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ORIGINAL PAPER

Proximity to competitors changes secondary metabolites of non-indigenous cup corals, *Tubastraea* spp., in the southwest Atlantic

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Abstract Competition for space changes species' distributions and community organization on tropical rocky shores, and the presence of secondary metabolites in the tissues of non-indigenous species may aid them in establishing and expanding their range through negative competitive interactions. The aim of this study was to describe the range of chemical substances produced by the non-indigenous cup corals *Tubastraea coccinea* and *T. tagusensis* and to test whether they varied in the field when the corals were placed in proximity to two local competitors. Cholest-5-en-3β-ol and 9-octadecanoic acid were two common secondary metabolites found in the tissues of *Tubastraea*. In the competition interaction experiment, necrosis was detected on the tissues of the coral *Mussismilia hispida,* and this species induced variation in sterol, alkaloid, and fatty acid production in *Tubastraea* tissues. In contrast, a sponge overgrew *Tubastraea* colonies. These results indicate that chemical defense may contribute to the ability of these non-indigenous corals to invade native communities.

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Introduction

The presence of secondary metabolites in benthic organisms may defend them from enemies (Coll 1992; Pawlik 1993; Nishiyama and Bakus 1999; López-Legentil et al. 2006; Kelman et al. 2009). Studies focusing on cnidarians have detected chemical substances that have negative effects on predators (Van Alstyne et al. 1994; O'Neal and Pawlik 2002), fouling species (Coll and Sammarco 1983; Maida et al. 2006), or competitors (Coll 1992; Sammarco and Coll 1992; Fleury et al. 2004). Other defensive mechanisms such as cnidocytes may be used by cnidarians to secrete chemical products that are released after an appropriate chemical and/or mechanical stimulus (Brusca and Brusca 2003; Özbek et al. 2009).

A question of primary interest to chemical ecologists has been to identify and quantify to what extent concentrations and types of secondary metabolites differ between individuals, within populations, or between populations of marine organisms (Van Alstyne et al. 1999). Studies have detected variation in secondary metabolites in seaweeds (Hay et al. 1988; Dworjanyn et al. 1999), sponges (Becerro et al. 1998; Schupp et al. 1999) and cnidarians (Van Alstyne and Paul 1992; Harvell et al. 1993; Maida et al. 1993; Kelman et al. 2000); however, there is no information concerning variation in chemical compounds due to competition for space between invasive corals and species in receptor communities.

It has been hypothesized that the use of chemical substances against predators and competitors may assist non-indigenous species to colonize, establish, and expand into

new areas, as the substances themselves may be novel to the receptor community (Pereira 2004; Parker and Hay 2005; Lages et al. 2006; Fleury et al. 2008). The absence of specialist enemies and the preferential consumption of native species by native generalists give non-indigenous species a further competitive advantage over their native counterparts (Parker and Hay 2005). Invasive species may therefore negatively impact natives that may lead to irreversible changes in the receptor community (Occhipinti-Ambrogi 2007).

The cup corals *Tubastraea coccinea* and *T. tagusensis*, which have invaded the Brazilian coast (De Paula and Creed 2004), produce chemical substances that influence interactions with potential predators and foulers (Lages et al. 2010) and modify local rocky shore communities (Lages et al. 2011). The advantage gained by the corals along with their diverse and precocious reproductive strategy (Glynn et al. 2007) could explain their success in invading new regions to the detriment of local fauna and flora. However, we still lack the experimental evidence that secondary metabolites are modified by *Tubastraea* spp. in order to facilitate their colonization.

The aim of the present study was to detect secondary metabolites produced by the cup corals *T. coccinea* and *T. tagusensis* and experimentally test whether chemical substances that potentially mediate competition varied when in close proximity to competitors. No previous studies have shown variability in secondary metabolite concentrations, which may mediate competition for space, in situ, in these corals.

Materials and methods

Study area

The study was carried out at Ilha dos Macacos, Ilha Grande Bay, which is located in the south of Rio de Janeiro State (23°04.713′S 44°13.479′W). Ilha Grande Bay possesses a number of marine protected areas although an oil terminal on the continent, a shipyard and a mineral ore terminal produce considerable shipping traffic (De Paula and Creed 2005).

Experiment design

Two commonly occurring native species were chosen for the competitive interaction experiment: (1) *Mussismilia hispida*, the most abundant hermatypic scleractinian coral in the region, is endemic to Brazil and was chosen because previous unpublished studies and observations by Creed (2006) suggested that this coral is negatively affected by the presence of *Tubastraea* spp. (2) the sponge *Desmapsamma anchorata* is an important space occupying organism at the site and was selected, because in previous studies, it was observed not to be affected by the presence of the *Tubastraea* spp. (De Paula 2007).

Colonies of about 25 g of live weight of both *T. coccinea* and *T. tagusensis* and the competitors were collected, and the experiments were run in April 2007 at a depth of approximately 3–4 m. The colonies were transplanted onto ceramic tiles and left for a 1-month acclimatization period before treatment. Partial controls (mimics) were used to identify any variation in concentration or class of secondary metabolites in *Tubastraea* tissues due to the presence of an inert volume similar to the living competitor. The mimics of *D. anchorata* were prepared by using flexible rubber sheets wrapped in synthetic sponge and mimics of *M. hispida* were made from concrete using a standard mold. For the experiment, five different treatments ($n = 8$ replicates) were performed on each *Tubastraea* species: (1) *Tubastraea* alone (control); (2) *Tubastraea* and *M. hispida*; (3) *Tubastraea* and *D. anchorata*; (4) *Tubastraea* and *M. hispida* mimic (partial control); (5) *Tubastraea* and *D. anchorata* mimic (partial control). The pairs of organisms/mimics were transplanted 2 cm apart onto ceramic tiles (15 × 15 cm) using Tubolit epoxy putty to attach the corals and coral mimics and elastic lines to attach the sponge and its mimics. All treatments were attached with cable ties onto concrete blocks at 2–4 m depth in a random order. The organisms were left to interact for 5 weeks. After this time, *M. hispida* and *D. anchorata* were inspected for the presence of necrosis (retraction of living tissue) or growth. To measure the evident necrosis in *M. hispida,* a tape measure was used to measure from the base of *M. hispida* colony in proximity to the *Tubastraea* colony to the opposite side of each *M. hispida* colony, and the linear proportion that was dead was expressed as percent dead colony.

Chemical extraction and analyses

After 5 weeks in the field, the colonies of *Tubastraea* were collected and halved with the side closest to the potential competitor being retained, labeled, and immediately individually frozen. The secondary metabolites of *Tubastraea* were extracted using standardized MeOH solvent and produced 749 mg of extract, on average. As the literature concerning extraction of compounds in coral tissues shows bioactive compounds such as terpenes, sterols, and fatty acids in non-polar extracts (Coll 1992; Maida et al. 1993; Yamashiro et al. 1999; Epifanio et al. 2007), a fixed aliquot (30 mg) of each MeOH extract was fractioned using distilled water and NaCl (sodium chloride) to produce a solution that aided transfer of organic compounds of each *Tubastraea* species to organic phase dichloromethane

(DCM) (salting out effect). After partitioning with DCM, *T. coccinea* and *T. tagusensis* produced mean weights of 10.6 mg and 11.8 mg of DCM extracts, respectively, which were dissolved with a fixed volume of DCM before being injected (1 µl) into a gas chromatography/mass spectrometry (GC/MS).

The GC/MS analysis was carried out on an Agilent 5973 model with electron impact ionization at 70 eV. An HP5 MS capillary column of 30 m length × 0.25 mm I.D. × 0.25 µm film thickness (J&W Scientific) was used. Sample volumes of 1 µl were injected in a split mode (1:20) using a manual syringe. Helium was employed as the carrier gas (1 mL/min). Initial oven temperature was programmed for 60 °C and was gradually increased to 290 °C at a rate of 10 °C/min (from 60 to 220 °C) and at a rate of 5 °C/min (from 220 to 290 °C). Subsequently, the oven temperature remained constant for 30 min. Injector and transfer line temperatures were kept constant at 280 and 290 °C, respectively. The identification of the substances by CG/MS was carried out by comparing the substances with others found in Budzikiewicz et al. (1964) and Yamashiro et al. (1999), the Wiley 275 Mass Library and by using standard co-injections.

Statistical analyses

Data from each GC/MS chromatogram were exported as peak tables and aligned to obtain a matrix where each line represents a sample and each column a peak due to the same substance. Before the matrices were submitted to multivariate analysis of variance (MANOVA), they were square root transformed. As there was some loss during the fieldwork period, the matrices generated had 46 samples and 28 peaks for all treatments of *T. coccinea* and *T. tagusensis* in the global data set. These analyses were used in order to detect variation in concentration of chemical substances between the two species (Wilk's lambda test). MANOVA was also used for each species of coral to detect differences in concentration of the group of chemical substances between treatments (Wilk's lambda test). One-way ANOVA and Tukey Multiple means comparison tests were used to identify differences between controls and treatments for individual substances of each species. These analyses were carried out using SPSS Version 17.0 for Windows.

Partial least squares discriminant analysis (PLS-DA) was carried out using the Unscrambler Version 9.1 program in order to classify different treatments. The matrices generated in this way had 12 samples and 28 peaks for *T. coccinea* control and *M. hispida* treatment, 11 samples and 28 peaks for *T. coccinea* control and *D. anchorata*, 9 samples and 26 peaks for *T. tagusensis* control and *M. hispida* treatment and for *T. tagusensis* control and *D. anchorata* treatment. Peak area was zeroed for peaks with zero areas or if they were too small to be integrated under the conditions used. Before submitting to PLS-DA, the matrices were pretreated by square root transformation, followed by normalization, and mean centering.

Results

The GC/MS analysis of DCM fractions of *T. coccinea* and *T. tagusensis* showed 28 and 26 substances, respectively (Table 1). Methyl 7,10,13-hexadecatrienoate and ergosta-5,7,22-trien-3β-ol were exclusive to *T. coccinea,* while the other 26 substances were common to both species; cholest-5-en-3β-ol and 9-octadecanoic acid were majority substances in both species (Table 1).

In general, for both species of *Tubastraea*, a variety of substances were found, where the sterols cholest-5-en-3β-ol (27 %), 27-norergosta-5,22-dien-3β-ol (7.37 %), stigmasta-5,24(28)-dien-3β-ol (2.36 %), ergosta-5,24-dien-3β-ol (1.47 %), ergosta-5,22-dien-3β-ol (1.13 %), cholest-5-en-3β-one (0.75 %), dihydrocholesterol (0.43 %), and ergosta-5,7,22-trien-3β-ol (0.21 %) represented 40.5 % of all substances found, on average. The fatty acids 9-octadecanoic acid (14.3 %), oleic acid (11.9 %), hexadecanoic acid (0.93 %), methyl 9,12-octadecadienoate (0.25 %), and methyl 7,10,13-hexadecatrienoate (0.04 %) represented 28.4 % of substances. The hydrocarbonates 1-hexadecene (9.8 %), 1-octadecene (8.8 %), and octadecane (0.71 %) represented 19.4 % of substances. The alkaloids 1-H-indole-3-carboxaldehyde (2.1 %), 5-bromoindole-3-carbaldehyde (0.98 %), and 5-bromoindole (0.41 %) represented 3.5 % of substances found. The esters methyl stearate (1.1 %), methyl oleate (0.93 %), methyl palmitate (0.88 %), and methyl arachidonate (0.17 %) represented 2 % of substances and the alcohols phytol (0.63 %), methoxyoctadecane (0.59 %), and 9-octadecen-1-ol (0.43 %) represented 1.7 % of substances found (Table 1).

The effects of *Tubastraea* were observed in the field as necrosis (Fig. 1a). The colonies of *M. hispida* possessed areas of necrosis when in proximity to *T. coccinea* and *T. tagusensis* colonies, and this represented 39.5 and 45.6 % of colonies, respectively. In contrast, the sponge *D. anchorata* overgrew *Tubastraea* colonies in the field (Fig. 1b).

There were significant differences in the chemical composition of the two species (MANOVA, $F = 4.945$, $P = 0.008$; Wilks' lambda test) when pooled but the test did not detect significant differences between treatments for each species analyzed separately (MANOVA, $F = 1.351$, $P = 0.145$; Wilks' lambda test). Significant differences were not detected in the overall chemical composition of

Table 1 GC-MS analysis of DCM fractions of *T. coccinea* and *T. tagusensis* and relative concentration of chemical compounds employing global data (control + treatment) for each coral

M[a]	Molecular formula	Substance[b]	Means of pooled data of all treatments (%) ±SD *T. coccinea*	Means of pooled data of all treatments (%) ±SD *T. tagusensis*
145	C_9H_7NO	1-H-indole-3-carboxaldehyde	2.98 ± 4.37	1.21 ± 1.08
194	C_8H_6BrN	5-Bromoindole	0.41 ± 0.27	0.42 ± 0.36
223	C_9H_6BrNO	5-Bromoindole-3-carbaldehyde	1.32 ± 1.92	0.64 ± 0.80
224	$C_{16}H_{32}$	1-Hexadecene	7.52 ± 3.04	12.13 ± 2.98
252	$C_{18}H_{36}$	1-Octadecene	7.65 ± 3.06	10.04 ± 2.15
254	$C_{18}H_{38}$	Octadecane	0.84 ± 1.27	0.58 ± 0.92
254	$C_{15}H_{30}N_2O$	n.i	4.48 ± 3.19	3.69 ± 2.25
264	$C_{17}H_{28}O_2$	Methyl 7,10,13-hexadecatrienoate	0.04 ± 0.10	–
268	$C_{18}H_{36}O$	9-Octadecen-1-ol	0.25 ± 0.28	0.61 ± 0.31
270	$C_{17}H_{34}O_2$	Methyl palmitate	1.13 ± 1.22	0.63 ± 0.52
282	$C_{18}H_{34}O_2$	Oleic acid	12.21 ± 18.31	11.59 ± 10.98
284	$C_{19}H_{40}O$	Methoxyoctadecane	0.49 ± 0.27	0.69 ± 0.28
294	$C_{19}H_{34}O_2$	Methyl 9,12-octadecadienoate	0.25 ± 0.28	0.24 ± 0.21
296	$C_{19}H_{36}O_2$	Methyl oleate	0.97 ± 1.20	0.89 ± 0.52
296	$C_{20}H_{40}O$	Phytol	0.75 ± 0.56	0.50 ± 0.47
298	$C_{19}H_{38}O_2$	Methyl stearate	1.37 ± 1.52	0.86 ± 0.68
318	$C_{21}H_{34}O_2$	Methyl arachidonate	0.16 ± 0.23	0.18 ± 0.39
384	$C_{27}H_{44}O$	27-Norergosta-5,22-dien-3β-ol	8.34 ± 3.03	6.39 ± 2.70
384	$C_{27}H_{44}O$	Cholest-5-en-3β-one	1.29 ± 1.28	0.20 ± 0.45
386	$C_{27}H_{46}O$	Cholest-5-en-3β-ol	28.24 ± 7.35	25.56 ± 9.49
388	$C_{27}H_{48}O$	Dihydrocholesterol	0.78 ± 2.38	0.08 ± 0.36
396	$C_{28}H_{44}O$	Ergosta-5,7,22-trien-3β-ol	0.21 ± 0.72	–
398	$C_{28}H_{46}O$	Ergosta-5,22-dien-3β-ol	1.21 ± 1.65	1.04 ± 1.75
398	$C_{28}H_{46}O$	Ergosta-5,24-dien-3β-ol	1.40 ± 1.80	1.54 ± 1.59
412	$C_{29}H_{48}O$	Stigmasta-5,24(28)-dien-3β-ol	0.90 ± 1.30	3.81 ± 10.35
480	$C_{32}H_{64}O_2$	Hexadecanoic acid	1.00 ± 2.17	0.86 ± 1.05
491	$C_{35}H_{70}$	17-Pentatriacontene	0.55 ± 0.29	0.38 ± 0.24
535	$C_{36}H_{69}O_2$	9-Octadecanoic acid	13.29 ± 7.80	15.23 ± 9.50

[a] Molecular mass; [b] Wiley 275 library and *SD* standard deviation

extracts between treatments for *T. tagusensis* (MANOVA, $F = 12.061$, $P = 0.223$; Wilks' lambda test). However, the lower concentration of the alkaloid 5-bromoindole-3-carbaldehyde in tissues of this coral species in proximity to *D. anchorata* colonies was significant when compared with the control (one-way ANOVA, $F = 4.508$, $P = 0.009$; Fig. 2). The higher concentration of stigmasta-5,24(28)-dien-3β-ol in tissues of the same cup coral in proximity to *M. hispida* colonies was also significant when compared with control (one-way ANOVA, $F = 3.412$, $P = 0.038$; Fig. 3). Overall, for *T. coccinea*, significant differences between treatments in the concentration of secondary metabolites of the suite of chemical substances was detected (MANOVA, $F = 2299.585$, $P = 0.016$; Wilks' lambda test). The higher concentrations of 5-bromoindole, 5-bromoindole-3-carbaldehyde, cholest-5-en-3β-ol, and hexadecanoic acid in the treatment employing *M. hispida* were not significant when compared with the control (one-way ANOVA, $F = 1.125$, $P = 0.371$; $F = 0.897$, $P = 0.483$; $F = 1.172$, $P = 0.352$; $F = 0.830$, $P = 0.521$ respectively; Fig. 4). However, according to the regression coefficients of the PLS-DA, these substances were important and positively correlated with this treatment. The brominated indole alkaloids, cholest-5-en-3β-ol and hexadecanoic acid, increased their concentrations in treatments when compared to controls. No significant differences in the concentration of substances between controls and mimics were detected for *T. coccinea* or *T. tagusensis* (MANOVA, $F = 92.303$, $P = 0.081$; $F = 4.660$, $P = 0.346$; Wilks' lambda test, respectively).

The PLS-DA was used on all treatments of *Tubastraea* to discriminate the treatments, and both controls and treatments were separated into two groups. Given the variation in concentration of the substances detected by GC/MS, these results demonstrated that secondary

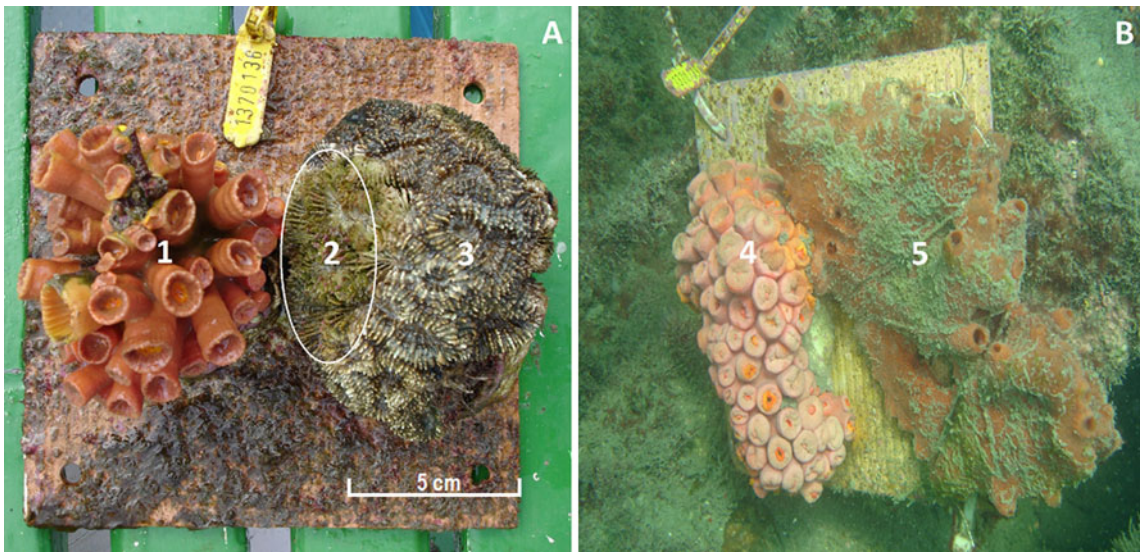

Fig. 1 Photographs of the experimental transplants. **a** Colony of *T. tagusensis* (1) caused necrosis (2) after action of allelopathic compounds on living tissues of *M. hispida* (3) after 5 weeks in the field; **b** Overgrowth of *D. anchorata* (5) on a *T. coccinea* colony (4) in the field experiment

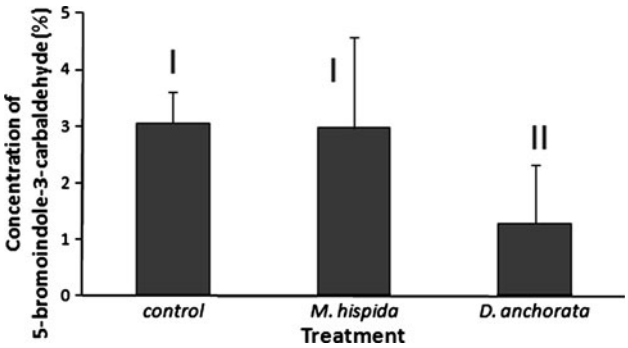

Fig. 2 Variation in the concentration of the alkaloid 5-bromoindole-3-carbaldehyde produced in living tissues of *T. tagusensis* in control colonies ($n = 8$) and in treatments transplanted beside colonies of the coral *M. hispida* ($n = 8$) and the sponge *D. anchorata* ($n = 8$) in the field experiment. *Vertical bars* Standard Error and different numerals represent a significant statistical difference

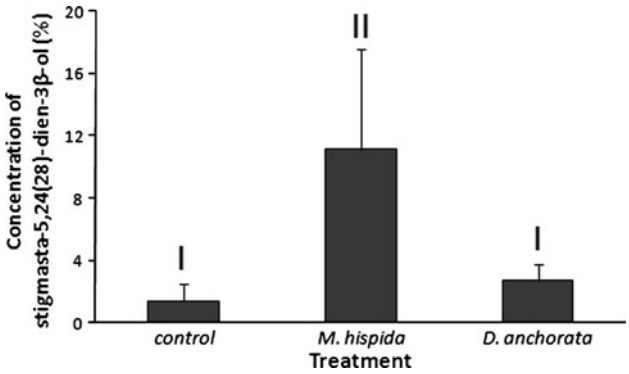

Fig. 3 Variation in the concentration of the sterol stigmasta-5,24(28)-dien-3β-ol produced in living tissues of *T. tagusensis* in control colonies ($n = 8$) and in treatments transplanted beside colonies of the coral *M. hispida* ($n = 8$) and the sponge *D. anchorata* ($n = 8$) in the field experiment. *Vertical bars* Standard Error and different numerals represent a significant statistical difference

metabolites produced by *Tubastraea* colonies varied in the presence of the competitors *M. hispida* and *D. anchorata* (Fig. 5).

Discussion

This study provides experimental evidence that necrosis of *M. hispida* tissues is caused by the close proximity of both species of *Tubastraea*. *Tubastraea faulkneri* produces allelochemicals that inhibit settlement and growth of coral competitors (Koh and Sweatman 2000), and these substances may allow *T. faulkneri* to persist among faster growing species. According to Creed (2006), the necrosis on *M. hispida* suggests that the two species of *Tubastraea* are competitively dominant and can reduce or exclude this native coral. Seeing as they are commonly found living in proximity, in the field, the interaction between native and invasive corals in Brazil will continue to occur as the invasive species increase their range. The genus *Tubastraea* is known to produce substances with negative ecological effects on other community components (Koh 1997; Koh and Sweatman 2000; Lages et al. 2010). Our results demonstrated that changes in substances produced by both species of *Tubastraea* were not stimulated by the presence of mimics, as there was an absence of necrosis in tissues of *M. hispida* when in proximity to mimics; also, there were no significant differences in concentration and/or class of substances between controls and partial controls.

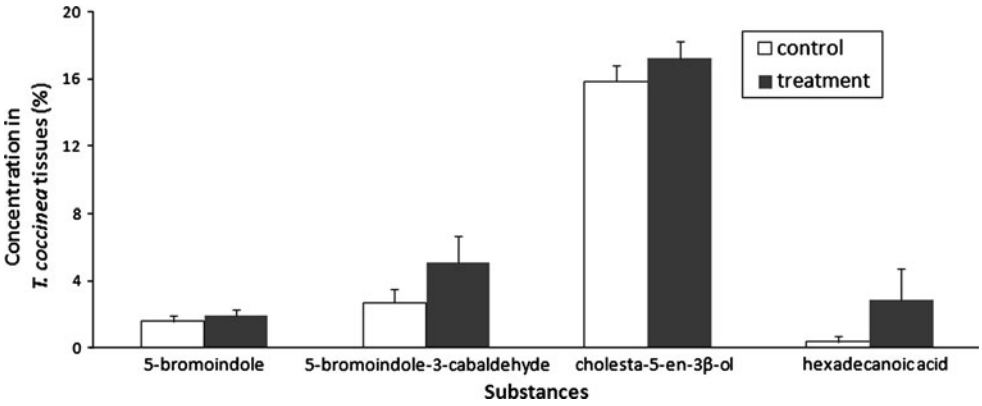

Fig. 4 Variation in the concentration of 5-bromoindole, 5-bromoindole-3-carbaldehyde, cholest-5-en-3β-ol and hexadecanoic acid produced in living tissues of the coral *T. coccinea* in control colonies ($n = 8$) and those transplanted nearby colonies of the coral *M. hispida* ($n = 8$) in the field experiment. *Vertical bars* Standard Error

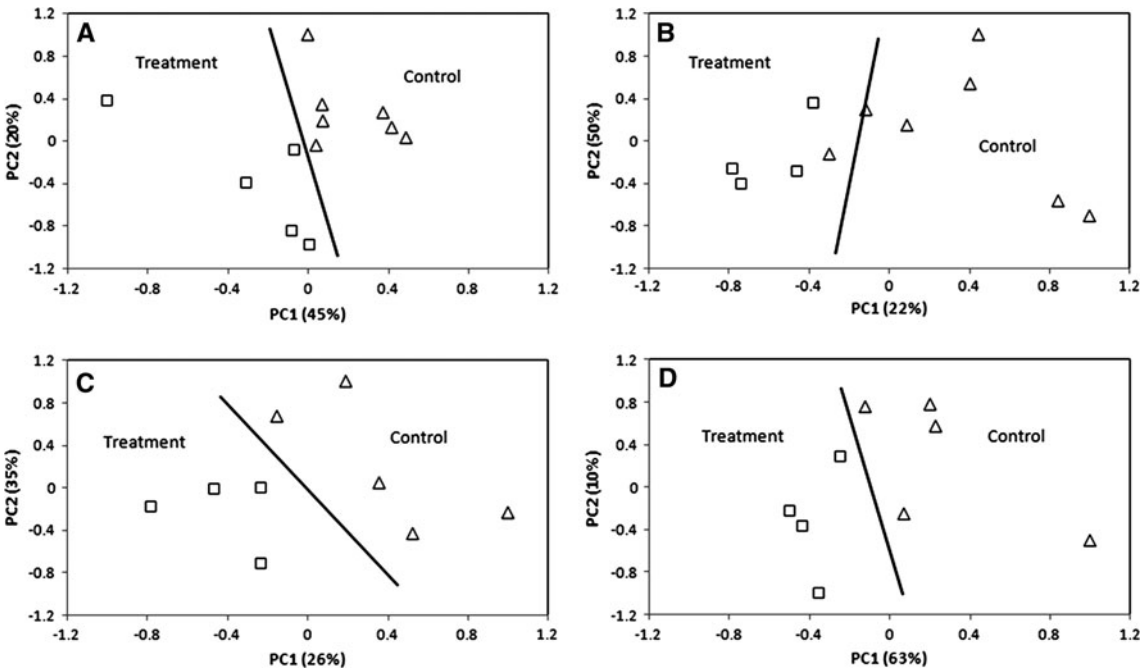

Fig. 5 Partial Least Square Discriminant Analysis score plots for secondary metabolite concentrations in *Tubastraea* spp.: **a** *T. coccinea* controls versus those transplanted close by colonies of the coral *M. hispida*; **b** *T. coccinea* controls versus those transplanted close by the sponge *D. anchorata* treatment; **c** *T. tagusensis* controls versus those transplanted close by colonies of the coral *M. hispida*; **d** *T. tagusensis* controls versus those transplanted close by the sponge *D. anchorata*. Control samples are represented by *triangles* and treatment samples by *squares*

Sponges are known to actively compete for space with scleractinian corals (Aerts and van Soest 1997; Hill 1998; Wulff 2005; Márquez et al. 2006), and many species produce diverse arrays of secondary metabolites, many of which are known to have defensive properties against foulers, predators, or competitors for space (Sears et al. 1990; Pawlik et al. 1995; Puyana et al. 2003; Paul and Ritson-Williams 2008). The sponge *D. anchorata* is the only competitor reported to be capable of damaging or causing the death in *Tubastraea* spp. (Meurer et al. 2010). The presence of *D. anchorata* effected the production of 5-bromoindole-3-carbaldehyde in *Tubastraea* spp. tissues. As well as *Tubastraea* spp., the sponge is known to overgrow and negatively affect other coral species, including the coral *Siderastrea siderea* (Mclean and Yoshioka 2008).

In our study, sterols represented about 40 % of all substances found for both species of *Tubastraea,* and the concentration of stigmasta-5,24(28)-dien-3β-ol produced by *T. tagusensis* was higher in the treatment employing *M. hispida* when compared with the control. Whether this substance is produced by *T. tagusensis* for defense is not clear, but its concentration did not stop the growth of the sponge. Fleury et al. (2008) reported a new sterol 23-ketocladiellin-A isolated from the introduced soft coral *Chromonephthea braziliensis* that exhibited potent in situ

feeding deterrence against a natural assemblage of fish. Within the sterols found here, cholest-5-en-3β-ol, predominant in both species of *Tubastraea*, may have played a role in the observed necrosis of *M. hispida* tissues, considering its higher concentration in this treatment when compared with controls and its positive correlation, according to PLS-DA, to that treatment. As both invasive species produce chemicals that negatively affect the benthos in the southwest Atlantic, we must consider the possibility that these chemicals contribute to the successful expansion of *Tubastraea* along the Brazilian coast.

Fatty acids are key structural components of cell membranes involved in photo-acclimation (in the laboratory) and acclimatization (in the field) (Latyshev et al. 1991; Harland et al. 1992), and they also contribute to the ability of organisms to tolerate temperature stress (Wada 1994). Our results show the importance of fatty acids in tissues of *Tubastraea* spp., since they represented more than 28 % of substances found in both species. The present study showed a higher concentration of hexadecanoic acid in the treatment employing *M. hispida* when compared with the control. In fact, fatty acids might serve as allelochemicals in aquatic organisms (Kakisawa et al. 1988; Suzuki et al. 1996; Chiang et al. 2004). Therefore, the high concentration of hexadecanoic acid found in tissues of *Tubastraea* may also have considerable ecological consequences for competitors, as necrosis occurred on tissues of *M. hispida*.

Previous studies have focused on the variation in secondary metabolites in some groups of cnidarians, including gorgonians (Harvell et al. 1993), soft corals (Maida et al. 1993; Kelman et al. 2000; Martí et al. 2005) and octocorals (Harvell and Fenical 1989; Van Alstyne and Paul. 1992). Leoni et al. (1995) showed a dramatic reduction in lipid content in tissues of the soft coral *Lobophytum compactum* when in contact with the red alga *Plocamium hamatum*. Direct contact with this alga caused necrosis of the soft-coral tissues that became less rich in organic material. In our study, some of the compounds produced by *Tubastraea* spp. also varied in concentration with proximity to *M. hispida* and *D. anchorata* despite the fact that no necrosis on tissues of *Tubastraea* was detected in the field.

In general, for both *Tubastraea* species, there were increases in alkaloids (16.2 %) and sterols (12.4 %); however, there was a decrease in fatty acid (−14.7 %) concentration in treatments in proximity to *M. hispida* when compared with controls. For both *Tubastraea* species, there was an increase in concentration of sterols (8.4 %) in treatments in proximity to *D. anchorata* when compared with controls. Nevertheless, there were decreases in alkaloid (−28.5 %) and fatty acid (−5.9 %) concentrations. The mechanisms behind these interactive effects remain to be elucidated.

Corals also use other specialized aggression mechanisms such as sweeper tentacles and mesenterial filaments. Sweeper tentacles have epidermii composed primarily of nematocysts used for feeding and for defense against predators and competitors (Sebens and Miles 1988). Witman (1993) suggested that damage to competitors by tentacular contact between *T. coccinea* and incrusting gorgonians and sponges in the US Virgin Islands may play an important role in the distribution and abundance of *Tubastraea*. In our study, allelochemicals and/or physical contact through cnidocytes (not observed in the field) may both be used by these non-indigenous species and could provide an alternative explanation for necrosis of areas observed on the tissues of the endemic coral *M. hispida*. Mariscal (1974) pointed out that it is difficult to separate experimentally the defensive effects of nematocysts from defensive effects of other cnidarian chemicals.

It is known that exploitative competition, which reduces resource availability due to indirect interactions between the competitors, may reduce the incorporation of energy by corals (Davies 1991; Kim and Lasker 1997). Additionally, variation in concentration of nutrients and food in the surrounding waters may also affect coral physiology, including the production of chemical defenses. The small size of competitors used in our experiment and multi-directional flow of water in the field were assumed not to have affected the supply of food and nutrients to *Tubastraea* spp.

To date, no studies have focused on the variability in composition and concentration of secondary metabolites in tissues of *Tubastraea* in close proximity to competitors. This study is therefore the first to show these species can change their chemistry and provides some insight into a mechanism that may mediate non-indigenous and native coral encounters. We conclude that the negative effects of the aggressive species of *Tubastraea* on *M. hispida* colonies seem to be chemically mediated, and these invasive species will probably also impact a suite of other species in the receptor communities along the southwest Atlantic coastline.

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