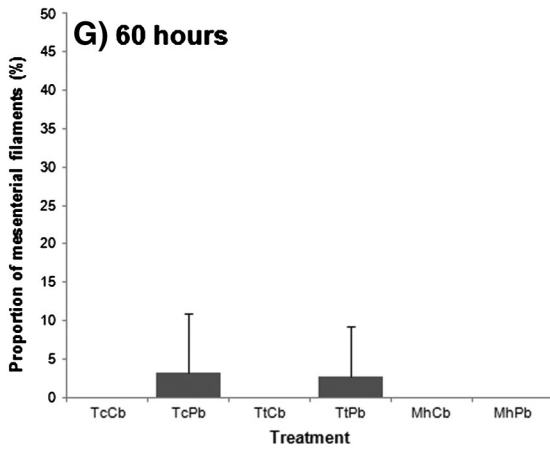
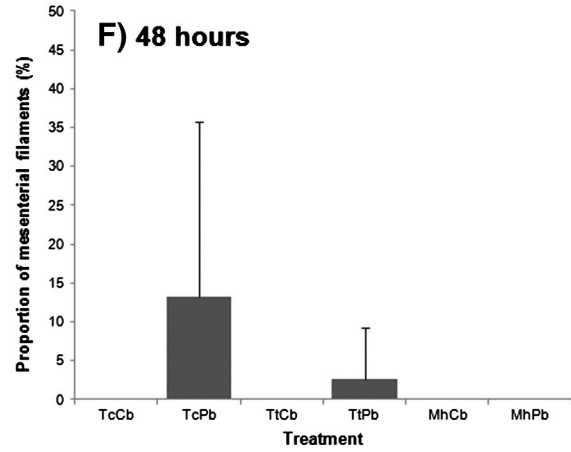
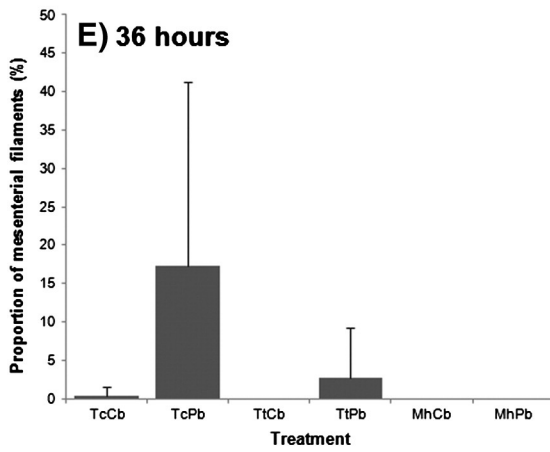
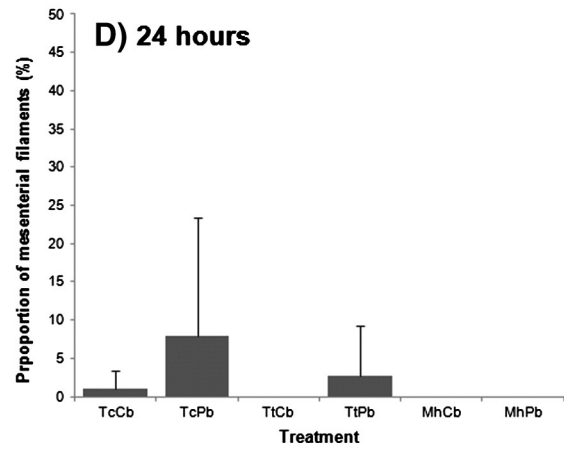
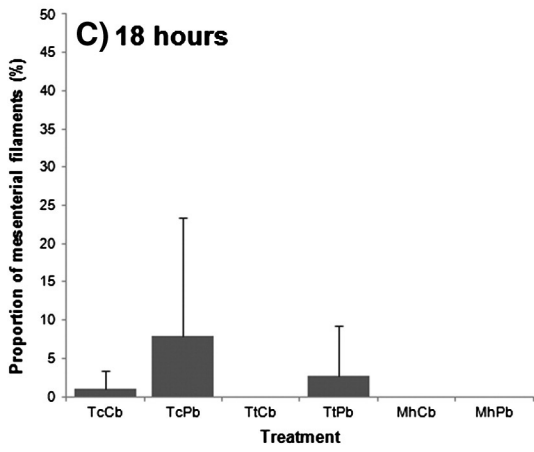
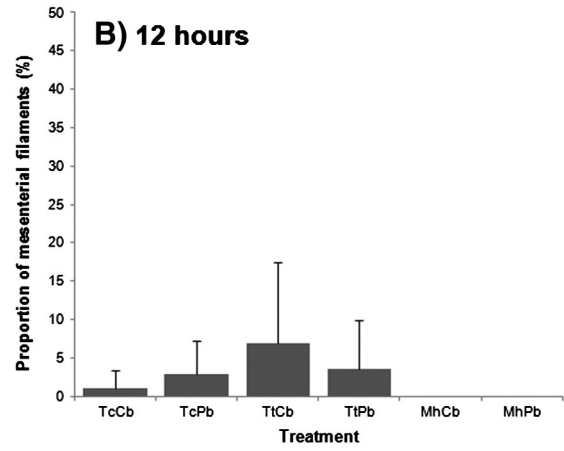
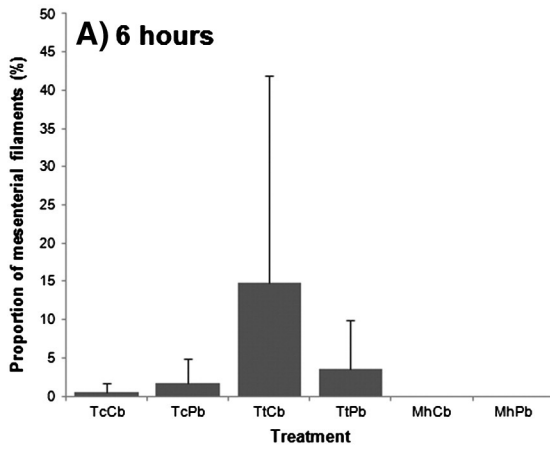


Fig. 2. Occurrence of mesenterial filaments (% of colonies) on the native *Mussismila hispida* over 60 hour interaction in a microcosm experiment with six treatments: complete barrier or partial barrier in three combinations over seven times.

filaments in our experiment occurred to a greater degree in the aquaria where the native coral was paired with the invasive species rather than the control, it seems probable that this was a response by *M. hispida* to the detection or recognition of *Tubastraea* spp. as a harmful threat. Many of the responses of other cnidarians to direct competition are thought to be stimulated by contact or recognition of opponent tissues (Chornesky, 1983). The mesenterial filaments extruded by *M. hispida* observed in aquaria were a first response to the recognition of the

presence of an interspecific competitor. Further responses may include the production of sweeper tentacles by either competitor: for example *Balanophyllia elegans*, from the same family as *Tubastraea*, can use tentacular contact to prevent its overgrown by an ascidian (Bruno and Witman, 1996). Moreover, the induced development of sweeper tentacles can lead to the reversal of the initial interaction outcome (Wellington, 1980). The short time scale used in the microcosm experiment was not sufficient for the development of sweeper

Fig. 3. Proportion of mesenterial filaments projected toward competitor (% of a perimeter of nearest one-quarter of colony) on the native *Mussismila hispida* over 60 h interacting in a microcosm experiment with six treatments: complete barrier or partial barrier in three combinations, over seven times. Means + SD.



Tc = *M. hispida* colonies with *T. coccinea*
 Tt = *M. hispida* with *T. tagusensis*
 Mh = *M. hispida* with *M. hispida* (control)
 Cb = complete barrier
 Pb = partial barrier

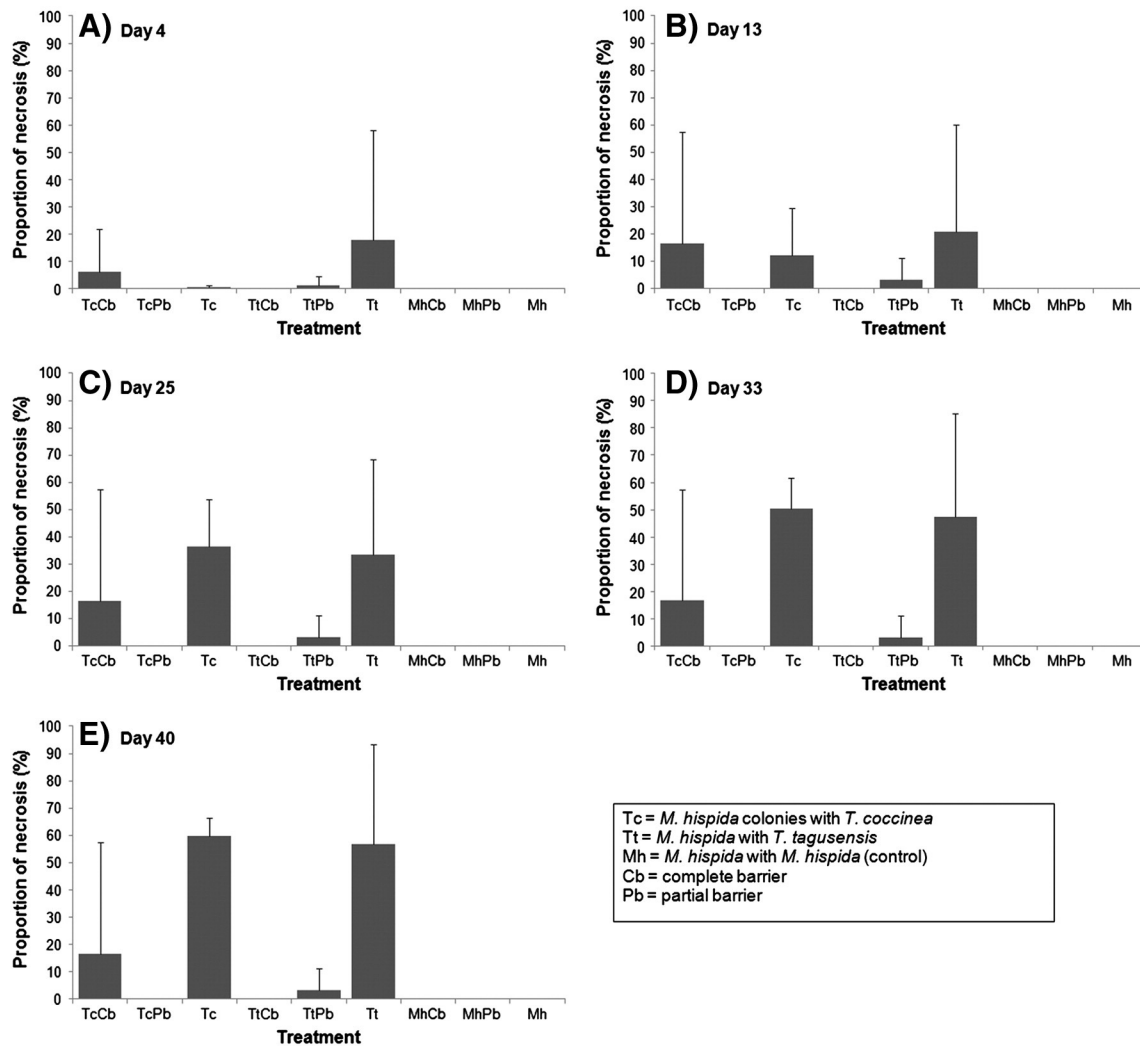


Fig. 4. Proportion of necrosis (%) on tissue of the native coral *Mussismila hispida* over 40 days interacting in a field experiment. The nine treatments were complete physical barrier, partial physical barrier and no barrier, in three species combinations, over five times. Means + SD. Day one is not shown, as no effects were observed.

tentacles which can take about 30 days (Chornesky, 1983; Lapid et al., 2004).

In contrast, during the field experiment and despite a similar experimental set-up, no mesenterial filaments were observed on *M. hispida* in the field, so the production of mesenterial filaments might have been stimulated by the confined microcosm conditions and/or enhanced chemical cues in the closed systems. Furthermore, despite the adequate time-frame (Chornesky, 1983) sweeper tentacles were not observed in any of the study species during monitoring of the field experiment. It has been reported that the contact with tissues or mesenterial filaments of the gorgonian *Erythropodium caribaeorum* can stimulate the development of sweeper tentacles by the scleractinian *Agaricia agaricites* in 30 days (Chornesky, 1983). This same period of time was observed for sweeper development in *P. daedalea* after contact with *F. complanata*, which caused increasing tissue damage to it over two months (Lapid et al., 2004). It is possible that we did not observe this competitive physical mechanism during our field study because we made observations during daylight; mesenterial filaments and sweeper tentacles may be extruded in the dark (Chornesky, 1983; Lang, 1973; Richardson et al., 1979). For example night observations of the interaction between the scleractinians *P. daedalea* and *F. complanata* have revealed confrontation in which both competitors expanded completely developed sweeper tentacles (Lapid et al., 2004). Another possible reason for not observing these structures is that the sweepers of some species retract and revert to their pre-encounter size and feeding function after destroying the

opponent's tissues (Wellington, 1980). In the microcosm experiment this behavior was noted for the mesenterial filaments released by *M. hispida*, which retracted back to their polyps. The mechanism of regression reduces the high energetic cost of the maintenance of these structures over time (Lapid et al., 2004). The observations in the field were only made 4 days after deployment when, according to the microcosm experiment, most mesenterial filaments had probably already retracted.

T. coccinea and *T. tagusensis* are known to produce allelochemicals which are active against several native marine organisms (Lages et al., 2010). Furthermore, the congener *T. faulkneri* is known to release toxic compounds which inhibit the settlement and growing of competitor corals (Koh and Sweatman, 2000). The physical barrier of the present study was designed to allow the passage of dissolved toxic secondary metabolites but not much necrosis occurred on the native coral in either the partial or complete barrier treatments and so there was little evidence of an allelochemical release mechanism. It is therefore likely that these *Tubastraea* species use physical defenses against *M. hispida* as the barrier prevented mesenterial filaments (or less likely) sweeper tentacles from reaching the competitor.

Observations by Bruno and Witman (1996) corroborate our observations which suggest that *T. coccinea* and *T. tagusensis* primarily use a physical rather than chemical defense strategy during competitive interactions with *M. hispida*. In an experiment using similar methods they observed that *B. elegans*, also a Dendrophylliid coral, uses tentacular contact to prevent overgrowth by the ascidian *Trididemnum opacum*.

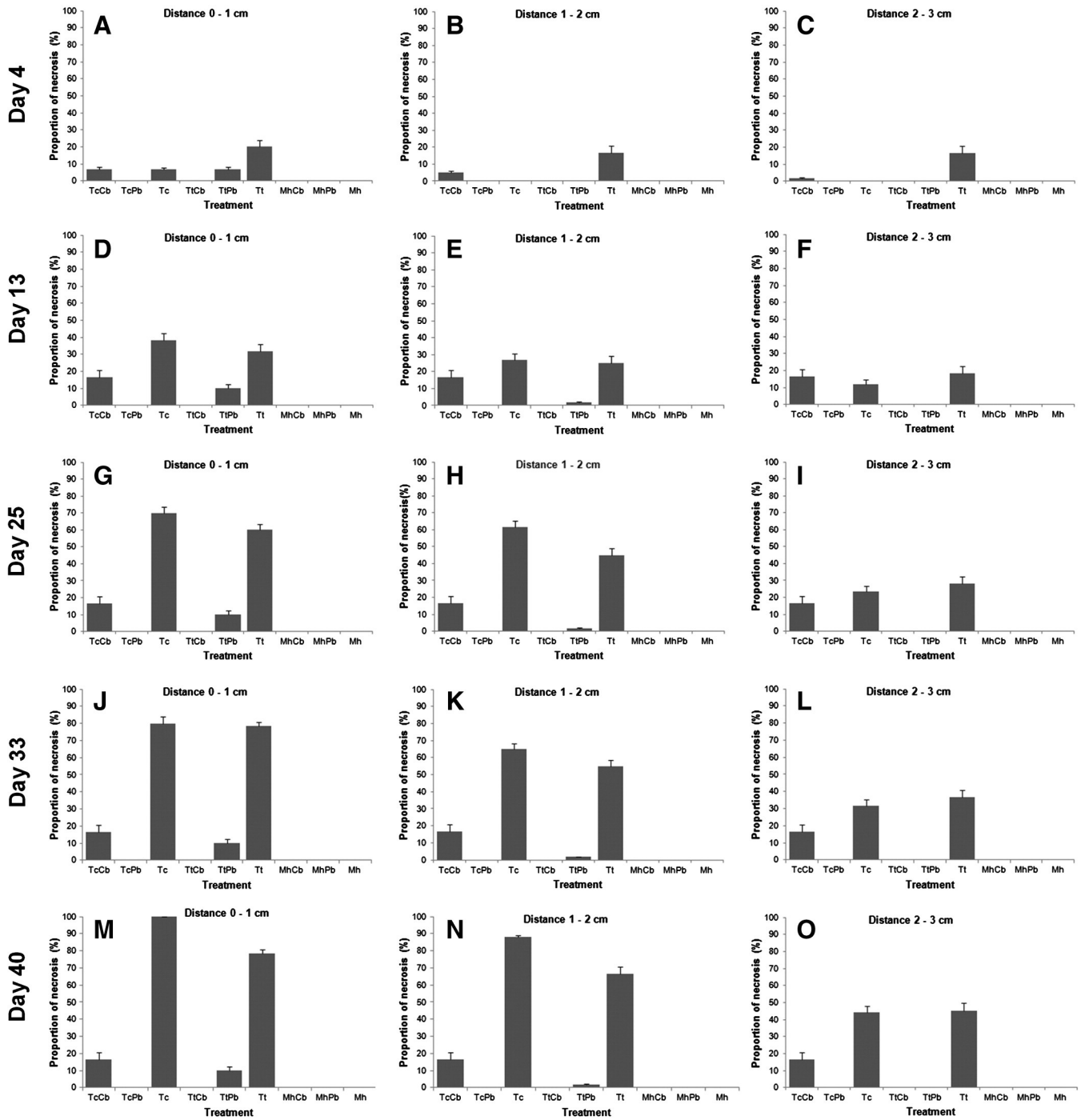


Fig. 5. Proportion of necrosis (%) at three distances on tissue of the native coral *Mussismila hispida* over 40 days interacting in a field experiment. The nine treatments were complete physical barrier (Cb), partial physical barrier (Pb), and no barrier, in each of the following combinations: 1) *M. hispida* colonies with *T. coccinea* (Tc); 2) *M. hispida* with *T. tagusensis* (Tt); 3) *M. hispida* with *M. hispida* (Mh, control). Means + SD.

M. hispida belongs to Mussidae, one of the most aggressive coral families in the Atlantic Ocean (Lang, 1973; Thomason and Brown, 1986), which might explain the rapid and sustained production of mesenterial filaments. *Tubastraea* spp. produced (very) few mesenterial filaments (Fig. 1B) when compared to *M. hispida*. However, the field experiment didn't reveal any negative competitive outcome by *M. hispida* over the invasive species, which remained healthy throughout the experiment. In a study conducted in Palau (Wellington and Trench, 1985), the nonsymbiotic *Tubastraea micrantha* and more abundant symbiotic corals were placed within tentacular contact for approximately 2 months: *T. micrantha* was able to withstand the attack or inflict damage on the predominant corals. It was concluded that

T. micrantha was resistant due to the combination of its rapid growth and aggressive competitive abilities.

The results obtained in the field show that the necrosis of *M. hispida* colonies began from the region of contact between the competitors and expanded over time. This fact reinforces observations that the biological invasion of *Tubastraea* spp. is bringing about long-term changes in native rocky shore communities (Lages et al., 2011) through negative competitive interactions with native species such as *M. hispida* and thus threatening whole benthic communities of Ilha Grande Bay (De Paula, 2007). The scleractinian *M. hispida* not only belongs to a genus endemic to Brazil but is also one of the most widely distributed coral species along the Brazilian coast (Laborel, 1969). These corals not only

act as a nursery for the marine community, providing protection to many associated species (Oigman-Pszczol and Creed, 2006) and supporting organisms that mostly feed on their debris and mucus (Hetzl and Castro, 1994; Nogueira, 2003) but they also help build Brazil's reefs. Recently published species distribution models (Riul et al., 2013) have shown that native and invasive corals have similar predicted distributions and thus similar habitat requirements, so as the range expansion of *Tubastraea* spp. continues it is highly probable that populations of *M. hispida* will be impacted on a widespread geographical basis. Recently *T. tagusensis* was reported for the first time on a coral reef at Salvador, Brazil, 1600 km distant from the present study (Sampaio et al., 2012). As Brazil's reefs are relatively poor in coral species but many of them, including *M. hispida*, are endemic (Leão et al., 2003) not only is *M. hispida* in jeopardy but other native reef building corals and the coral reefs themselves may succumb to the biological invasion of *Tubastraea* spp. over the forthcoming years. This makes management steps to slow the spread of *Tubastraea* spp. imperative in order to protect coral reefs from biological invasion and consequent changes in ecosystem function that is implied by the substitution of hermatypic corals by ahermatypic species.

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