


How does the proliferation of the coral-killing sponge *Terpios hoshinota* affect benthic community structure on coral reefs?

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Abstract *Terpios hoshinota* is an encrusting sponge and a fierce space competitor. It kills stony corals by overgrowing them and can impact reefs on the square kilometer scale. We investigated an outbreak of *T. hoshinota* in 2014 at the island of Mauritius to determine its impacts on coral community structure. Surveys were conducted at the putative outbreak center, an adjacent area, and around the island to determine the extent of spread of the sponge and which organisms it impacted. In addition, quadrats were monitored for 5 months (July–December) to measure the spreading rates of *T. hoshinota* and *Acropora austera* in areas both with and without *T. hoshinota*. The photosynthetic capabilities of *T. hoshinota* and *A. austera* were also measured. *Terpios hoshinota* was well established, covering 13% of an estimated 416 m² of available hard coral substrate at the putative outbreak center, and 10% of an estimated 588 m² of available hard coral substrate at the adjacent area. The sponge was observed at only one other site around Mauritius. *Terpios hoshinota* and *A. austera* increased their planar areas by 26.9 and 13.9%, respectively, over five months. No new colonies of *T. hoshinota* were recorded in adjacent sponge-free control areas, suggesting that sponge recruitment is very low during austral winter and spring. The sponge was observed to overgrow five stony corals; however, it showed a preference for branching corals, especially *A. austera*. This is the first

time that a statistically significant coral substrate preference by *T. hoshinota* has been reported. *Terpios hoshinota* also had a significantly higher photosynthetic capacity than *A. austera* at irradiance >500 μmol photons m⁻² s⁻¹, a possible explanation for its high spreading rate. We discuss the long-term implications of the proliferation of *T. hoshinota* on community structure and dynamics of our study site.

Keywords Mauritius · Encrusting sponges · Competition · Photosynthesis · nMDS

Introduction

Benthic organisms in coral reef ecosystems use diverse physical and chemical mechanisms to compete for space. Stony corals can exhibit aggressive behavior by using mesenterial filaments to perform extracoelenteric digestion on their neighbors or sweeper tentacles to cause tissue destruction and cell death (Lang 1973; Richardson et al. 1979; Hidaka 1985). Free-living fungiids can use locomotion to acquire open spaces or overtop competitors (Chadwick-Furman and Loya 1992; Hoeksema et al. 2014a), while soft corals can use allelopathic compounds to cause local mortality in the competitors (Coll et al. 1982; Sammarco et al. 1983). Filamentous algae have been observed to physically interfere with the settlement of invertebrate larvae and reduce their recruitment success (Birrell et al. 2005). Crustose coralline algae have also been observed to reduce recruitment success of competitors by either sloughing off their epithelial cells (Johnson and Mann 1986; Keats et al. 1997) or using allelopathic compounds (Suzuki et al. 1998; Kim et al. 2004). The degree to which species interact depends on their relative abundance and spatial configuration (Vermeij et al. 2010). Interactions

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on the reef are diverse, and the outcomes of competitive interactions are species specific.

Sponges are important space competitors in coral reef communities. Their diversity and biomass can sometimes exceed those of stony corals (Diaz and Rützler 2001; Rützler 2002). They are important filter feeders that affect secondary production and help control nutrient fluxes in their surrounding waters (Pile et al. 1996; Yahel et al. 2003). Some sponges compete for space with stony corals by coming in direct or indirect contact and releasing allelopathic compounds that kill coral tissues and significantly reduce photosynthetic potential of the symbiotic zooxanthellae (Porter and Targett 1988; Pawlik et al. 2007; Chaves-Fonnegra et al. 2008). Others seem to rely on physical means to kill stony corals. For example, they can excavate coral skeletons from below the surface, deprive the coral polyps of support, and afterward grow on the skeleton of the dying corals (Schonberg and Wilkinson 2001; Rützler 2002; López-Victoria et al. 2006). Sponges have been observed to successfully overgrow several stony corals species using these mechanisms (Aerts and Van Soest 1997; Aerts 1998; Coles and Bolick 2007; Ávila and Carballo 2008; Rossi et al. 2015). Standoff interactions, where there is no clear winner, are also common on the reef (Aerts 2000). However, these have been found to be dynamic with both sponges and stony corals alternately losing and gaining space when observations were done over a period of months (Aerts 2000). Many stony corals have been observed to successfully maintain their space against sponge attacks (Aerts and Van Soest 1997; Schonberg and Wilkinson 2001; Rützler 2002) by fighting back (McKenna 1997).

There are numerous factors that influence the outcomes of sponge–coral interactions. If the sponge uses a confrontational strategy, its level of aggressiveness, whether physical (Lang 1973) or chemical (Porter and Targett 1988), can be a strong determinant of who will win the confrontation. If the sponge uses a non-confrontational strategy, growth form could play an important role. For example, sponges have also been observed to stop their progression or retreat when stony corals escaped by growing upwards (López-Victoria et al. 2006). Similarly, sponges were able to escape aggressive corals by also growing upwards (Aerts 2000). Growth rate can also provide a competitive advantage. A high growth rate can facilitate the acquisition of substratum, and the seeking or avoidance of competition (Hoppe 1988). Some sponges have been observed to very quickly take over space vacated by dead coral polyps (Aerts 2000). The angle of confrontation between the sponges and stony corals can also be important for lateral advancement. For example, confrontational angles $\geq 180^\circ$ enabled boring sponges to overgrow stony corals (López-Victoria et al. 2006). The

fitness of the species can also matter. Tissue damage in stony corals can increase their susceptibility to overgrowth by encrusting sponges (Aerts 2000).

The sponge *Terpios hoshinota* Rützler and Muzik, 1993 is an aggressive space competitor and is particularly good at overgrowing stony corals (Fig. 1a, b; Plucer-Rosario 1987; Rützler and Muzik 1993). *Montipora* and *Porites* corals and crustose algae are among a few that have been observed occasionally to overgrow the sponge (Fig. 1c; Plucer-Rosario 1987; Wang et al. 2012; Elliott et al. 2015). *Terpios hoshinota* is a very thin (<1 mm) encrusting sponge with a gray to black coloration (Fig. 1), which is attributed to a high density of photosynthetic cyanobacterial symbionts within its mesohyl (Rützler and Muzik 1993). It was originally thought that *T. hoshinota* overgrew stony corals to obtain nutritional benefits from their tissues (Bryan 1973), a hypothesis subsequently disproven (Plucer-Rosario 1987). The success of *T. hoshinota* has been attributed to its ability to propagate asexually, bridge coral branches and regrow from broken branches (Rützler and Muzik 1993).

There are three possible mechanisms that *T. hoshinota* could be using to defeat its coral competitors. The first and most likely mechanism involves physically overgrowing the stony corals. The growing front of *T. hoshinota* produces hairy tips or tendrils (Wang et al. 2012; Elliott et al. 2015) that progressively extend and grow over the healthy coral polyps. Cytotoxic compounds have also been isolated from *T. hoshinota* (Teruya et al. 2004), which suggests that the sponge could potentially use a chemical mechanism to acquire space. However, since no tissue discoloration or necrosis has been observed in the corals during these interactions, it is unlikely that the sponge uses chemical warfare against stony corals (Wang et al. 2012; Elliott et al. 2015). A third potential mechanism involves the indirect use of microbes by *T. hoshinota*. When *T. hoshinota* overgrew stony corals, the corals' microbial communities were observed to shift and become more similar to those found on corals suffering from black band disease (Tang et al. 2011). These observations suggest that harmful bacteria could weaken the corals, which then provides a competitive advantage to *T. hoshinota*.

The sponge has proven to be a threat to coral reefs through its effectiveness in overgrowing and killing large numbers of colonies of several stony coral species across the Indo-Pacific region (Bryan 1973; Plucer-Rosario 1987; Rützler and Muzik 1993; Fujii et al. 2011; Shi et al. 2012; de Voogd et al. 2013; Hoeksema et al. 2014b; Van der Ent et al. 2015). A *T. hoshinota* outbreak can impact reefs on the square kilometer scale (Bryan 1973). The sponge has been reported to have a linear growth rate of 11.5 mm month⁻¹ (Elliott et al. 2015) to 23 mm month⁻¹ (Bryan 1973). Moreover, it seems to be progressively

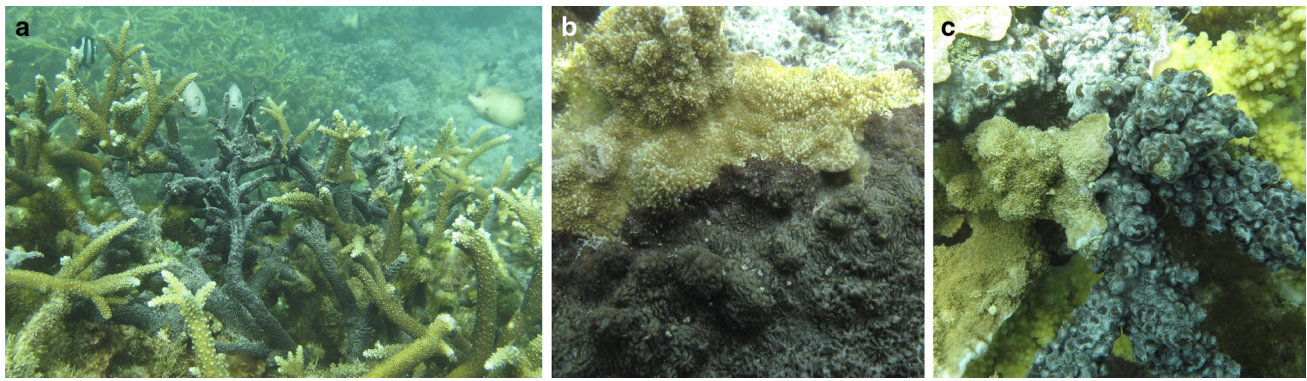


Fig. 1 **a** Coral-killing sponge *Terpios hoshinota* overgrowing *Acropora* corals. **b** *T. hoshinota* overgrowing *Montipora aequituberculata*. **c** *M. aequituberculata* overgrowing *T. hoshinota*

extending its global range, migrating westwards through the Indian Ocean (Elliott et al. 2015; Montano et al. 2015).

The first anecdotal observations of *T. hoshinota* in Mauritius (southwestern Indian Ocean) were made in 2010. By 2014, the sponge was one of the most conspicuous organisms at our study site. There is much debate as to why we are seeing this outbreak now. Was the sponge recently introduced, e.g., through ballast water, or was it a rare species that is now becoming prevalent due to changes in local environmental conditions? A large number of merchant ships from the Indo-Pacific region where *T. hoshinota* is native stop in Mauritius. Thus, it seems possible that *T. hoshinota* could have arrived to Mauritius through anthropogenic activities. In the Caribbean, removal of sponge-eating fishes by overfishing led to an over threefold increase in sponges overgrowing corals (Loh et al. 2015). If *T. hoshinota* was a rare species, it could now be proliferating in Mauritius where overfishing is widespread because of a predator release effect. Elsewhere, *T. hoshinota* outbreaks have been linked to pollution (Rützler and Muzik 1993) and iron enrichment of seawater (Schils 2012). This occurrence is not unique to *T. hoshinota*; other sponges have also been seen to overgrow stony corals after a change in local environmental conditions due to anthropogenic activities (Rose and Risk 1985; Rützler 2002).

At present, no study has assessed the ecological impacts of *T. hoshinota* on benthic community structure and dynamics of coral reefs. We investigated an outbreak of the sponge around the island of Mauritius to determine how it impacts the community over different spatial and temporal scales. We hypothesized that (1) *T. hoshinota* density is higher at the putative outbreak center compared to the adjacent area, (2) *T. hoshinota* has a higher growth rate than *Acropora austera* Dana, 1846 that helps it to overgrow this dominant branching coral, (3) *T. hoshinota* is more likely to be found on branching corals than non-branching coral, (4) *T. hoshinota* is more likely to be found on

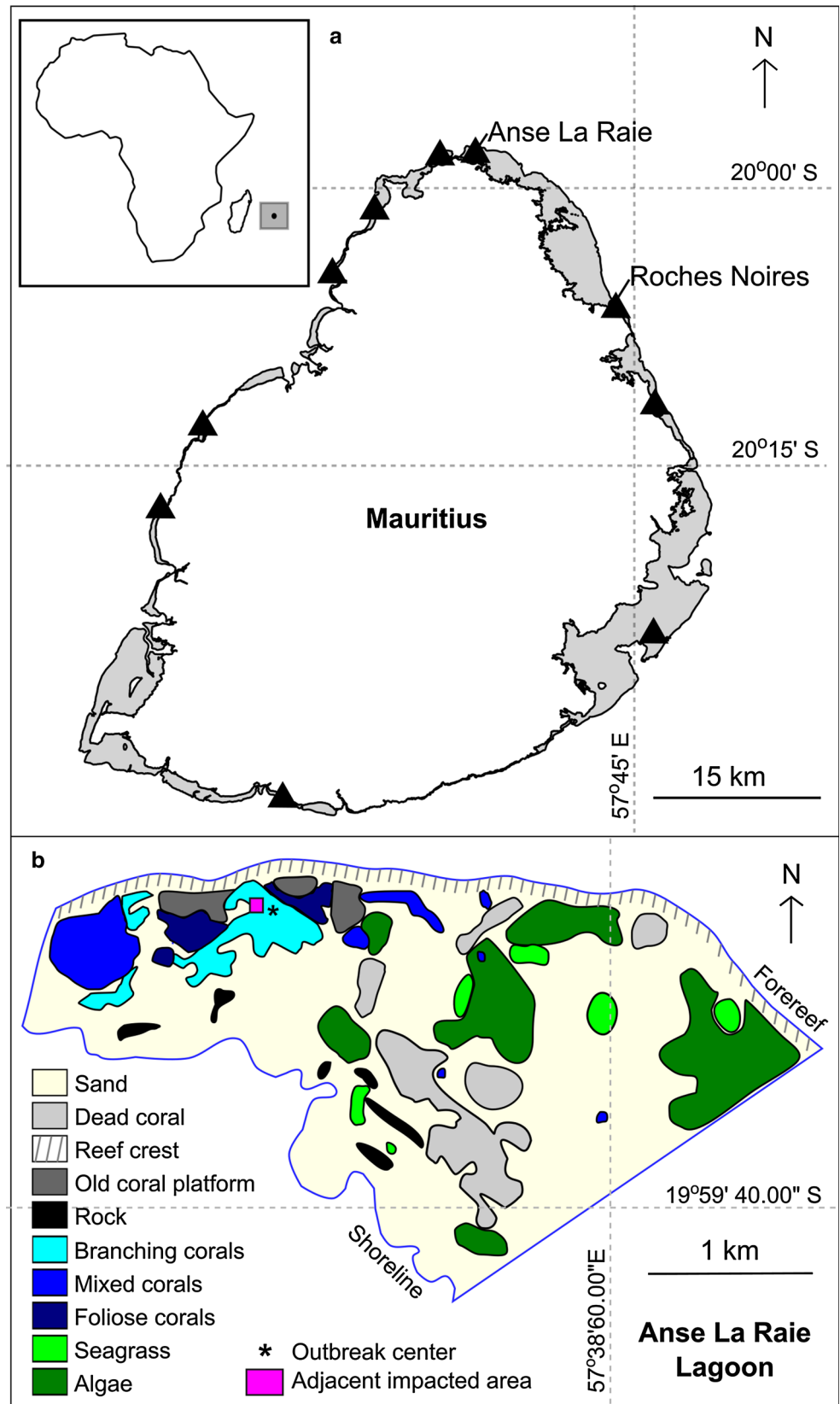
A. austera than any other coral species, (5) *T. hoshinota* has a higher photosynthetic capacity than healthy *A. austera*, (6) *A. austera* partially overgrown by *T. hoshinota* has a lower photosynthetic capacity than healthy *A. austera*, and (7) in a coral community, *T. hoshinota* is more likely to be present in areas dominated by branching corals than areas dominated by non-branching corals. We discuss the long-term implications of the proliferation of *T. hoshinota* on community structure and dynamics at our study site.

Materials and methods

Study site

The island of Mauritius is found in the southwestern Indian Ocean (20°10'S, 57°31'E; Fig. 2a). The island is mostly surrounded by shallow (<3 m) and narrow (<1 km) fringing reefs and has a small barrier reef (10 km) on the southeast coast (Fig. 2a; Turner and Klaus 2005). The lagoonal reefs consist mainly of branching and tabular *Acropora*, massive *Porites*, foliaceous *Montipora* and *Pavona*, and consolidated sea grass (Turner and Klaus 2005). Our principal field site was at Anse La Raie lagoon (ALR; Fig. 2a), the location of the only confirmed *T. hoshinota* sighting in Mauritius at the start of our study. A habitat map of ALR was created in 2011 using satellite remote sensing and field surveys (Fig. 2b). The total area of the lagoon surveyed was 6.53 km². We calculated that there was a total of 0.50 km² of live coral of which 0.21 km² were branching corals, 0.08 km² were foliose corals, and 0.21 km² were mixed corals. Live branching corals covered 35% of the branching coral areas, and live foliose corals covered 60% of the foliose coral areas. In the mixed coral areas, there was no dominant coral growth form. We also calculated that there were 0.10 km² of sea grass, 0.81 km² of algae, 0.46 km² of dead coral/rubble,

Fig. 2 **a** Island of Mauritius with its surrounding reefs and lagoons (gray). The inset shows the position of the island in the Indian Ocean. The black triangles show the field sites around the island. **b** Habitat map of Anse La Raie lagoon where most of this study was done. The asterisk shows the position of the putative outbreak center of *Terpios hoshinota*. The pink square shows the adjacent impacted area that was surveyed. The square representing the surveyed area is not to scale



0.41 km² of reef crest, 0.06 km² of rocks, and 0.10 km² of old coral platform. Sand was the most abundant type of substrate with an area of 4.08 km². The dead coral zones had mostly intact skeletons of dead corals with less than 2% live stony coral (Fig. 2b). Macroalgae, mostly *Padina* sp., covered 45% of the dead zones.

Spatial survey: community composition at the putative outbreak center

In June 2014, we assessed the extent of spread of *T. hoshinota* by conducting a small-scale high-resolution survey at the putative outbreak center of the sponge at ALR (Fig. 2b; 19°58'43"S, 57°37'52"E). A rapid survey of ALR identified an area in the northwest that had a much higher density of *T. hoshinota* colonies relative to adjacent areas; this location was declared the putative outbreak center. Four 10-m radius circular plots were established 30–35 m apart. Across the four plots, a total area of 1256 m² was surveyed. Within these plots, the Braun–Blanquet method (McAuliffe 1990) was used to estimate percent cover of six benthic groups: stony corals; *Cespitularia* sp. (soft coral); crustose coralline algae (CCA); turf algae–rubble; sand; and other. Additionally, each circular plot was divided into 18 sectors of 20°. All colonies of *T. hoshinota* within each sector were mapped (Fig. 3). The following measurements were taken for each *T. hoshinota* colony: (1) the sector within which it was found; (2) distance from the center of the plot; (3) length and width, multiplied to obtain a liberal estimate of its surface area; and (4) the coral species on which it was growing. Because of the high abundance of the colonies, we could not assign an exact bearing to each colony. Instead, depending on the sector that they were found in, colonies were assigned one of the following bearings: 10°, 30°, 50°, 70°, 90°, 210°, 230°, 250°, 270°, 290°, 310°, 330°, or 350°. Polar plots were made using the assigned bearing and the distance from center to visualize spatial distribution and abundance of *T. hoshinota*. The surface area of the sponge colonies was categorized into four size groups (<0.05, 0.05–0.15, 0.15–0.30, and >0.30 m²) and was represented as circles on the map. Because of the common bearing per sector, the circles formed one line per sector and sometimes overlapped. Each sector was also color-coded to represent percent of available hard substrate that was obtained from the survey using the Braun–Blanquet method.

Spatial survey: community composition of the area adjacent to the outbreak

A second survey was made at the same time to determine the extent to which the community adjacent to the putative center of *T. hoshinota* outbreak was affected by the sponge

(Fig. 2b). We characterized a 2000 m² area (19°58'41"S to 19°58'43"S; 57°37'49"E to 57°37'5"E) by conducting four 50-m video transects that were perpendicular to the beach and 10 m apart. Twenty-five quadrats evenly spaced over each 50 m transect were analyzed using Coral Point Count with Excel Extensions (CPCe) (Kohler and Gill 2006). Due to variations in depth, the area of the quadrats analyzed ranged from 0.70 to 1.10 m². A total area of 99 m² was analyzed. Overlays of 150, 200, and 250 points per m² were tested, and percent cover estimates compared using Pearson's product–moment correlation (Guinan et al. 2009). We aimed for a data analysis efficiency given by a correlation coefficient (r) ≥ 0.95 . The r was 0.92 ($p < 0.001$) for the 150 versus 200 points per m², and 0.97 ($p < 0.001$) for the 200 versus 250 points per m². Therefore, percent cover for the entire data set was extracted using a density of 200 points per m². Results were organized to show the percent cover of (1) major benthic groups, (2) stony corals, and (3) stony corals overgrown by *T. hoshinota* at ALR.

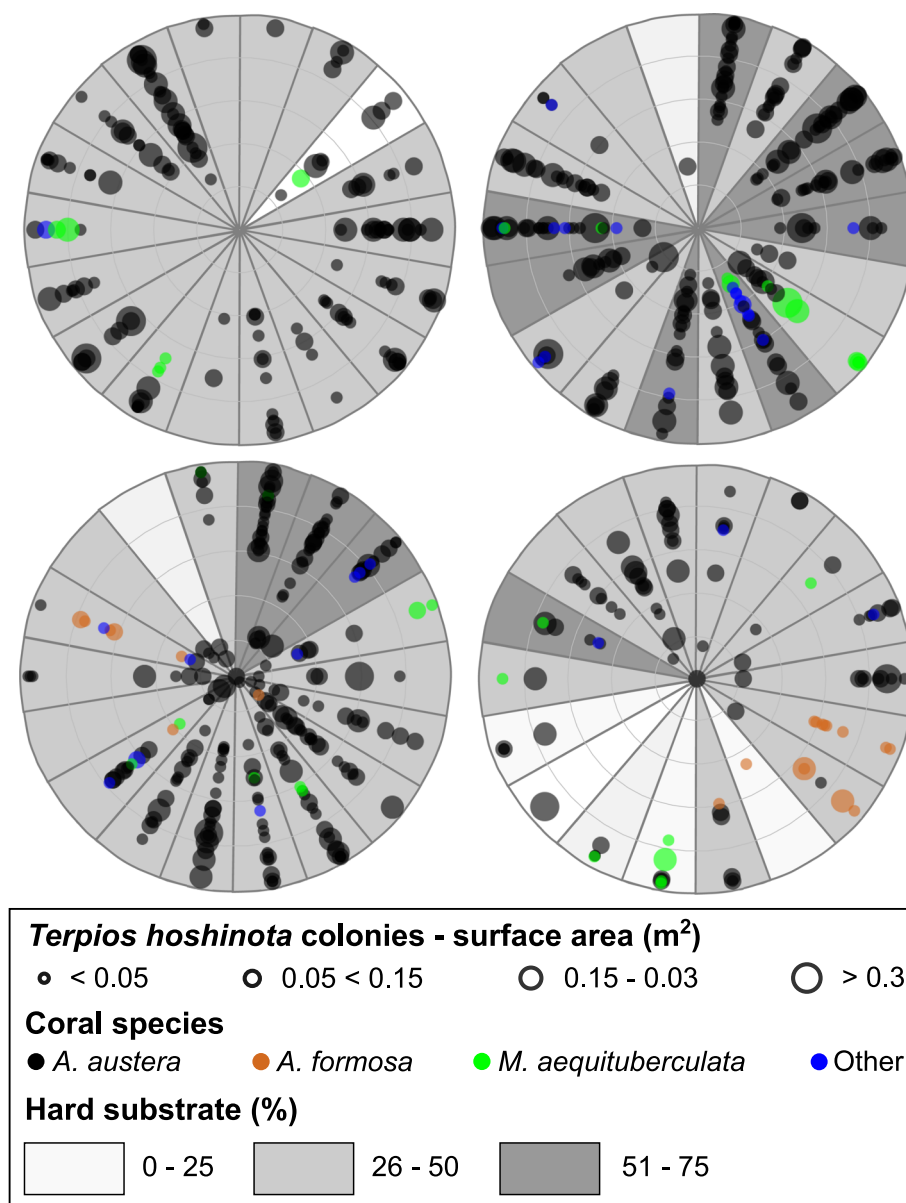
Spatial survey: *T. hoshinota* around Mauritius

In December 2014, we did a third and final survey to determine the extent of spread of *T. hoshinota* around Mauritius. A total of nine shallow back reef lagoons were surveyed (Fig. 2a): one in the north (Bain Boeuf); one in the south (St. Félix); three on the east coast (Belle Mare, Roches Noires, Mahébourg); and four on the west coast (Trou aux Biches, Pointe aux Piments, Albion, Flic en Flac). With the exception of Mahébourg lagoon, all the other sites were surveyed by starting from the beach and running a series of parallel transects perpendicular to the beach. Each survey lasted 60 min. Major coral patches were targeted along the way, and the presence/absence of *T. hoshinota* was noted. Mahébourg lagoon is one of the largest and widest lagoons in Mauritius. A small boat was used to do this survey, and eight major coral patches were targeted. At each coral patch, spot checks were done by snorkeling for 5 min, and the presence/absence of *T. hoshinota* was noted.

Temporal survey: spreading rates

We measured the spreading rates of *T. hoshinota* and *A. austera*, which appeared to be the coral species most affected by the sponge. At the putative outbreak center, thirty 25 × 25 cm quadrats were set up in July 2014. Fifteen quadrats had 20–40% cover of *T. hoshinota*, and the other 15 did not have any *T. hoshinota* at the start of the experiment. Similarly, we set up another thirty 25 × 25 cm quadrats to measure the spreading rate of *A. austera* with ($n = 15$) and without ($n = 15$) *T. hoshinota* over a 5-month period. All quadrats were at least 2–3 m

Fig. 3 Spatial distribution and abundance of *Terpios hoshinota* at the putative outbreak center. Each plot has a diameter of 10 m. Colored circles represent the planar area of *T. hoshinota* colonies and which species they overgrew (*Acropora austra*, black; *A. formosa*, orange; *Montipora aequituberculata*, green; other, blue). Sector color represents percent of available substrate



apart. A photograph of each quadrat was taken at the time of setup and again five months later (December 2014). We also inspected the control quadrats to determine whether new sponge colonies settled over a 5-month period. Spreading rates of the sponge and coral were calculated as a percent change in their planar area over time using ImageJ (Abramoff et al. 2004). One-way ANOVAs were used to test how the presence or absence of *T. hoshinota* affected the spreading rate of the sponge and the coral.

Substrate preference of *T. hoshinota*

Using data obtained from the community survey of the area adjacent to the outbreak, a Chi-square goodness-of-fit test was done to test whether *T. hoshinota* was equally likely to

overgrow any stony coral species it encountered. We compared the observed proportions of *T. hoshinota* overgrowing branching corals and non-branching corals to expected proportions predicted by the observed proportions of each group in the coral community. Similarly, we compared the observed proportions of *T. hoshinota* overgrowing *A. austra*, *Montipora aequituberculata* (Bernard, 1897) and other (all other stony coral species recorded) to the expected proportions predicted by the observed proportions of the coral community made up by each species/group.

Photosynthetic capacity of *T. hoshinota*

We measured the photosynthetic capacity of (1) *T. hoshinota*, (2) healthy *A. austra*, and (3) *A. austra* partially

overgrown by *T. hoshinota* using a pulse amplitude modulated fluorometer (Diving PAM, Walz, Germany) to determine whether the sponge was more effective at harvesting solar energy than *A. austera*. The rapid light curve (RLC) function of the diving PAM was used to measure the effective quantum yield of PSII in darkness. PAM works by measuring light under ambient conditions (F), subjecting the sponge/coral to a saturating pulse of actinic light, and remeasuring fluorescence (Fm'). Samples were exposed to eight incremental steps of irradiance ranging from 0 to 2346 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, and each step consisted of 10 s of irradiance. The relative electron transport rate (rETR) at each irradiance intensity of the RLCs was estimated by the equation $rETR = \phi p \times PAR$, where ϕp was the effective quantum yield of PSII ($FPSII = (Fm' - F)/Fm'$) and PAR was the photosynthetically available irradiance reaching the sponge/coral ($\mu\text{mol photon m}^{-2} \text{s}^{-1}$). From the rETR, the maximal rETR at light saturation (rETR_{max}) and the initial slope of the light-limited relationship (α) were calculated by fitting the observed data to the negative exponential curve $rETR = rETR_{\text{max}} \times (1 - e^{(-\alpha \times PAR/rETR_{\text{max}})})$ (Finelli et al. 2007). Curve fitting was achieved using a nonlinear least squares model. A 95% confidence interval band was also plotted for each curve. All measurements were taken in complete darkness on a single night at ALR in January 2015. The measurement was repeated three times ($n = 3$) on a sponge or coral colony that was 5 m from all others that had been measured. The fiber optic probe was held 5 mm away from sponge/coral and positioned on the downstream side relative to the prevailing currents. Measurements on *A. austera* partially overgrown by *T. hoshinota* were always taken at least 2–3 cm away from the growing front of the sponge.

Impacts of *T. hoshinota* on community structure

We performed a non-metric multidimensional scaling (nMDS) analysis on Bray–Curtis distance (Borcard et al. 2011) on the community data obtained from the area adjacent to the outbreak to investigate the impacts of *T. hoshinota* on community structure at ALR. We assumed that community dynamics were not dependent on quadrat size over the range of 0.70–1.10 m². Quadrats were color-coded based on their spatial location (east or west), and a 95% confidence interval ellipse was fitted around each set of location scores to investigate any geographical patterns in community composition. Quadrats on the east side were closer to the putative outbreak center.

Statistical analysis

All graphs and statistical analyses were done using R 3.2.0 (R Core Team 2015) except when mentioned otherwise.

Results

Community composition at the putative outbreak center

The Braun–Blanquet survey showed that the putative outbreak center of *T. hoshinota* was dominated by stony corals, rubble–turf, and the soft coral *Cespitularia* sp. (Table 1). The polar plots showed that *A. austera* was the most impacted by *T. hoshinota*, followed by *A. formosa* and *M. aequituberculata* (Fig. 3). Other taxa overgrown by the sponge include *M. digitata*, *M. spongiosa*, *Pocillopora damicornis*, and CCA, all of which are grouped under ‘other’ (Fig. 3). Overall, out of the 1256 m² surveyed, there was an estimated 416 m² of available hard coral substrate of which 55 m² had been overgrown by *T. hoshinota* (Table 1; Fig. 3). This constitutes a 13% loss of live coral to the sponge. A total of 762 *T. hoshinota* colonies were recorded of which 158, 251, 248 and 105 were <0.05, 0.05–0.15, 0.15–0.30, and >0.30 m² in size, respectively. The maximum colony size recorded was 0.75 m².

Community composition of the area adjacent to the outbreak

The benthic community in the area adjacent to the putative outbreak center was composed mainly of stony corals and turf algae, followed closely by rubble and the soft coral *Cespitularia* sp. (Figure 4a). Overall, of the 2000 m² surveyed, there was an estimated 588 m² of available hard coral substrate of which an estimated 59 m² had been overgrown by *T. hoshinota*. This constitutes a 10% loss of live coral to the sponge. *Acropora austera* was the dominant stony coral species in this area, representing 71% of all stony corals observed (Fig. 4b). Moreover, *T. hoshinota* was observed to primarily overgrow *A. austera* (92% of all *T. hoshinota* observed; Fig. 4c).

Terpios hoshinota around Mauritius

The island-wide survey revealed only one other site where *T. hoshinota* was present, namely Roches Noires (Fig. 1). A solitary *T. hoshinota* colony of about 15 × 15 cm was observed on a colony of *Porites lutea*.

Table 1 Community composition in the circular plots at the putative outbreak center of *Terpios hoshinota* based on the Braun–Blanquet estimate

	Cover (%)					Area (m ²)
	Plot 1	Plot 2	Plot 3	Plot 4	Average	
Stony corals ^a	29	42	38	23	33	416
<i>Cespitularia</i> sp.	24	30	12	37	26	321
Rubble–Turf	28	22	35	22	27	334
Crustose coralline algae	6	4	6	10	6	79
Sand	12	2	3	2	5	60
Other	2	1	6	6	4	45
Total	100	100	100	100	100	1256

^a Stony corals with and without *T. hoshinota* grouped together

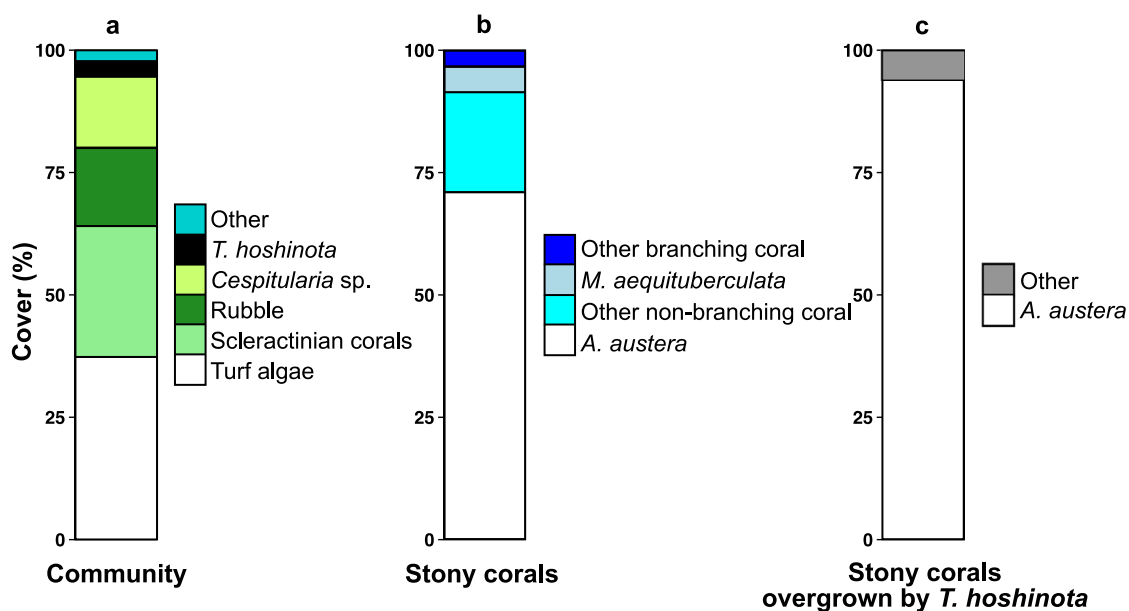


Fig. 4 **a** Overall composition of the community at the area adjacent to the putative outbreak center of *Terpios hoshinota*; **b** composition of stony corals; and **c** identity of stony corals overgrown by *T. hoshinota*

Spreading rates

Five of the quadrats could not be relocated for the experiment measuring the spreading rate of the sponge. The sample sizes were 12 and 13, respectively, for quadrats with and without *T. hoshinota*. Over 5 months, planar area of *T. hoshinota* increased by a mean of 26.9%, and no new colonies of *T. hoshinota* were observed in quadrats without *T. hoshinota*.

Four of the quadrats could not be relocated for the experiment measuring the spreading rate of *A. austera*. The sample sizes were 13 and 13, respectively, for quadrats with and without *T. hoshinota*. There was a significant difference in changes of coral planar area over five months between quadrats with and without *T. hoshinota* ($p < 0.05$). Over 5 months, the planar area of *A. austera*

increased by 13.9% in quadrats without *T. hoshinota* and decreased by mean of 19.6% in quadrats with *T. hoshinota*.

Substrate preference of *T. hoshinota*

Terpios hoshinota overgrew branching corals in preference to non-branching corals ($\chi^2 = 16.84$, $df = 1$, p value = 4.1×10^{-5}) and preferentially overgrew *A. austera* more than any other stony coral species at ALR ($\chi^2 = 18.372$, $df = 2$, p value = 1.0×10^{-4}).

Photosynthetic capacity of *T. hoshinota*

There was no significant difference in the fitted slope (α) for *T. hoshinota* ($\alpha = 0.19$), healthy *A. austera* ($\alpha = 0.20$) and partially overgrown *A. austera* ($\alpha = 0.27$) (Fig. 5).

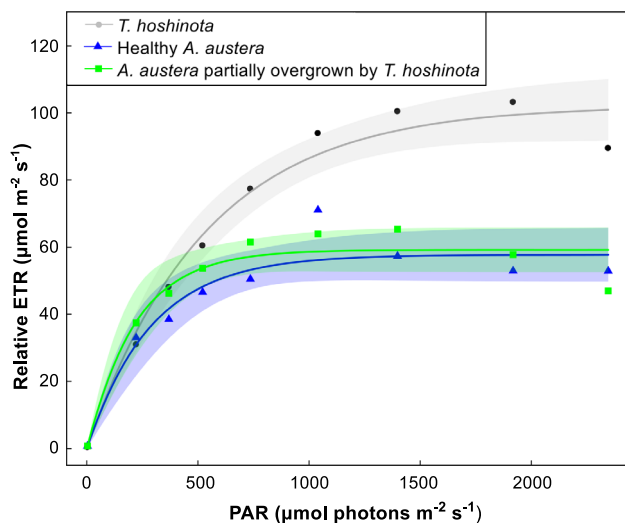


Fig. 5 Photosynthetic capacity ($rETR_{max}$) of *Terpios hoshinota* (black) compared to healthy (blue) and partially overgrown *Acropora austra* (green). Shaded areas represent 95% confidence interval band for each curve

However, there was a significant difference in the relative ETR maximum for *T. hoshinota* ($rETR_{max} = 102.19$) compared to both healthy *A. austra* ($rETR_{max} = 57.72$) and partially overgrown *A. austra* ($rETR_{max} = 59.19$), which is $>40\%$ higher for *T. hoshinota*. This implies that *T. hoshinota* had a significantly higher photosynthetic capacity than *A. austra* when irradiance was $>500 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ($p < 0.05$; Fig. 5). There were no significant differences in photosynthetic capacity of healthy and partially overgrown *A. austra*.

Impacts of *T. hoshinota* on community structure

There was a significant difference in community composition between quadrats on the east versus those on the west of Mauritius (Fig. 6). Quadrats on the east were characterized by relatively high abundances of *T. hoshinota*, branching coral (BC), turf, and other (all other organisms), while those on the west contained mostly rubble, sand, CCA, *Cespitularia* sp. (CS), and non-branching corals (NBC). The smaller 95% ellipse also indicated that community composition in quadrats located on the east were more similar to each other than those on the west.

Discussion

Spatial scale

Our investigation showed that *T. hoshinota* was well established in 2014 at ALR, with 13 and 10% of all available stable hard substrate overgrown by the sponge at the putative

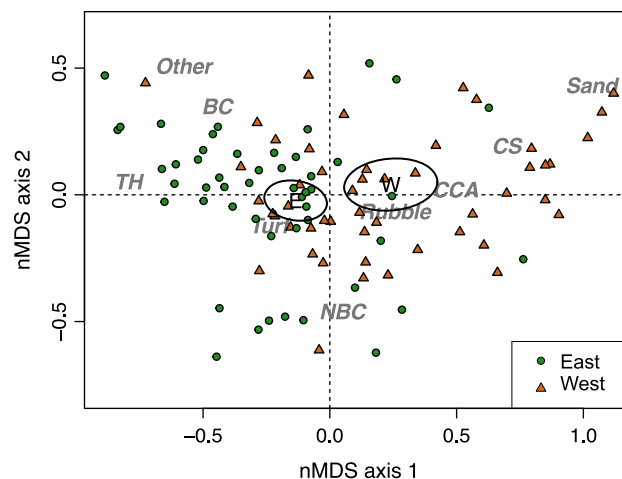


Fig. 6 Non-metric multidimensional scaling (nMDS) plot for the benthic community at Anse La Raie lagoon (2-D stress = 0.12). Data used were from the area adjacent to the putative outbreak center of *Terpios hoshinota*. BC branching coral, CCA crustose coralline algae, CS *Cespitularia* sp., NBC non-branching coral, Other other living non-coral organisms, TH: *T. hoshinota*. A 95% confidence interval ellipse was fitted around each set of location scores

outbreak center and the adjacent area, respectively. As we hypothesized, there was a higher density of *T. hoshinota* at the putative outbreak center than the adjacent area, but the two percentages were very close. This suggests that there is a higher abundance of *T. hoshinota* at ALR and that the sponge is more evenly spread than previously thought. A 50–89.7% overgrowth by *T. hoshinota* was reported in Japan (Reimer et al. 2010). Studies in Guam and Japan also showed that *T. hoshinota* could spread to several lagoons around small islands and that the spread could extend from a few small patches (<30 cm in diameter) to extensive, large patches (>50 cm in diameter) covering most of the available hard substrate (Bryan 1973; Reimer et al. 2011). Our sponge colonies had a mean and maximum diameter of 15 and 49 cm, respectively. Our measurements indicate that the outbreak at ALR could be at an intermediate stage, i.e., that there were more than a few small patches, but the community was not completely dominated by *T. hoshinota*. Although concentrated in the northern lagoon of ALR, the sponge appears to have spread to only one other lagoon (Roches Noires; Fig. 1). The limited distribution of *T. hoshinota* supports the idea that the outbreak started at ALR, although identifying the exact position of the center remains difficult. Observations in Guam and Japan indicate the potential for *T. hoshinota* to spread to other lagoons around Mauritius.

Temporal scale

Terpios hoshinota increased its planar area by asexual propagation by 26.9% over a 5-month period, which is

almost a 5% increase per month if we assume a constant rate of increase. Interestingly, during the same period no new sponge colonies recruited to the adjacent area without *T. hoshinota*. These observations suggest that sponge recruitment is very low during July–December, which is winter to late spring at our study site. The sponge's linear growth rate of 11.5 mm month⁻¹ (Elliott et al. 2015) was also 1.5–2 times higher than two encrusting sponges that are potential threats to stony corals (Rützler 2002; Rossi et al. 2015). Over a 5-month period, *A. austera* increased its planar area by 13.9%. Thus, the sponge spread twice as fast as the coral over 5 months. As we predicted, *T. hoshinota* had a higher growth rate than *A. austera*. The linear growth rate of the sponge was also 2–10 times higher than other stony coral species (Gladfelter and Monahan 1978). This faster spreading rate could be attributed partly to not needing to bear the material and energetic costs of building a calcium carbonate skeleton (Brusca and Brusca 2003). Therefore, the spreading/growth rate of *T. hoshinota* could contribute to its higher competitive ability.

Substrate preference

As we hypothesized, *T. hoshinota* was found overgrowing branching corals more often than non-branching corals, and it was also found more often on *A. austera* than any other coral species. This has also been observed in Indonesia (Van der Ent et al. 2015), but this is the first report of a statistically significant coral substrate preference by *T. hoshinota*. Different stony coral species have different levels of aggression (Lang 1973), but it seemed that however aggressive branching corals may be, they were not able to defend themselves against *T. hoshinota*, with *A. austera* the least able to defend itself. A study examining the interface between *T. hoshinota* and 19 stony coral species with different morphologies reported that some species fired their nematocysts on contact with *T. hoshinota*, but that they were generally ineffective at stopping the progression of the sponge (Wang et al. 2012). Growing upwards to escape *T. hoshinota* did not seem to work for *A. austera* probably because of the higher growth rate of the sponge, its encrusting growth form, and ability to bridge coral branches (Rützler and Muzik 1993). *Montipora aequituberculata* was the only stony coral to occasionally overgrow *T. hoshinota* at our study site. Its morphological plasticity enabled redirection of growth and maintenance of space (Elliott et al. 2015). An encrusting morphology enabled *M. aequituberculata* to win over *T. hoshinota*.

We did not observe such morphological plasticity in *A. austera*, which could potentially explain why it could not escape from the sponge. One very noticeable feature of the overgrowth of *T. hoshinota* on branching corals was that the overgrowth would always start at the base of the coral

branch, at the interface of the coral and turf algae, and progressed upwards toward the tips of coral branches. The interface between live coral tissues and turf algae could be a surface where *T. hoshinota* larvae may have higher recruitment success. An ex situ experiment showed that freshly released larvae would always settle on dead coral or the bottom of the petri dish, and never on live coral (Hsu et al. 2013). Additionally, damselfishes are known to vigorously guard their algal patches and can indirectly provide a refuge for some invertebrate microfauna (Ferreira et al. 1998). This possible combination of recruitment surface and indirect protection could potentially explain why *T. hoshinota* was found more often on branching stony corals.

Photosynthetic capacity

As we predicted, *T. hoshinota* had a higher photosynthetic capacity than healthy *A. austera*. However, there were no significant differences in photosynthetic capacity between healthy *A. austera* and *A. austera* partially overgrown by *T. hoshinota*, suggesting that *T. hoshinota* did not affect photosynthesis in healthy coral tissues that were not in direct contact with it. Photosynthetic sponges can obtain a large part of their energy budget for growth and reproduction through photosynthesis (Wilkinson 1983). Therefore, if a mutualistic relationship exists between *T. hoshinota* and its symbionts, the high photosynthetic capacity of the symbionts could partly explain the high growth rate of the sponge host. We measured irradiance >2000 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ in December at ALR (1100–1200 hrs, clear sunny sky, 3.0 m deep). At irradiance levels >500 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, *T. hoshinota* had a greater rETR than *A. austera* (Fig. 5). This ability to take greater advantage of high levels of irradiance could potentially explain *T. hoshinota*'s higher competitive ability against the coral at ALR. Many encrusting sponges with photosynthetic symbionts have also been observed to be good space competitors (Rützler and Muzik 1993).

Impacts on community structure

The high proliferation rate of *T. hoshinota* will bring some significant changes to the community structure and dynamics of ALR. The nMDS analysis confirmed that *T. hoshinota* at the area adjacent to the outbreak was more often found in areas dominated by branching corals than areas dominated by non-branching corals (Fig. 6). The sponge was also found closely associated with turf algae and other live non-coral organisms and rarely associated with sand, *Cespitularia* sp., CCA, rubble, and non-branching coral. This propensity of *T. hoshinota* to overgrow branching coral areas suggests that the community could have a lower abundance of branching corals in the

long term, and possibly also a lower structural complexity when the dead corals break down. The current trends also suggest that there could be a major decrease in *A. austera* abundance, the preferred target of *T. hoshinota*, at ALR. *Terpios hoshinota* could replace *A. austera* to become one of the most dominant species over time. However, observations in Guam suggest that this dominance could be of short duration because after the sponge dominated a reef area and killed almost all the corals, *T. hoshinota* also died with very few colonies surviving 2 yr after the coral mortality (Bryan 1973). Therefore, long-term survival of *T. hoshinota* could be dependent on availability of live stony coral as substrate.

Although rarely observed, a community dominated by *T. hoshinota* can return to coral dominance (Reimer et al. 2010), suggesting that even under optimal proliferation conditions, other factors can control the spread of *T. hoshinota*. CCA is an important substrate for coral larval settlement (Harrington et al. 2004). We have rarely seen *T. hoshinota* overgrow CCA, and contact between the two has been reported to cause retrogression in the sponge (Plucer-Rosario 1987). Thus, availability of CCA in communities highly impacted by *T. hoshinota* could play an even more important role in controlling the spread of the sponge by supporting stony coral recruitment and survival. Although there are reports of the sponge overgrowing rubble (Plucer-Rosario 1987; Rützler and Muzik 1993), we did not observe any *T. hoshinota* growing on rubble at ALR. However, *Cespitularia* sp. was often found in high rubble areas. This soft coral is an opportunistic colonizer of disturbed habitats (McFadden et al. 2014). Its success in colonizing new space has been attributed to its toxicity (Coll et al. 1982; Sammarco et al. 1983) and ability to overgrow adjacent organisms (Benayahu and Loya 1981). Thus, *Cespitularia* sp. seemed to be controlling the spread of *T. hoshinota* in the community at ALR, especially in rubble areas. However, almost nothing else was observed to grow in its presence.

Our study provides more evidence that the encrusting growth form and high spreading rate of *T. hoshinota* contribute to make the sponge a fierce space competitor in coral reef communities. We report for the first time a statistically significant coral substrate preference by *T. hoshinota*. Long-term monitoring is needed to better understand how *T. hoshinota* will change the competitive balance on the reef, and how community structure and dynamics will change over time.

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References

- Abràmoff MD, Magalhães PJ, Ram SJ (2004) Image processing with ImageJ. *Biophotonics International* 11:36–42
- Aerts LAM (1998) Sponge/coral interactions in Caribbean reefs: analysis of overgrowth patterns in relation to species identity and cover. *Mar Ecol Prog Ser* 175:241–249
- Aerts LAM (2000) Dynamics behind standoff interactions in three reef sponge species and the coral *Montastraea cavernosa*. *Mar Ecol* 21:191–204
- Aerts LAM, Van Soest RWM (1997) Quantification of sponge/coral interactions in a physically stressed reef community, NE Colombia. *Mar Ecol Prog Ser* 148:125–134
- Ávila E, Carballo JL (2008) A preliminary assessment of the invasiveness of the Indo-Pacific sponge *Chalinula nematifera* on coral communities from the tropical Eastern Pacific. *Biol Invasions* 11:257–264
- Benayahu Y, Loya Y (1981) Competition for space among coral-reef sessile organisms at Eilat, Red Sea. *Bull Mar Sci* 31:514–522
- Birrell CL, McCook LJ, Willis BL (2005) Effects of algal turfs and sediment on coral settlement. *Mar Pollut Bull* 51:408–414
- Borcard D, Gillet F, Legendre P (2011) *Numerical ecology with R*. Springer, New York, NY, USA
- Brusca RC, Brusca GJ (2003) *Phylum Porifera: the sponges. Invertebrates*. Sinauer Press, Sunderland, MA, pp 179–208
- Bryan PG (1973) Growth rate, toxicity, and distribution of the encrusting sponge *Terpios* sp. (Hadromerida: Suberitidae) in Guam. *Mariana Islands. Micronesica* 9:238–242
- Chadwick-Furman N, Loya Y (1992) Migration, habitat use, and competition among mobile corals (Scleractinia: Fungiidae) in the Gulf of Eilat, Red Sea. *Mar Biol* 114:617–623
- Chaves-Fonnegra A, Castellanos L, Zea S, Duque C, Rodríguez J, Jiménez C (2008) Clionapyrolidine A—a metabolite from the encrusting and excavating sponge *Cliona tenuis* that kills coral tissue upon contact. *J Chem Ecol* 34:1565–1574
- Coles SL, Bolick H (2007) Invasive introduced sponge *Mycale grandis* overgrows reef corals in Kāneʻohe Bay, Oʻahu, Hawaiʻi. *Coral Reefs* 26:911–911
- Coll JC, La Barre S, Sammarco PW, Williams WT, Bakus GJ (1982) Chemical defences in soft corals (coelenterata: octocorallia) of the Great Barrier Reef: a study of comparative toxicities. *Mar Ecol Prog Ser* 8:271–278
- de Voogd NJ, Cleary DFR, Dekker F (2013) The coral-killing sponge *Terpios hoshinota* invades Indonesia. *Coral Reefs* 32:755–755
- Diaz MC, Rützler K (2001) Sponges: an essential component of Caribbean coral reefs. *Bull Mar Sci* 69:535–546
- Elliott J, Patterson M, Vitry E, Summers N, Miteronique C (2015) Morphological plasticity allows coral to actively overgrow the aggressive sponge *Terpios hoshinota* (Mauritius). *Mar Biodiv, Southwestern Indian Ocean*. doi:10.1007/s12526-015-0370-4
- Ferreira C, Gonçalves J, Coutinho R (1998) Herbivory by the dusky damselfish *Stegastes fuscus* (Cuvier, 1830) in a tropical rocky shore: effects on the benthic community. *J Exp Mar Bio Ecol* 229:241–264
- Finelli CM, Helmuth BS, Pentcheff ND, Wethey DS (2007) Intra-colony variability in photosynthesis by corals is affected by water flow: role of oxygen flux. *Mar Ecol Prog Ser* 349:103–110
- Fujii T, Keshavmurthy S, Zhou W, Hirose E, Chen CA, Reimer JD (2011) Coral-killing cyanobacteriosponge (*Terpios hoshinota*) on the Great Barrier Reef. *Coral Reefs* 30:483–483

- Gladfelter EH, Monahan RK (1978) Growth rates of five reef-building corals in the northeastern Caribbean. *Bull Mar Sci* 28:728–734
- Guinan J, Grehan AJ, Dolan M, Brown C (2009) Quantifying relationships between video observations of cold-water coral cover and seafloor features in Rockall Trough, west of Ireland. *Mar Ecol Prog Ser* 375:125–138
- Harrington L, Fabricius K, De'ath G, Negri A (2004) Recognition and selection of settlement substrata determine post-settlement survival in corals. *Ecology* 85:3428–3437
- Hidaka M (1985) Nematocyst discharge, histoincompatibility, and the formation of sweeper tentacles in the coral *Galaxea fascicularis*. *Biol Bull* 168:350–358
- Hoeksema BW, Dekker F, de Voogd NJ (2014a) Free-living mushroom corals strike back by overtopping a coral-killing sponge. *Mar Biodiv* 44:3–4
- Hoeksema BW, Waheed Z, de Voogd NJ (2014b) Partial mortality in corals overgrown by the sponge *Terpios hoshinota* at Tioman Island, Peninsular Malaysia (South China Sea). *Bull Mar Sci* 90:989–990
- Hoppe WF (1988) Growth, regeneration and predation in three species of large coral reef sponges. *Mar Ecol Prog Ser* 50:117–125
- Hsu C-M, Wang J-T, Chen CA (2013) Larval release and rapid settlement of the coral-killing sponge, *Terpios hoshinota*, at Green Island, Taiwan. *Mar Biodiv* 43:259–260
- Johnson CR, Mann KH (1986) The crustose coralline alga, *Phymatolithon* Foslie, inhibits the overgrowth of seaweeds without relying on herbivores. *J Exp Mar Bio Ecol* 96:127–146
- Keats DW, Knight MA, Pueschel CM (1997) Antifouling effects of epithelial shedding in three crustose coralline algae (Rhodophyta, Corallinales) on a coral reef. *J Exp Mar Bio Ecol* 213:281–293
- Kim M-J, Choi J-S, Kang S-E, Cho J-Y, Jin H-J, Chun B-S, Hong Y-K (2004) Multiple allelopathic activity of the crustose coralline alga *Lithophyllum yessoense* against settlement and germination of seaweed spores. *J Appl Phycol* 16:175–179
- Kohler KE, Gill SM (2006) Coral Point Count with Excel extensions (CPCe): a Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Comput Geosci* 32:1259–1269
- Lang J (1973) Interspecific aggression by scleractinian corals. 2. Why the race is not only to the swift. *Bull Mar Sci* 23:260–279
- Loh TL, McMurray SE, Henkel TP, Vicente J, Pawlik JR (2015) Indirect effects of overfishing on Caribbean reefs: sponges overgrow reef-building corals. *PeerJ* 2015:e901
- López-Victoria M, Zea S, Weil E (2006) Competition for space between encrusting excavating Caribbean sponges and other coral reef organisms. *Mar Ecol Prog Ser* 312:113–121
- McAuliffe JR (1990) A rapid survey method for the estimation of density and cover in desert plant communities. *J Veg Sci* 1:653–656
- McFadden CS, Reynolds AM, Janes MP (2014) DNA barcoding of xeniid soft corals (Octocorallia: Alcyonacea: Xeniidae) from Indonesia: species richness and phylogenetic relationships. *System Biodivers* 12:247–257
- McKenna SA (1997) Interactions between the boring sponge, *Cliona lampa* and two hermatypic corals from Bermuda. *Proc 8th Int Coral Reef Symp* 2:1369–1374
- Montano S, Chou W-H, Chen CA, Galli P, Reimer JD (2015) First record of the coral-killing sponge *Terpios hoshinota* in the Maldives and Indian Ocean. *Bull Mar Sci* 91:97–98
- Pawlik JR, Steindler L, Henkel TP, Beer S, Ilan M (2007) Chemical warfare on coral reefs: sponge metabolites differentially affect coral symbiosis in situ. *Limnol Oceanogr* 52:907–911
- Pile AJ, Patterson MR, Witman JD (1996) In situ grazing on plankton <10 µm by the boreal sponge *Mycale lingua*. *Mar Ecol Prog Ser* 141:92–105
- Plucer-Rosario G (1987) The effect of substratum on the growth of *Terpios*, an encrusting sponge which kills corals. *Coral Reefs* 5:197–200
- Porter JW, Targett NM (1988) Allelochemical interactions between sponges and corals. *Biol Bull* 175:230–239
- R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Reimer JD, Nozawa Y, Hirose E (2010) Domination and disappearance of the black sponge: a quarter century after the initial *Terpios* outbreak in southern Japan. *Zool Stud* 50:394
- Reimer JD, Mizuyama M, Nakano M, Fujii T, Hirose E (2011) Current status of the distribution of the coral-encrusting cyanobacteriosponge *Terpios hoshinota* in southern Japan. *Galaxea* 13:35–44
- Richardson CA, Dustan P, Lang JC (1979) Maintenance of living space by sweeper tentacles of *Montastrea cavernosa*, a Caribbean reef coral. *Mar Biol* 55:181–186
- Rose CS, Risk MJ (1985) Increase in *Cliona delitrix* infestation of *Montastrea cavernosa* heads on an organically polluted portion of the Grand Cayman fringing reef. *Mar Ecol* 6:345–363
- Rossi G, Montori S, Cerrano C, Calcinaï B (2015) The coral killing sponge *Chalinula nematifera* (Porifera: Haplosclerida) along the eastern coast of Sulawesi Island (Indonesia). *Ital J Zool* 82:143–148
- Rützler K (2002) Impact of crustose clionid sponges on Caribbean reef corals. *Acta Geologica Hispanica* 37:61–72
- Rützler K, Muzik K (1993) *Terpios hoshinota*, a new cyanobacteriosponge threatening Pacific reefs. *Sci Mar* 57:395–403
- Sammarco PW, Coll JC, La Barre S, Willis B (1983) Competitive strategies of soft corals (Coelenterata: Octocorallia): allelopathic effects on selected scleractinian corals. *Coral Reefs* 1:173–178
- Schils T (2012) Episodic eruptions of volcanic ash trigger a reversible cascade of nuisance species outbreaks in pristine coral habitats. *PLoS One* 7:e46639
- Schonberg C, Wilkinson C (2001) Induced colonization of corals by a clionid bioeroding sponge. *Coral Reefs* 20:69–76
- Shi Q, Liu GH, Yan HQ, Zhang HL (2012) Black disease (*Terpios hoshinota*): a probable cause for the rapid coral mortality at the northern reef of Yongxing Island in the South China Sea. *Ambio* 41:446–455
- Suzuki Y, Takabayashi T, Kawaguchi T, Matsunaga K (1998) Isolation of an allelopathic substance from the crustose coralline algae, *Lithophyllum* spp., and its effect on the brown alga, *Laminaria religiosa* Miyabe (Phaeophyta). *J Exp Mar Bio Ecol* 225:69–77
- Tang S-L, Hong M-J, Liao M-H, Jane W-N, Chiang P-W, Chen C-B, Chen CA (2011) Bacteria associated with an encrusting sponge (*Terpios hoshinota*) and the corals partially covered by the sponge. *Environ Microbiol* 13:1179–1191
- Teruya T, Nakagawa S, Koyama T, Arimoto H, Kita M, Uemura D (2004) Nakiterpiosin and nakiterpiosinone, novel cytotoxic C-nor-D-homosteroids from the Okinawan sponge *Terpios hoshinota*. *Tetrahedron* 60:6989–6993
- Turner J, Klaus R (2005) Coral reefs of the Mascarenes, western Indian Ocean. *Philos Trans R Soc Lond A* 363:229–250
- Van der Ent E, Hoeksema BW, de Voogd NJ (2015) Abundance and genetic variation of the coral-killing cyanobacteriosponge *Terpios hoshinota* in the Spermonde Archipelago, SW Sulawesi, Indonesia. *J Mar Biol Assoc UK* 96:453–463
- Vermeij MJA, van Moorselaar I, Engelhard S, Hörnlein C, Vonk SM, Visser PM (2010) The effects of nutrient enrichment and

- herbivore abundance on the ability of turf algae to overgrow coral in the Caribbean. PLoS One 5:e14312–e14318
- Wang JT, Chen YY, Meng PJ, Sune YH, Hsu CM, Wei KY, Chen CA (2012) Diverse interactions between corals and the coral-killing sponge, *Terpios hoshinota* (Suberitidae: Hadromerida). Zool Stud 51:150–159
- Wilkinson CR (1983) Net primary productivity in coral reef sponges. Science 219:410–412
- Yahel G, Sharp JH, Marie D, Häse C, Genin A (2003) In situ feeding and element removal in the symbiont-bearing sponge *Theonella swinhoei*: bulk DOC is the major source for carbon. Limnol Oceanogr 48:141–149