Coral reef status in Mauritius: historic trends and recent perturbations

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Dedication

To my husband *Stephen Elliott* whose love, support and many sacrifices have made this work possible.
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Abstract of Dissertation

Coral reefs are under pressure from numerous natural and anthropogenic stressors that are changing drastically the structure and functioning of these important ecosystems. This dissertation investigated impacts of human development, and an invasive sponge species on the benthic community structure of fringing coral reefs around the Mascarene island of Mauritius, in the southwestern Indian Ocean. The research used historical datasets, field surveys, and laboratory manipulations to understand the tempo and scale of changes in Mauritius. The dissertation is divided into three chapters: Chapter 1 examined a 13-year dataset on benthic community cover from 22 sites around Mauritius. The goal was to not only investigate the spatiotemporal trends in the benthic community structure and stability, but to also discriminate between the effects of four local and four global stressors on the coral reef communities. The results showed that there was a general decline in total live coral cover at many sites, both on back- and fore-reefs. However, most sites did not experience a phase shift to macroalgal dominance. Sea surface temperature (SST) and tourism were the two most important stressors affecting community structure. Physical location with respect to oceanographic conditions was another important factor structuring the benthic communities. Unlike the back-reef sites, the fore-reef sites did not appear to respond to any of the local stressors, but they were still sensitive to SST. Chapter 2 addressed aspects of the autoecology of Terpios hoshinota, a sponge likely to be a recent arrival in Mauritius. T. hoshinota is an encrusting sponge and a fierce space competitor. It is a poorly studied organism that kills stony corals by overgrowing them, and can impact reefs on the square kilometer scale. This is the first documentation of this sponge in Mauritius (published in Marine
The success of *T. hoshinota* as an invader on coral reefs has been attributed to its relationship with its symbiotic cyanobacteria. An ex-situ experiment using light and dark treatments was performed to investigate the photosymbiotic relationship between the sponge host and its cyanobacterial symbionts. The results showed that variation in weight change (growth rate) of the sponge hosts was not driven by the abundance of the cyanobacteria at least in the short term. Chapter 3 investigated an outbreak of *T. hoshinota* at one lagoon in Mauritius to determine its impacts on coral reef community structure (published in *Coral Reefs* - Elliott et al. 2016), and complemented the historical investigation of decadal change in Chapter 1. The results showed for the first time a statistically significant preference by *T. hoshinota* to overgrow the stony coral *Acropora austera*. *T. hoshinota* also had a higher photosynthetic capacity than *A. austera*, a possible explanation for its high spreading rate. The long-term implications of *T. hoshinota*’s proliferation on coral reef community structure are discussed. To conclude this dissertation, recommendations are provided to improve conservation management strategies for coral reefs in Mauritius.
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Introduction

Coral reefs worldwide are declining through the impacts of many different types of natural and anthropogenic stressors. Natural stressors such as storms, diseases and freshwater from floods have always impacted coral reefs, however, these natural patterns are now being modulated by anthropogenic activities. The frequency and intensity of storms and diseases have been increasing (Nugues et al. 2004; Emanuel 2005; Madin et al. 2008; Donner 2009). Global climate change is also increasing rainfall variability leading to more intense droughts and floods in different parts of the world (De'ath et al. 2012).

Anthropogenic activities, in particular, the burning of fossil fuels and the release of carbon dioxide have been causing the ocean’s temperature to increase and pH to drop at an unprecedented rate (Hughes et al. 2003; De'ath et al. 2009; Hughes et al. 2010). Species living at the limits of their thermal tolerance are very sensitive to these temperatures changes (IPCC 2014). Additionally, many species in the oceans are calcifiers, and are therefore also having difficulty maintaining and renewing their exoskeletons as the aragonite saturation state falls throughout the world ocean (Przeslawski et al. 2008).

Global warming is causing reef-building corals, the foundational species of coral reef ecosystems, to bleach and die on a large scale (Roberts et al. 2002; Gardner et al. 2003; Pandolfi et al. 2003; Bellwood et al. 2004; Graham et al. 2006; Bruno and Selig 2007). These bleaching events has been observed to often coincide with positive El Niño Southern Oscillation (ENSO) events, which are characterized by abnormally high and persistent sea surface temperature (SST) not only in the Central Pacific, but also in other
ocean basins (van Oppen and Lough 2008; Vargas-Ángel et al. 2011). Ocean acidification is also causing an increase in the bioerosion of the reef-building corals (De’ath et al. 2009; Fang et al. 2013; Enochs et al. 2015). Additionally, the reproductive phenology and fecundity of corals and other marine invertebrates on coral reefs are being disrupted by the rising seawater temperatures as the timing for their reproduction is tightly linked to temperature cues (Przeslawski et al. 2008).

More than 60% of the world’s coral reefs are under direct threat from anthropogenic activities (Burke et al. 2012). Many of these stressors originate directly from land. Land clearing for agricultural practices and coastal urbanization have led to sediments, nutrients, and pollutants being discharged through runoff into these coastal ecosystems (Smith et al. 1981; Fabricius 2005; Markey et al. 2007; Brodie et al. 2012). In general, sediments impact phototrophic organisms by reducing irradiance and thus their ability to photosynthesize (Fabricius 2005). Sedimentation has also been reported to reduce abundance, growth and fecundity of reef-building corals as well as decrease juvenile coral settlement and recruitment (Kojis and Quinn 1984; Rogers 1990; Babcock and Smith 2000).

Nutrient enrichment has variable effects on coral reef communities (Szmant 2002). It can reduce growth and reproduction success in reef-building corals, recruitment of benthic crustaceans, and CCA growth (Koop et al. 2001; Belliveau and Paul 2002). Nutrient enrichment can, however, increase the abundances of turf algae, macroalgae, and filter feeders such as sponges, bryozoans, ascidians, mollusks and some polychaetes (Smith et al. 1981; Rose and Risk 1985; Costa et al. 2000). Chemical pollutants such as those used in pesticides can impair fertilization and metamorphosis in reef-building coral larvae.
Mercury and copper have also been reported to impair reproduction in ascidians and mollusks (Franchet et al. 1997; Fitzpatrick et al. 2008).

Overfishing is another anthropogenic activity that has led species to extinction, caused significant changes in ecological communities, and contributed to the collapses of some coastal ecosystems (Jackson et al. 2001). The effects of overfishing on benthic coral communities are primarily indirect. Overfishing of herbivorous fishes coupled with loss of other herbivores (e.g. Diadema die-off) have led to a reduction in the top-down control of algae on the reefs, and have been identified as being principal causes of coral reef communities shifting from coral to macroalgal dominance (Carpenter 1990; McCook et al. 2001). However, such phase shifts have been shown to be much less common than previously thought (Bruno et al. 2009). Another example of overfishing having devastating effects on coral reefs is the case of the crown-of-thorns starfish (COTs). Overfishing of its natural predators coupled with the release of larval food limitation due to nutrient enrichment, have led to outbreaks of COTs, a predator of reef–building corals; and consequently to the loss of large areas of these corals (Lucas 1982; Fabricius et al. 2010).

Introduced invasive species are another type of threat to coral reefs. International shipping and aquaculture have been identified as being the two main pathways of species introduction (Godwin 2003; Molnar et al. 2008). These introductions have significant environmental and economic costs (Pimentel et al. 1995; 2005). Invasive species can alter community composition and structure, and there is increasing evidence that they can also alter ecosystem properties such as productivity and nutrient cycling (Vitousek 1990; Allison and Vitousek 2004; Rahel and Olden 2008). They are, moreover, widely accepted
as being one of the leading causes of biodiversity loss in many different terrestrial and marine ecosystems (Didham et al. 2005). Introduced invasive species belong to many different taxonomic groups. A few examples include: the tunicate Didemnum sp, the sponge Mycale grandis, and the lionfish Pterois volitans. Didemnum sp. is a fouling organism observed to cover pontoons, ropes, chains and boat hulls (Minchin and Sides 2006). M. grandis has been observed to overgrow reef corals in Hawaii (Coles and Bolick 2007). Pterois volitans was accidentally introduced in the Atlantic; it has now spread to the Caribbean and has been sighted as far north as on the coast of Rhode Island in the United States (US). It has been reported to interfere with the recruitment of native reef fishes (Albins and Hixon 2008). Environmental damages and losses in the US due to terrestrial and marine invasive species have been estimated to add up to $120 billion per year (Pimentel et al. 2005). It is therefore very important to understand the causes and consequences of dominance by introduced invasive species because they can potentially displace native species, alter ecosystem functioning (Vitousek 1990), and can have very high economic costs (Pimentel et al. 2005).

These multiple stressors are acting simultaneously on coral reefs, and they are changing the community structure and functioning of these ecosystems. Some coral reef communities have, however, been observed to be more resilient than others to the same stressors. The concept of ecosystem resilience consists of two components. The first one is resistance that is the ability of a system to absorb shocks and resist phase shifts; the second is the ability of a system to return to its original state after natural and human-induced disturbances (Bellwood et al. 2004).
Physical factors that enable resistance to thermally stressful events on coral reefs include localized upwelling that can cool heated surface water (Glynn and D'Croz 1990), vertical mixing and upwelling due to island mass effect (Glynn 1993), water movement and flushing of toxins (Nakamura and Van Woesik 2001; 2005), and decreased light stress, e.g., in the form of shading or cloud cover (Hoegh-Guldberg 1999). Physiological tolerance of stony corals to resist bleaching has been attributed to acclimation to high temperature after regularly exposure to thermally stressful environment (Dunne and Brown 2001), and to selection of tolerant genotype over time (West and Salm 2003). The *Symbiodinium* clades harbored by the stony corals (Baker et al. 2004; Oliver and Palumbi 2009), and the heterotrophic plasticity exhibited by the corals themselves (Palardy et al. 2006; Grottoli et al. 2006) may also contribute to making these foundation species more resilient to thermal stress.

Intrinsic factors that enable coral reef ecosystems to return to their original states after disturbance include availability and abundance of local larvae for recruitment success (West and Salm 2003). These factors can also include a biological component such as having sufficient grazing fish populations to keep macroalgal growth in check (Bythell et al. 2000). Extrinsic factors include physical factors such as currents or other processes that distribute larval supply among sites (Dayton et al. 2000), or the physical location of coral reef communities with regards to oceanographic conditions (West and Salm 2003). Reefs with more effective management in place may also be more resilient because local chronic anthropogenic impacts are reduced (Hughes and Connell 1999).

Coral reefs are among the most diverse ecosystems of the world. They provide invaluable ecosystem and economic services (Costanza et al. 1997) to hundreds of millions of
people especially from many developing countries (Cinner et al. 2009). There is therefore a pressing need to better understand the interactive and cumulative effects of these multiple stressors if we want to improve conservation management and protect these important ecosystems for the longer-term.
Chapter 1: Relative importance of local and global drivers of change: an analysis of benthic coral reef communities around Mauritius from 1998 to 2010

Abstract

Coral reefs worldwide are declining and numerous anthropogenic impacts have been linked to their demise. Discriminating among stressors impacting coral reefs is important to develop targeted conservation strategies. I studied a 13-year long dataset (1998 – 2010) gathered by the government of Mauritius, an island in the southwestern Indian Ocean. I examined spatiotemporal trends at 18 back- and four fore-reef sites in this fringing reef system to investigate changes in benthic community structure and stability. I also assessed the effects of four local and four global stressors on benthic community structure using univariate and multivariate analyses. The goal was to discriminate between the different stressors and determine their relative importance in shaping community structure over time. The results showed that there were significant changes in the benthic communities over the 13 years, with a general decline in total live coral at many sites both on back- and fore-reefs. However, change in community structure over time was different for different sites, with a few sites being able to maintain a fairly stable community over time. Moreover, with the exception of one study site, all others did not experience a phase shift to macroalgal dominance. Windward sites were among ones with the highest community stability, and highest long-term mean in total live coral cover. At the island-wide level, four local stressors (population, agriculture, tourism index, Catch Per Fisherman Day (CPFD), and two global stressors (Sea Surface Temperature, rainfall) correlated significant with community structure on the back-reefs only. At the site level, population, agriculture, tourism, and SST were the stressors that
more often correlated significantly with community structure. When all stressors were considered together, SST was the most important stressor affecting community structure on both the back- and fore-reefs. Tourism index and CPFD were the second and third most significant stressor impacting communities on the back-reefs. Interestingly, none of the four local stressors that I tested explained much of the variance in the data for five of the study sites, which were all found on the windward site, indicating that other factors such physical location with respect to oceanographic conditions could be very important factors for coral reef resilience. Moreover, spatial differences were larger than temporal shifts in communities across the island. Long-term management strategies need to take into account these large spatial differences and also consider local oceanographic conditions. The growing tourism industry is also another local stressor that needs to be addressed.

Introduction

Coral reefs worldwide are declining; reef-building corals, the foundational species of these ecosystems are bleaching and dying on a large scale (Roberts et al. 2002; Gardner et al. 2003; Pandolfi et al. 2003; Bellwood et al. 2004; Graham et al. 2006; Bruno and Selig 2007). More than 60% of the world’s coral reefs are under direct threat from anthropogenic activities (Burke et al. 2012). The burning of fossil fuels and release of carbon dioxide indirectly impact all coral reef communities through global warming and ocean acidification (Hughes et al. 2003; De'ath et al. 2009; Hughes et al. 2010). Species living at the limits of their thermal tolerance are threatened with extinction as the oceans continue to warm at an unprecedented rate (IPCC 2014). The reproductive phenology and fecundity of many marine invertebrates are being disrupted by the rising seawater
temperatures as the timing for their reproduction is tightly linked to temperature cues (Przeslawski et al. 2008). Benthic calcifiers are having difficulty maintaining and renewing their exoskeletons as the aragonite saturation state falls throughout the world’s oceans (Przeslawski et al. 2008). Ocean acidification is also causing an increase in the bioerosion of reef-building corals (De'ath et al. 2009; Fang et al. 2013; Enochs et al. 2015).

Global climate change is not the only factor affecting coral reef communities. Numerous anthropogenic stressors that impact coral reef communities directly originate from land. Land clearing for agricultural practices and coastal urbanization have led to sediments, nutrients, and pollutants being discharged through runoff into these coastal ecosystems (Smith et al. 1981; Fabricius 2005; Markey et al. 2007; Brodie et al. 2012). Sediments impact algae and other phototrophic organisms by reducing irradiance and thus reducing their ability to photosynthesize (Fabricius 2005). Sedimentation can also reduce abundance, growth and fecundity of reef-building corals as well as decrease juvenile coral settlement and recruitment (Kojis and Quinn 1984; Rogers 1990; Babcock and Smith 2000). Turf algae have also been observed to be more effective at outcompeting crustose coralline algae (CCA) in high sedimentation areas (Steneck 1997).

Nutrient enrichment has variable effects on coral reef communities (Szmant 2002). It can reduce growth and reproduction success in reef-building corals, recruitment of benthic crustaceans, and CCA growth (Koop et al. 2001; Belliveau and Paul 2002). Nutrient enrichment can increase abundances of turf algae, macroalgae, and filter feeders such as sponges, bryozoans, ascidians, mollusks and some polychaetes (Smith et al. 1981; Rose and Risk 1985; Costa et al. 2000). Chemical pollutants such as those used in pesticides
can impair fertilization and metamorphosis in reef-building coral larvae (Markey et al. 2007). Mercury and copper have also been reported to impair reproduction in ascidians and mollusks (Franchet et al. 1997; Fitzpatrick et al. 2008).

Overfishing is another anthropogenic activity that has led species to extinction, caused significant changes in ecological communities, and contributed to the collapses of some coastal ecosystems (Jackson et al. 2001). The effects of overfishing on benthic coral communities are primarily indirect. Overfishing of the natural predators of the crown-of-thorns starfish (COTs) coupled with the release of larval food limitation due to nutrient enrichment, have led to outbreaks of COTs that have had devastating effects on coral reefs (Lucas 1982; Fabricius et al. 2010). Overfishing of herbivorous fishes, when coupled with loss of other herbivores (e.g. Diadema die-off) and/or nutrient enrichment, has been identified as being a principal cause of coral reef communities shifting from coral to macroalgal dominance (Carpenter 1990; McCook et al. 2001). However, such phase shifts have been shown to be much less common than previously thought (Bruno et al. 2009).

Natural stressors have always impacted coral reefs, but now these global naturals patterns are being modulated by human activities. With global climate change, the frequency and intensity of tropical storms are predicted to increase (Emanuel 2005; Madin et al. 2008; IPCC 2014). Moreover, disease outbreaks are also becoming more prevalent (Bruno et al. 2003; Nugues et al. 2004; Donner 2009). Global climate change is also increasing rainfall variability leading to more intense droughts and floods (De'ath et al. 2012). Unusually strong positive El Niño Southern Oscillation (ENSO) are characterized by abnormally high and persistent sea surface temperature (SST), which is severely impacting coral
reefs by causing large scale coral bleaching (van Oppen and Lough 2008; Vargas-Ángel et al. 2011).

There is increasing evidence that these global scale diseases and anthropogenic driven climate change are becoming more important contributors to coral mortality than overfishing, pollution or sedimentation (Aronson and Precht 2006). These multiple stressors are also acting simultaneously on coral reefs communities, the outcomes of which can at times be synergistic, and at other times antagonistic (Crain et al. 2008). For example, the collapse of coral reefs in Jamaica has been attributed to the interaction of multiple stressors, namely cyclone Allen, white band disease of *Acropora* corals, die-off of the sea urchin *Diadema antillarum*, and historical overfishing (Gardner et al. 2003). There is a pressing need to better understand the interactive and cumulative effects of these multiple stressors (Crain et al. 2008). All these direct and indirect impacts are changing the community structure and functioning of corals reef ecosystems.

It is often difficult to discriminate among the impacts of multiple simultaneous stressors and assess their relative impact on coral reef communities, however discriminating among stressors is essential to developing targeted conservation strategies and reverse degradation (Aronson and Precht 2006; Mora 2008). Long-term datasets and meta-analyses have been used to study how reef-building corals change over time at a regional level. All these studies linked causes of coral decline to a variety of direct and/or indirect anthropogenic stressors (Gardner et al. 2003; Bruno and Selig 2007; Ateweberhan et al. 2011), but they have rarely attempted to link quantitative land use data to changes in the community structure of adjacent coral reefs. Work in the Northern Line Islands in the Pacific has focused on separating local impacts from global impacts by comparing
benthic cover data from isolated reefs along a gradient of human habitation and fishing (Sandin et al. 2008). The work by Mora et al. (2008) is among rare efforts that were able to discriminate between the effects of different local stressors such as agricultural land use and coastal development on fish, coral and macroalgal abundance. In order to obtain their gradient of human impact, these studies in the Northern Islands and in the Caribbean were conducted on the 1000 km scale. I wanted to know if I could discriminate between the effects of different local stressors on a much smaller (100 km) scale, while accounting for global stressors. This would only be possible if higher resolution data on local anthropogenic activities could be paired with higher resolution data on the state of corresponding lagoons.

For this study, I used a 13-year dataset of benthic community cover from 22 coral reef sites around the southwestern Indian Ocean island of Mauritius (20° 10’ S, 57° 31’ E; Fig. 1.1a). The goal was to determine the relative importance of four local and four global drivers of change in shaping the community structure of back- and fore-reefs during this time period. Mauritius has 1869 km² of land area, 258 km of coastline length, and 240.4 km² of reef habitats. In 2005, the average live coral cover was estimated to be 11.8% (Turner and Klaus 2005).

I used the catchment area map of Mauritius (Proag 1995) to link local land use impacts to the study sites (Fig. 1.1). Mauritius has one of the densest human populations on earth, with 601 individuals km⁻² in 2004 (middle of study period; data.worldbank.org). I used total population by catchment area as the first local stressor. Large areas of Mauritius are under foodcrop and sugarcane cultivation. I used total area under foodcrop and sugarcane cultivation per catchment area as the second local stressor. In the 1970s, Mauritius
diversified its economy by investing in the tourism industry, which continue to contribute significantly to the economy of Mauritius (Durbarry 2004; Lincoln 2006). I developed a tourism index as the third local stressor to measure the impacts of tourism. Although I did not have any data on overfishing, I used catch per fisherman day (CPFD), which is an indirect measure for fish abundance for Mauritius, as the fourth local stressor.

I used the average satellite derived sea surface temperature (SST) as the first global stressor. The El Niño Southern Oscillation (ENSO) is the most important ocean-atmosphere phenomenon to cause global climate change variability on seasonal to inter-annual time scales (Wolter and Timlin 2011). I therefore also considered the multivariate ENSO Index as the second global stressor. This allowed me to test for any teleconnection that this phenomenon could have with the benthic communities in Mauritius. I developed a cyclonic index to study the impacts that this natural phenomenon, which I used as the third global stressor. For the fourth global stressor, I used total rainfall by catchment area, which was the proxy for terrestrial runoff.

I hypothesized that (1) there would be a general decline in live coral cover and an increase in macroalgal abundance over the 13-year period due to these multiple stressors; (2) different sites will respond to different stressors; (3) sites impacted by higher magnitude of stressors would have a lower community stability; (4) out of the four global stressors, SST would be the most likely one to impact both back- and fore-reefs communities as positive temperature anomalies have been observed to contribute to mass coral bleaching; (5) given the scale of relentless pressures on coral reefs, I expected temporal shifts in community structure over the 13-year period to be greater than spatial differences in community structure across the island.
Materials and Methods

Study sites

This study was carried out at 18 back- and four fore-reef sites around Mauritius (20° 10′ S, 57° 31′ E). Fore-reefs sites were found only on the west coast (leeward), while back-reef sites were spread around the island (Fig. 1.1). The fringing reefs around Mauritius are broken up by natural breaks that result in a series of distinct lagoons (Fig. 1.1). Most lagoons are < 3 m deep and 1 – 8 km wide. They contain habitats that include beaches, mangroves, channels, sand, seagrass beds, sparse coral heads, patch reefs and coral reefs. Lagoon reefs consist mainly of branching and tabular *Acropora*, massive *Porites*, foliaceous *Montipora* and *Pavona*, and sand consolidated with seagrass. There is also a 10 km long and 0.5 – 2.0 km wide barrier reef on the southeast coast with a deep channel (15 – 30 m) separating it from the shore (Fig. 1.1b) (Turner and Klaus 2005).

Narrow reef flats consist of dead coral platform, hard corals and macroalgae, and the shallow fore reefs are dominated by *Acropora* corals. The outer slopes consist of spurs and grooves with a diverse range of hard and soft coral genera (*Pocillopora*, *Favia*, *Porites*, *Sarcophyton* and *Lobophyton*). The fore-reefs have gradual to steep slopes, and at greater depths (20 – 50 m), basalt is colonized by hard corals, soft corals, sponges and algae (Turner and Klaus 2005). The fore-reef sites were found in 10 – 20 m deep waters. Some 160 scleractinian corals species have been reported in Mauritius (Moothien Pillay et al. 2002).

Using the catchment area map of Mauritius (Fig. 1.1b) (Proag 1995) and the position of rivers and mountain ranges, I assigned specific catchment area(s) to each lagoon where
there were study sites. Catchment areas were connected to specific study sites and were color-coded identically (Fig. 1.1b). I used the catchment area map to link data on stressors originating from land to each of the study sites.

Datasets

(a) Benthic communities

Benthic coral reef monitoring data spanning from 1998 to 2010 were obtained from the Albion Fisheries Research Center (AFRC), Government of Mauritius. The data were collected by a small group of staff from the AFRC, which minimizes the observer error in the dataset. The data were collected from three permanent 20 m long transects at each site, using a line intercept method (Kaiser 1983). The benthic data were converted to percent cover data, where each transect was set equal to 100%. The three transects were considered as three replicates for each site. Most sites had 10 – 13 years of observations, with a few having only 7 – 8 years.

The benthic cover data were recorded as one of the following 25 categories: Acropora branching, Acropora digitate, Acropora encrusting, Acropora submassive, Acropora massive, non-Acropora branching, non-Acropora encrusting, non-Acropora foliaceous, non-Acropora submassive, non-Acropora massive, fungid corals, turf algae (filamentous), macroalgae, crustose coralline algae (CCA), Millepora spp., Heliopora spp., sponges, soft coral, zoanthid, other live, dead coral, rubble, sand, silt, rock. For some of the statistical tests, it was necessary to further group the 25 categories into fewer categories to facilitate interpretation of results and extract main trends from the spatiotemporal data. I grouped the 25 categories into the following eight: Acropora
corals, non-Acropora corals, other live (all live categories except reef-building corals and algae), dead coral (dead coral and rubble), non-live (sand, silt, rock), turf algae, macroalgae, and CCA.

(b) Local stressors

Data for three of the local stressors (land-use data) for 1998 – 2010 were obtained from the governmental organization ‘Statistics Mauritius’ (statsmauritius.govmu.org). I used the highest resolution data available. The land area of Mauritius is divided into nine districts, which are then further divided into smaller council areas. The island is also divided into four main sugarcane factory areas (see maps in Appendix 1). I used the following data: total human population per year by council area, total number of hotels per year by council area, total number of tourist nights per year for the whole island, total area under sugarcane cultivation by factory zone, and total area under foodcrop cultivation by district. Using a geographic information system (GIS; QGIS Lyon 2.12), these data were superimposed over the catchment area map, and reorganized by catchment area. The final data used in this study were: (1) total number of people per catchment area per year; (2) the total number of hotels by catchment area was divided by the total number of hotels across the island and multiplied by total number of tourist nights to have a tourism index by catchment area per year; (3) sugarcane and foodcrop were added to have total area under agriculture by catchment area per year. I assumed that all the land-use data were evenly distributed across space.

Data for the fourth local stressor, the mean annual ‘catch per fisherman day’ (CPFD) for 1998 – 2010, were obtained from the AFRC and used as a proxy for fish abundance.
island-wide per year. The CPFD consists of artisanal fishery that makes use of basket trap, line, harpoon, large nets and gill nets inside and outside (fore-reef) lagoons. The list of species provided by the AFRC showed that the majority of the fishes/groups caught by the fisherman were carnivorous.

(c) Global stressors

Four global stressors were tested. Daily sea surface temperature (SST; AVHRR Pathfinder Version 5.2) were obtained from the US National Oceanographic Data Center and GHRSSST (http://pathfinder.nodc.noaa.gov) (Casey et al. 2010). All SST data points found in a square surrounding the island (19.96° – 20.53° S, 57.29° – 57.82° E) were used to calculate a mean annual SST per year for the whole island. All SST of 18°C and below were removed prior to calculating the annual mean because the seawater temperature around tropical Mauritius does not reach below 18 °C. These spurious SST were points very close to the landmass. The annual mean of the multivariate El Niño Southern Oscillation (ENSO) Index were obtained from the National Oceanic and Atmospheric Administration (http://www.esrl.noaa.gov/psd/enso/mei/table.html), and was used as a proxy for climate change.

An annual cyclonic index for Mauritius was calculated by adding the intensity of each cyclone that passed within 2° latitude from the island per year. The intensity of the cyclones was based on the Saffir–Simpson hurricane wind scale, which ranges from 1 to 5, with 5 being the highest intensity. I also considered tropical depressions and tropical storms, which are the two stages prior to becoming a cyclone. I, therefore pushed the Saffir–Simpson hurricane wind scale to 3 – 7, and considered tropical depressions and
storms to respectively have a scale of one and two. For example, if in one year there were a tropical storm (scale 2) and a cyclone of scale 3, then the cyclonic index would be 5. Cyclonic data from 1998 – 2010 were obtained from the WikiProject Tropical Cyclones (https://en.wikipedia.org/wiki/Wikipedia:WikiProject_Tropical_cyclones).

Rainfall was used as a proxy for terrestrial runoff. Rainfall data for Mauritius were obtained from the monthly meteorological summaries (Mauritius Meteorological Services) that were made available by the Mauritius Sugar Industry Research Institute (MSIRI) archives department. Monthly rainfall totals (2000 - 2011) from 85 stations, a digital elevation model (DEM), and location-specific landscape characteristics were used to calculate linear relationships between mean rainfall and landscape characteristics on Mauritius. The time and space-varying nature of the modeled relationships were then explored by estimating separate models for each month (Staub et al. 2014). Finally, monthly rainfall totals for 1998 – 2010 were generated by removing the variability characteristic to each month from the observed data, interpolating these values across space using ordinary kriging, and adding these back to the spatial mean model for the corresponding month (Staub et al. 2014). For this study, these monthly rainfall totals were averaged across months then by catchment area for 1998 – 2010.

Statistical analysis

(a) Trends in benthic cover over time and space

Island-wide changes in benthic cover over time for the 25 categories on the back- and fore-reefs were examined by plotting mean annual percent cover and their respective standard errors against time. Benthic community composition by site was also examined
by averaging percent cover of the eight consolidated categories for the period of 1998 – 2010.

To further investigate changes in live coral cover between sites over time, I averaged the percent cover of the total live coral for the 13-year period to obtain a long-term mean per site. I then subtracted this long-term mean from the annual mean of each site to create anomaly plots for total live coral cover for each year and for each site. Anomaly plots tell whether the mean cover of corals for a particular year and site was above or below the mean for the 1998 – 2010 period. I also investigated how macroalgae abundances changed by site by plotting percent change by time for each site.

I used a mixed effects model (more details) in R (R Core Team 2015) to test if there were significant effects of time and site on the benthic cover of the eight categories. I used year and site as fixed factors, and transects collected within each site as the random factor.

(b) Benthic community structure and stability

A non-metric multidimensional scaling (nMDS) analysis on Bray-Curtis distances (Borcard et al. 2011) was done to investigate differences in community structure between the back- and fore-reefs. Only four sites namely Albion, Ile aux Benitiers, Trou aux Biches and Pointe aux Sables were used for this test because they were the only ones with data for both the back- and fore-reefs. A 95% confidence interval ellipse was fitted around each set of location scores to determine if community composition was significantly different between the two types of reefs.

Resistance is the ability of a system to absorb shocks and resist phase shifts (Bellwood et al. 2004). One way of studying resistance is to measure the stability of a stressed system
over time. I investigated community stability at the study sites by producing a Euclidean distance matrix of all possible pairings using the eight dimensions of the benthic data (Acropora corals, non-Acropora corals, dead coral, macroalgae, turf algae, CCA, other live, non live). I then averaged all the pairwise distances to produce a mean interannual Euclidean distance for each site that I then used as an instability index. A relatively small number indicates that community structure did not change or fluctuate much over a decadal time scale, and thus it is rather stable. Based on these results, I carried out an nMDS analysis on Bray-Curtis distances (Borcard et al. 2011) for sites with the lowest and the highest instability to observe how different their community structures were. All statistical tests were done using R (R Core Team 2015).

To determine if reef type (back-reef or fore-reef) had a significant effect on the instability index, a mixed effects model was used. Reef type was used as fixed factor and site as a random factor. Only the four sites for which I had data for both the back- and fore-reefs were used. This test was done using R (R Core Team 2015).

I wanted to also determine if spatial differences were greater than temporal shifts in the benthic community structure across Mauritius. I averaged the data temporally and spatially, and then calculated an instability index for each using the above Euclidean distance methods.

(c) Drivers of change in reefs around Mauritius

Local and global stressors

I plotted a graph with the eight stressors using a Z-scale to examine their relative trends over time (see Appendix 2 for the data).
Impacts of stressors on the community island-wide (spatial averaging)

The benthic cover data were spatially averaged to derive an island-wide mean for benthic cover for each year (one observation per year). Using a nMDS analysis on Bray-Curtis distances (Borcard et al. 2011), the data were plotted in 2-D space to investigate how the benthic community on the back- and fore- reefs changed over this 13-year period. A line was also drawn to link each year to the next to better follow the trajectory of the benthic communities over time. Using the ‘envfit’ function of the package Vegan in R (Oksaken et al. 2015), I fitted the data from the eight stressors onto these ordinations to determine which ones had a significant correlation with the placement of benthic community observations in ordination space. The direction of the resulting vector indicates the type of benthic community that the stressor is positively correlated with and the length of the vector indicates the strength of the correlation. The vector is colored red when there is a 95% confidence that the stressor is positively correlated with the placement of each benthic observation in ordination space.

Additionally, a permutational multivariate analysis of variance (PERMANOVA) was computed on the benthic data that were spatially averaged (one observation per year). Back- and fore-reefs were analyzed separately because of the significant differences in community structure between the two. I also tested for any correlation between the eight stressors as highly collinear variables, typically with an $|r| > 0.7$, can lead to spurious results (Dormann et al. 2012). Agriculture was strongly correlated with tourism index and rainfall ($r > 0.8$). The remaining correlation pairs had an $|r| < 7$. To determine the most parsimonious model that would explain community structure, I ran the statistical model by including data from one stressor at a time to determine if they individually contributed
to explaining significant variance in the data. Only the stressors that contributed to explaining some variance were included in the final model. Agriculture, tourism index and rainfall were never present together in any of the model runs, and thus I did not have any issues with collinearity.

*Impacts of stressors on the community island-wide (temporal averaging)*

Benthic cover data were temporally averaged to obtain a long-term mean in benthic cover per site (one observation per site). Benthic cover data for sites that were connected by the same catchment area(s) (e.g., BM, BM2) were further averaged, because I had only one set of data for the eight stressors for both. When benthic cover data from two sites were averaged, I labeled them by ‘.c’, e.g., BM.c consisted of data from BM and BM2. A nMDS analysis on Bray-Curtis distances (Borcard et al. 2011) was then used to investigate spatial variability among sites. The envfit function (Oksaken et al. 2015) was again used to determine which of the four variables for which I had spatial resolution (data organized by catchment area; population, tourism index, agriculture, rainfall) correlated with the placement of benthic observations in ordination space. Moreover, I used the physical location of the sites, windward or leeward, as an additional driver of change and a proxy for wind driven currents for these sites. Wind forcing has been shown to drive ocean circulation within fringing reef lagoons (Lowe et al. 2009; Taebi et al. 2012).

*Impacts of stressors on the community by site (spatial averaging)*

I wanted to determine which stressors would be most commonly correlated to benthic community structure by site since there were some inherent differences between them. I
performed an nMDS analysis on Bray-Curtis distances (Borcard et al. 2011) and applied the envfit function (Oksaken et al. 2015) to fit the eight stressors to each dataset. Bonferroni corrections were applied to counteract the problem of multiple comparisons.

Results

(a) Trends in benthic cover over time and space in Mauritius

The most abundant reef-building corals on the back reefs were Acropora branching, Acropora tabulate, non-Acropora foliose and non-Acropora sub massive, all of which showed a noticeable decrease in percent cover from 1998 to 2010 (Fig. 1.2). Rubble and dead coral percent cover increased over time. Turf and macroalgal percent cover fluctuated, but did not increase in abundance over time. The remaining categories constituted a very small percentage of the island-wide communities.

The most abundant reef-building corals on the fore reefs were non-Acropora encrusting, non-Acropora massive and non-Acropora sub massive, all of which showed a noticeable decrease in percent cover the 13-year period (Fig. 1.3). Turf, macroalgae, rubble and dead coral percent cover fluctuated, but did not appear to increase in abundance over time. The remaining categories constituted a very small percentage of the island-wide communities. There was, however, a higher percentage of sand and rock on the fore- compared to the back-reefs.

Benthic community cover for the eight categories was highly variable among sites (Fig. 1.4). There were more Acropora corals and dead corals on the back-reefs compared to the fore-reefs. The fore-reefs had relatively more non-Acropora corals and a substantial percent cover of non-living components compared to the back-reefs. Most sites had a
very small percent of CCA and other live components. Macroalgae cover was highly variable between sites, with most sites having < 5% and a few reaching 15 – 20%.

Sites on the windward side of the island (E, N, S) had higher long-term total live coral means for the periods of 1998 – 2010 (Fig. 1.5). The total live coral anomaly plots (Fig. 1.6) showed that > 15 out of 22 sites had total live coral cover means above their longer-term means for 1998 to 2004 (with the exception of 2001). In 2005, < 10 sites had means above their long-term means. In 2009, only one site had a mean above the long-term means, and finally in 2010, all the 22 sites had coral cover means below their long-term means. The years 2005 and 2009 appeared to be two years during which there were visible decrease in total live coral for a majority of the sites around Mauritius.

Macroalgae cover was highly variable among sites (Fig. 1.7). Ile aux Benitiers2, Belle Mare2, Trou d’Eau Douce, and Trou d’Eau Douce2 were the four sites that had majors in macroalgae at the end of the 1998 – 2010 period. Bel Ombre and Bambous Virieux 2 were the two sites with the highest percent cover of macroalgae (20 - 30%) that fluctuated over time. The fore-reefs sites had much lower percentages of macroalgae than the back-reef sites, and none of these fore-reef sites showed visible increases or decreases over time.

On the back-reefs, there were significant effects of year, site, and the interaction of year-site on the percent cover of all the eight benthic categories with a few exceptions. There were no effects of year or any interactive effects of year-site on CCA and the non-living components (Tab. 1.1).
On the fore-reefs, there were significant effects of year and site, but no interactive effects of year-site for percent cover of *Acropora* and non-*Acropora* corals (Tab. 1.1). Only site had significant effects on the percent cover of dead corals. There were also no significant effects of year or site or interaction of year-site on macroalgae, turf algae and CCA. Year, site and interaction of year-site had significant effects on other live, and only year had a significant effect on non-live.

(b) *Benthic community structure and stability around Mauritius*

Sites on the fore reefs (red) aggregate together and away from sites from the back reefs (blue), and the 95% confidence ellipses do not overlap, showing that the community structure of fore-reef sites were significantly from that of back-reef sites (Fig. 1.8). The instability index showed that Bambous Virieux (BV) was the least instable (most stable) site and ALB the most instable (least stable) site over the 13-year period (Fig. 1.9). The community of BV is found on the windward side of the island and also on the only barrier reef of the island, while the community of Albion is found on the leeward side. Both the lagoons of BV and Albion have < 3 m deep seawater. As expected, the nMDS plot showed that BV had a very tight cluster of observation points (little fluctuations over time) that were positioned halfway between *Acropora* and non-*Acropora* corals (Fig. 1.10). Cover at BV for both the *Acropora* and non-*Acropora* remained fairly stable over time (Fig. 1.10). Albion, however, had observation points that were scattered all over the ordination space (large fluctuations over time), with half of them positioned closer to dead coral and macroalgae (Fig. 1.10). Its coral cover started to crash in 2005, and progressively got worse (Fig. 1.10). In 2010, non-*Acropora* corals were starting to come back to replace a community that largely consisted of *Acropora* corals (Fig. 1.10).
There were no significant effects of reef type on the instability index (p = 0.001).

When benthic cover data were averaged spatially, the instability index was 25.74 (back-reefs) and 6.72 (fore-reefs). When benthic cover data were averaged temporally, the instability index was 38.52 (back-reefs) and 15.72 (fore-reefs). The results showed that spatial differences were larger than temporal shifts across the island for 1998 – 2010.

(c) Drivers of change in reefs around Mauritius

Local and global stressors

Figure 1 shows the trends over time of the four local and four global stressors used in this study. SST, population and the tourism index showed a general increasing trend over time. Land under agricultural cultivation also increased, but then decreased as from 2006. Rainfall fluctuated over time over the 13-year period. The cyclonic index, however, fluctuated a lot and there was no increasing trend over time. The year 2002 was the year with the most intense cyclones, and there were no cyclones in 2001 and 2004. The ENSO index had three high peaks respectively in 1998, 2002, and 2009. CPFD, the proxy for fish abundance, had a peak in 2000, after which it declined. It started to increase again in 2007 and peaked in 2009 -2010.

Impacts of stressors on the community island-wide (spatial averaging)

Over the 13-year period, back-reef benthic communities island-wide changed from having more *Acropora* and non-*Acropora* corals to more dead corals and macroalgae (Fig. 1.12a; green line linking years). Fore-reef benthic communities changed from having more *Acropora* corals, non-*Acropora* corals and macroalgae to having more dead
corals, CCA and non-living components (Fig. 1.12b; green line linking years).

Population, tourism index, agriculture, rainfall and SST showed a strong positive correlation with dead coral and non-living components on the back reefs. CPFD also showed a strong positive correlation with macroalgae on the back reefs. On the fore reefs, there were no significant effects of any local and global stressors on benthic community structure.

The most parsimonious models that explained most of the variability in the changes in community structure over time were as follows (Table 1.2):

Community structure ~ SST + CPFD + Tourism index (back-reefs)

Community structure ~ SST (fore-reefs)

SST was the strongest stressor of temporal change for both back- and fore-reefs.

*Impacts of stressors on the community by site (spatial averaging)*

There was only one factor that had a significant effect on community structure, and it was wind, the proxy for wind-driven currents. Wind stress creates waves, which affect flows over benthic communities both in the back-reef where circulation is set up by the stress and in the fore-reef where wave orbital motions can be routinely felt at depth of coral cover. Wind had a strong positive correlation on sites found in three lagoons positioned on the windward side of Mauritius (BV.c, BO.c, ALR.c; Fig. 1.14). Some of these sites have among the highest long-term mean coral cover (Fig. 1.5), and generally lower instability indices (Fig. 1.9). There was a positive correlation between population and
dead corals, but it was not significant. Agriculture, rainfall and tourism index did not explain much of the variance in the benthic community structure averaged temporally.

*Impacts of stressors on the by site (spatial averaging)*

Population, tourism index, agriculture (local stressors), and SST (global stressor) were the four most important stressors that correlated significantly with change in community structure when sites were considered individually (Table 1.3). CPFD and Rainfall rarely correlated with change in community structure, and ENSO and cyclones never correlated significant with change in community structure. Interestingly, none of the stressors explained any variance in the data for Belle Mare, Bel Ombre, Bambous Virieux, Bambous Virieux2 and Trou d’Eau Douce.

**Discussion**

*Temporal and spatial trends*

Over the 13-year period, there was a significant decline in *Acropora* and non-*Acropora* coral abundance on both the back- and fore-reefs in Mauritius, with complementary increases in abundance of dead coral. This is similar to trends observed in the coral reefs of the Caribbean and Indo-Pacific region (Gardner et al. 2003; Bruno and Selig 2007). The decline in reef-building corals in Mauritius was, however, not uniform across sites. A few sites, particular those on the windward side of the island, were able to maintain a relatively stable community structure over time. Bambous Virieux (east), Bel Ombre (south), and Anse La Raie (north) are all found on the windward side, and they were among sites with the highest long-term mean for total live coral cover, and among sites with the lowest instability index (i.e. most stable).
The higher community stability of these three sites could be due to their physical location with respect to oceanographic conditions (West and Salm 2003). The prevailing south-east trade winds are important drivers of ocean circulation within the lagoons (Lowe et al. 2009; Taebi et al. 2012), and their effects on ocean circulation are strongest on the south, east and north, and weakest on the west side of Mauritius. Water circulation can help make coral reefs more resistant to local and global stressors (West and Salm 2003).

Water movement can help flush toxins (Nakamura and Van Woesik 2001; 2005). Bambous Virieux is found next to a deep channel (15 - 30 m) (Turner and Klaus 2005). This deep channel flushes seawater containing terrestrial runoff away from the benthic communities, and may contribute to making this site most stable. Vertical mixing and upwelling can cool heated surface seawater (Glynn and D'Croz 1990; Glynn 1993).

Upwelling due to weak island mass effect has been detected around Mauritius (Elliott et al. 2012), and could be contributing to local water mixing and circulation, although this effect is not restricted to a particular side of the island. The fore-reef sites are found in deeper waters with higher water mixing and circulation that could also be contributing to making their communities more stable relative to some back-reef communities.

Albion and Point aux Sables were the two sites with the highest instability index, and therefore with the least stable benthic communities. Both sites are found on the leeward side where the South East Trade Winds have weaker effects on water circulation. The two sites are also found in very shallow lagoons (< 3 m deep), where exposure to greater temperature and light fluctuations that could contribute to making the coral communities more sensitive to bleaching (Hoegh-Guldberg 1999). In shallow depths, focusing by waves can expose corals to irradiance much greater than that arriving at sea level (Veal et
Community species composition and sensitivity of species to bleaching could be a second factor contributing to the observations (Hughes et al. 2010). The *Symbiodinium* clades harbored by the reef-building corals (Baker et al. 2004; Oliver and Palumbi 2009), and their heterotrophic plasticity (Palardy et al. 2006; Grottoli et al. 2006) may also contribute to making these foundation species of coral reef communities resilient to thermal stress. Bambous Virieux, the site with the most stable community, is also found in < 3 m deep water. However, it is also found on the only barrier reef found in Mauritius. Coral species living on barrier reef could potentially have genotypes that are more tolerant of stressful conditions because of longer periods of adaptations (West and Salm 2003) relative to species found on the fringing reefs.

There were significant changes in macroalgal abundance over time on the back-reefs, but not on the fore-reefs. Changes in macroalgal abundance were highly variable among sites on the back-reefs. Although macroalgal abundance increased at a few sites, only one site, Ile aux Benitiers2, appeared to have undergone a phase-shift to macroalgal dominance in 2010. The presence of sufficient herbivores (e.g., fish and sea urchins) has been attributed to keeping macroalgae abundance in check (Carpenter 1990; Bythell et al. 2000; McCook et al. 2001). Therefore, it appears that there were enough herbivores at most sites to provide some top-down control on the macroalgae. There were a very low percent of macroalgae at all fore-reef sites that remained more or less the same for the 13-year period. Therefore, the study on coral reef communities around Mauritius also support that phase shift to a macroalgal dominance is less common than previously thought (Bruno et al. 2009; Dudgeon et al. 2010).

*Drivers of change*
Island-wide, when local stressors were considered one at a time, all four stressors had significant effects on the back-reef communities, but not on the fore-reef communities. This could be due to the fact that these sites were relatively closer to land, and thus more heavily impacted by stress coming from land. Population, tourism index, and agriculture showed a positive correlation with abundance of dead coral and non-living components. This was similar to observations in the Caribbean where human population, land under cultivation and coastal development contributed to coral mortality (Mora 2008).

Interestingly, CPFD, a proxy for abundance of carnivorous fishes, was positively correlated with macroalgal abundance. A recent study reported a positive relationship between fish excretion and macroalgal cover on a coral depauperate reef in Florida; increasing nutrient availability from the more abundant fishes was found to decrease the efficiency of top-down control by herbivores when coral cover is low (Burkepile et al. 2013). Another study report that higher density of macroalgal patches supported a higher biomass of carnivores, presumably because the macroalgae provided a visual barrier that enabled the carnivores to ambush their prey (Hoey and Bellwood 2011). These could potentially explain the CPFD-macroalgae observations in Mauritius.

Island-wide, when all global stressors were considered one at a time, SST and rainfall had significant effects on coral reef communities on the back-reefs. No global stressor effects were detected on the fore-reefs. The negative impacts of temperature increases and pollutants reaching coral reefs through terrestrial runoffs are well documented and therefore the negative impacts from these two stressors were expected (Markey et al. 2007; van Oppen and Lough 2008; Brodie et al. 2012). Cyclones did not have any significant effects on the community structure. This was similar to other studies that
showed that cyclones were relatively less important in causing loss of coral (Gardner et al. 2005; Mora 2008). It was not surprising that the multivariate ENSO index did not significantly affect the benthic communities in Mauritius since the island is not located in the Indo-Pacific region. ENSO effects in Mauritius are thus muted and indirect. For example, the anomaly plots revealed that > 55% of the study sites had an annual mean cover of live coral that were lower than the long-term mean in 2005 and 2009. These two years coincided with two strong positive ENSO years, which could partially explain why a lot of the corals died. Other coral reefs worldwide were also impacted by the positive ENSO in 2005 (van Oppen and Lough 2008) and 2009 (Vargas-Ángel et al. 2011).

Island-wide, when all eight stressors were considered at the same time, SST, CPFD and tourism had significant effects on the back-reef communities. Surprisingly, SST this time had significant effects on the fore-reef communities. However, the SST effects were lower on the fore-reefs when compared to the back-reefs suggesting that the fore-reef communities are more isolated from the changes in SST over time. This could be due to the fact that fore-reef communities are found in deeper seawater where temperature changes are less than those at the surface. Additionally, fore-reef communities have greater connectivity with cool open seawater (West and Salm 2003). Given these results, I expected the fore-reefs communities to have lower instability indices compared to their corresponding back-reef communities. However, there were no significant differences between back and fore-reef instability indices likely due to the small sample size.

The analysis also indicated that tourism had significant effects on the back reef communities, but not human population nor agriculture. Unlike human population and agriculture, tourism development in Mauritius is concentrated in the coastal areas.
Coastal development has been shown to impact significantly coral reefs in the Caribbean (Mora 2008). Moreover, tourists participate in water sports that can have higher impacts on the reef-building corals (Hawkins and Roberts 1992; Allison 1996). These could explain why tourism had a higher impact compared to the other two stressors.

When sites were considered individually and each stressor considered one at a time, agriculture, population and SST were the three stressors that most commonly correlated with changes in benthic communities on both the back- and fore-reefs. This was not surprising as these three stressors are known to significantly impact coral reefs (Hughes et al. 2003; Mora 2008). Interestingly, none of the stressors correlated with changes in the benthic communities for quite a few sites, indicating that other factors that I did not consider were controlling changes in benthic communities at these sites.

Analysis of the temporally integrated data provided some insights on one other factor that could be shaping community structure. It indicated that physical location with regards to oceanographic conditions could be really important (West and Salm 2003). Moreover, differences in the long-term average intensities of the stressors did not influence long-term average community structure. This is surprising as I expected sites with higher stressor intensities to have a very different community structure compared to ones with lower stressor intensities. More studies are needed to tease apart which physical characteristics of particular sites are driving these different responses to the same stressors.

Conclusions
This is the first study done on a 100 km scale to distinguish between local and global stressor impacts on coral reefs. Even at such a small scale, spatial differences were larger than temporal shifts in communities across the island. Therefore, long-term monitoring needs to be done on a large number of sites to fully capture spatial variability and get a more accurate picture in community changes over time around Mauritius. The impacts of the rapidly expanding tourism industry need to be addressed by conservation managers. Also, ecological studies on fishing impacts on coral reef community structure could help elucidate the surprising positive correlation that I observed between fish abundance (CPFD) and macroalgae. Reducing local stressor impacts will help increase the resilience of coral reef communities only on the back-reefs, but not the fore-reefs around Mauritius. Therefore, working together with the international community to curb global warming remains critical to the protect corals reef ecosystems of Mauritius and elsewhere.

Acknowledgements

I would like to thank the Albion Fisheries Research Center and the Ministry of Fisheries, Government of Mauritius for providing me with the dataset for this work. Special thanks go to all those who have provided helpful discussion. Support was provided by US National Science Foundation Awards #1412462 and #1146056, and by Northeastern University. This is contribution number xxx from the Marine Science Center, Northeastern University.
Table 1.1. Changes in benthic community cover.

Results of the mixed-effects models.

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Table 1.2. Drivers of reef change in Mauritius.

Spatial averaging was conducted island-wide for back-reefs and fore-reefs. Results from PERMANOVA. SST: Sea Surface Temperature; CPFD: Catch Per Fisherman Day.

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Table 1.3. Drivers of reef change by site in Mauritius as analyzed by nMDS.

Sites that did not have sufficient data for the nMDS analysis were not included. B: back-reef; F: fore-reef; SST: Sea Surface Temperature; CPFD: Catch Per Fisherman Day; ENSO Index: multivariate El Nino Southern Oscillation Index. Bonferroni corrections applied: * p < 0.05/8 (p < 0.006)

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<th>Population</th>
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Figure 1.1. Mauritius.

(a) Position of the island in the southwestern Indian Ocean. (b) Map of the island showing study sites on the back- and fore-reefs. Land area is divided into several catchment areas. Study sites are connected to specific catchment area(s) and are color-coded identically. Back-reef sites colored white are connected to adjacent shaded catchment areas.
Figure 1.2. Island-wide changes in benthic community cover on the back-reefs.

Reef-building corals were recorded based on their morphology.

Code: acro.br – *Acropora* branching, acro.di – *Acropora* digitate, acro.en – *Acropora* encrusting, acro.s.m – *Acropora* submassive, acro.ta – *Acropora* tabulate, nacro.br – non-*Acropora* branching, nacro.en – non-*Acropora* encrusting, nacro.fo – non-*Acropora* foliose, nacro.m – non-*Acropora* massive, nacro.s.m – non-*Acropora* submassive, fungid – Fungid, other.live – all other live organisms other than reef-building coral or algae, cca: crustose coralline algae, macro.a – macroalgae, turf.a – turf algae.
Figure 1.3. Island-wide changes in benthic community cover on the fore-reefs.

See Fig. 2 for codes.
Figure 1.4. Benthic community composition by site.

Mean cover for 1998 – 2010. Most sites have 10-13 years of data. BM and BM2 having 7 years of data, and PDOR, PDOR2 have 8 years of data. Codes with ‘.f’ indicate fore-reef sites. Site codes: ALR – Anse La Raie, Albion – Albion, BENI - Ile aux Benitiers, BM – Belle Mare, BO – Bel Ombre, BT – Baie du Tombeau, BV - Bambous Virieux, PDOR – Poudre D’Or, PSAB – Pointe aux Sables, TBIC – Trou aux Biches.

Benthic cover codes: acro – *Acropora* corals, cca – crustose coralline algae, non.acro – non-*Acropora* corals, live – all other live organisms other than reef-building coral or algae, non.live – sand and silt and rock, macro.a – macroalgae, turf.a – turf algae, dead – dead corals.
Figure 1.5. Long-term means for total live coral cover around Mauritius for 1998 to 2010.

Circles represent sites surveyed. Hashed circles indicate fore-reef sites.
Figure 1.6. Total live coral anomaly plots around Mauritius for 1998 – 2010.

Circles represent surveyed sites. Warm colors indicate the percent of total live coral that was above the long-term average (see Fig. 5).

Back-reef site codes: #1 Anse La Raie2; #2 Anse La Raie; #3 Poudre D’Or2; #4- Poudre D’Or; #5 Belle Mare; #6 Belle Mare2; #7 Trou d’Eau Douce2; #8 Trou d’Eau Douce; #9 Bambous Virieux2; #10 Bambous Virieux; #11 Bel Ombre2# 12 Bel Ombre; #13 Ile aux Benitiers; #14 Ile aux Benitiers2; #15 Albion; #16 Pointe aux Sables; #17-Baie du Tombeau; #18 Trou aux Biches. Fore-reef site codes: #19 Ile aux Benitiers; 20 Albion; #21 Pointe aux Sables; #22 Trou aux Biches.
Figure 1.7. Macroalgae mean percent cover over time by site.

The code ‘.f’ denotes fore-reef sites. Refer to Fig. 4 for code names.
Only sites that had complementary back- and fore-reefs were used. Back- and fore-reef sites are colored respectively blue and red. The 95% confidence ellipses (colored black) showed that the community structure at sites on fore- and back-reefs were significantly different. Codes: acro – Acroporal corals; non.acro – Non-Acropora corals; dead.c – Dead corals; macro.a – Macroalgae; turf.a – Turf algae; cca – Crustose coralline algae; live – all other live; non.live – Sand, rock and silt. 2-D Stress = 0.14.
Figure 1.9. Instability index for benthic communities around Mauritius for 1998 – 2010.

This index indicates how stable the communities were for this time period. Relatively small numbers indicate more stable communities. Bars colored red represent sites on the windward side of the island. All other sites are found on the leeward side of the island. Sites with a ‘.F’ are found on the fore-reefs.
Figure 1.10. Communities with the lowest and highest instability indices around Mauritius.

(a) nMDS plots (2-D Stress = 0.20), (b) community composition for Bambous Virieux (BV) has an instability index of 31 and Albion has an instability index of 63. Codes: acro – *Acropora* corals; non.acro – Non-*Acropora* corals; dead.c – Dead corals; macro.a – Macroalgae; turf.a – Turf algae; cca – Crustose coralline algae; live – all other live; non.live – sand, silt, and rock.
Figure 1.11. Local and global stressors through time in Mauritius.

Because of the wide differences in the range of the different stressors, a standardized (Z) scale was used.
Figure 1.12. nMDS analysis of factor influence around Mauritius using spatial averaging.

Arrow is colored red when stressor is significantly correlation with observations in ordination space. Back-reef 2-D Stress = 0.08. Fore-reefs 2-D Stress = 0.12. Codes: acro – *Acropora* corals; non.acro – Non-*Acropora* corals; dead.c – Dead corals; macro.a – Macroalgae; turf.a – Turf algae; cca – Crustose coralline algae; live – all other live; non.live – Sand, rock and silt.
Figure 1.13. nMDS analysis of factor influence around Mauritius using temporal averaging.

Arrow is colored red when stressor is significantly correlation with observations in ordination space. 2-D Stress = 0.06. BO.c (Bel Ombre and Bel Ombre2), BM.c (Belle Mare, Belle Mare2), BV.c (Bambous Virieux, Bambous Virieux2), ALR.c (Anse La Raie, Anse La Raie2), BENI.c (Ile aus Benitiers, Ile aux Benitiers2), PDOR.c (Poudre D’Or, Poudre D’Or2).
Supplemental materials

Appendix 1. Map of Mauritius. (a) Governmental districts, (b) Factory areas (4 main areas; gray indicates areas where no sugarcane is grown).
Appendix 2: Local and global stressors – annual means – see methods section for the source of each dataset

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Chapter 2A. Morphological plasticity allows coral to actively overgrow the aggressive sponge \textit{Terpios hoshinota} (Mauritius, Southwestern Indian Ocean)

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Abstract

\textit{Terpios hoshinota} is a threat to coral reefs. It is an encrusting sponge that kills scleractinian corals by overgrowing them. Predominantly reported from the Indo-Pacific region, the sponge seems to be progressively expanding its range by moving towards the western Indian Ocean. It is still unclear what causes its outbreaks. We report for the first time its presence at our study site at the southwestern Indian Ocean island of Mauritius (20°10′S, 57°31′E). Our surveys showed that \textit{T. hoshinota} could grow linearly by 11.5 ± 3.60 mm month\(^{-1}\). In 2014, \textit{T. hoshinota} had covered 11% out of 500 m\(^2\) of available hard substrate. We also report a rare encounter with \textit{Montipora aequituberculata}, a scleractinian coral species that was able to successfully overgrow established sponge colonies. The sponge colonies did not react to the overgrowth by putting out tendrils and made no attempt to cover the \textit{Montipora aequituberculata}. The coral was able to overgrow \textit{T. hoshinota} because it did not directly attack the growing front of the sponge. The high growth rate and high plasticity of \textit{M. aequituberculata} helped the coral to overgrow and take the space of the sponge.

Keywords: coral-killing sponge, competition, adaptation, plasticity
**Introduction**

*Terpios hoshinota* is a very thin (< 1 mm thick) encrusting sponge, and its spicules have a characteristic quadriloba head (Rützler and Muzik 1993). Its gray to black coloration has been attributed to a high density of photosynthetic cyanobacteria that are suspected to contribute significantly to its energetic budget (Rützler and Muzik 1993). *T. hoshinota* is a big threat to many tropical coral reefs. The sponge is a space competitor that kills coral colonies by overgrowing them (Plucer-Rosario 1987). *T. hoshinota* cover can extend from a few small patches to areas that extend over 1000 meters squared (Bryan 1973; Liao et al. 2007). Once it invades a system, it persists for years, and can become a permanent feature on the reef (Reimer et al. 2011).

Outbreaks of the sponge have been reported primarily in the Indo-Pacific region. It was seen in Guam (Bryan 1973), American Samoa, Taiwan, Philippines, Northern Marianas Islands, Western Caroline Islands, Thailand (Plucer-Rosario 1987), Ryukyu Archipelago, Japan (Rützler and Muzik 1993), Yongxing Island, China (Shi et al. 2012), the Great Barrier Reef (Fujii et al. 2011), Java, Indonesia (de Voogd et al. 2013; Van der Ent et al. 2015), and Malaysia (Hoeksema et al. 2014a). It was more recently sighted in the Maldives (Montano et al. 2015). The sponge seems to be progressively increasing its distribution range, moving towards the western Indian Ocean. We report for the first time its presence at the Southwestern Indian Ocean island of Mauritius (20°10’S, 57°31’E), which is at present the most westerly and southerly report of this sponge (Fig. 2.1).

The factors leading to outbreaks of *T. hoshinota* remain unclear. But once the sponge starts to overgrow a coral, the most likely outcome of this interaction is the death
of the coral, as has been reported by several of the papers cited above. We, however, observed the opposite happening on a few occasions at our study site in Mauritius. While taking measurements to assess the extent of spread of *T. hoshinota*, we encountered four coral colonies of *Montipora aequituberculata* that were able to actively overgrow the sponge even while they were being partially overgrown by the sponge. This species-specific interaction between a scleractinian coral and *T. hoshinota* has not been reported before. The extent of these interactions will affect spatial competition on a reef, and how it may change in the future.

**Materials and Methods**

In June 2013, tissues were collected to confirm the identity of the encrusting sponge by using Scanning Electron Microscopy and DNA analysis. Tissues were stored in 95% ethanol at 4°C. DNA was extracted using the DNeasy Blood and Tissue kit (Qiagen) following the manufacturer’s protocol. The mitochondrial Cytochrome Oxydase I (COI) region was amplified using the universal primers HCO (5’-TAAACTTCAGGGTGACCAAAAAATCA-3’) and LCO (5’-GGTCAACAAAAATCATAAAAGATATTGG-3’), and the following thermal cycle: 94°C for 3 minutes, 94°C for 30 seconds and 54°C for 30 seconds and 72°C for 90 seconds repeated 35 times, 72°C for 10 minutes. PCR products were then sequenced bi-directionally using direct sequencing. The resulting 625 base-pair long sequences were then searched in GenBank to identify the species.

In June 2014, we performed a small-scale high-resolution survey of reef habitats at the Anse La Raie lagoon, Mauritius, Indian Ocean (19°59'02"S, 57°38'15"E). Four
circular plots with a radius of 10 m were set up, and a total of 1256 m² were surveyed. The quadrats were placed 30-35 m apart in an area where *T. hoshinota* was highly abundant. All coral species overgrown by the sponge were recorded. The length and width of each *T. hoshinota* colony were measured and multiplied to compute surface area per colony. The surface areas of all the colonies were added to determine the density of *T. hoshinota*. The Braun-Blanquet method (McAuliffe 1990) was used to determine cover-abundance of six substrate types: hard corals, soft corals, crustose algae, turf algae-rubble, sand, and other. Within the circular quadrats, we randomly set up 12 25x25 cm quadrats with the aim of measuring linear growth rate of specific colonies of *T. hoshinota* growing on *Acropora australis* and *Acropora nobilis*. Those quadrats were photographed in June and again five months later. Unfortunately, most colonies of the *Acropora* corals were completely covered by the sponge by the time we took the second set of pictures. We were only able to get linear growth measurements of *T. hoshinota* growing on three branches of one colony of *A. nobilis* (N=3). During our surveys, we came across four colonies of the scleractinian coral *M. aequituberculata* that were successful at overgrowing *T. hoshinota*. We documented this uncommon interaction between the coral and the sponge through macrophotography, and discuss possible mechanisms by which the coral is able to overgrow the sponge.

**Results**

The examination of spicules and COI mitochondrial DNA sequences confirmed that the identity of the sponge was *T. hoshinota*. 
T. hoshinota was observed to overgrow the following scleractinian corals: A. austera, A. formosa, A. nobilis, M. aequituberculata, M. digitata, M. spongiosa, Pocillopora damicornis, Galaxea fascicularis and also on free-living fungiids. The sponge was also observed to overgrow crustose algae and the plastic tags marking our study plots. Our surveys in 2014 showed that out of the 1256 m$^2$ surveyed, there were 500 m$^2$ of available hard substrate (hard corals and crustose algae) of which 11% had been overgrown by T. hoshinota. Our measurements also showed that a colony of T. hoshinota could grow linearly by an average of 11.5 ± 3.6 (S.D.) mm month$^{-1}$.

During our surveys, we saw four colonies of M. aequituberculata that were actively overgrowing T. hoshinota (Fig. 2.2a, b, white arrows). M. aequituberculata has been observed to have two growth forms at our study site, foliose and encrusting, but it was more often seen in a foliose form. It is, however, the encrusting form that allowed it to compete more effectively against T. hoshinota and take its space. Interestingly, one of the colonies of M. aequituberculata was simultaneously being attacked by T. hoshinota (Fig. 2.2b, black arrows). When T. hoshinota overgrows its competitor, it uses tendrils that allow it to colonize new areas (Fig. 2.2c).

**Discussion**

T. hoshinota is an emergent threat in the southwestern Indian Ocean. Our surveys in 2014 showed that 55 m$^2$ (11% of 500 m$^2$) of available hard substrate at our study site had already been covered by the sponge. It is still unclear what causes outbreaks of this sponge. Outbreaks have been linked to pollution stress (Rützler and Muzik 1993), iron enrichment of seawater, e.g., a shipwreck (Schils 2012), and predator release (Pawlik et
al. 2007). Population genetic analyses remain to be done to determine if the sponge was recently introduced to Mauritius or whether it was a rare species that is now becoming more prevalent.

The fast growth rate of *T. hoshinota* is an asset allowing it to be an effective space competitor against scleractinian corals, and rapidly increase its cover on coral reefs. Our results showed that the sponge has an average growth rate of 11.5 ± 3.6 (S.D.) mm month\(^{-1}\) (N=3), which is close to the 16.8 mm month\(^{-1}\) (N=10) reported by Plucer-Rosario (1987). Bryan (1973) reported an average growth rate of 23 mm month\(^{-1}\) (N=1), which is about two times higher. We also compared *T. hoshinota*’s growth rate with coral growth rates. We found that the growth rate of the sponge is at least two times higher than the estimated growth rates of branching corals such as *Acropora cervicornis* (6.42 mm month\(^{-1}\)) and *Acropora palmata* (3.92-8.25 mm month\(^{-1}\)), and at least 4 -10 times higher than the estimated growth rate of massive corals such as *Montastrea annularis* (0.55-0.74 mm month\(^{-1}\)) and *Porites astreoides* (0.25-0.29 mm month\(^{-1}\)) (Gladfelter and Monahan 1978). The sponge can grow much faster than the scleractinian corals partly because it does not need to bear the energetic and material costs of building a calcium carbonate skeleton (Brusca and Brusca 2003).

There are three possible mechanisms that *T. hoshinota* could be using to defeat its coral competitors. The first mechanism involves growing over the corals. The growing front of *T. hoshinota* consists of several observable tendrils (Fig. 2.2c) that progressively extend and overgrow the healthy coral polyps. Corals obtain a large part of their energy requirement from the symbiotic phototropic *Symbiodinium* (Grottoli et al. 2006), and thus are highly impacted when overgrown. The second mechanism involves using allelopathic
compounds. Encounters between corals and sponges often result in damage to the corals due to the negative effects of allelopathic compounds produced by the sponges (Porter and Targett 1988; Pawlik et al. 2007). Although cytotoxic compounds are produced by *T. hoshinota* (Teruya et al. 2004), it is unlikely that the sponge used such compounds as we did not observed any discoloration or tissue necrosis at the interface between the coral and the sponge. Observations from previous work (Wang et al. 2012b) also support the idea that allelopathic compounds may not be a major mechanism by which *T. hoshinota* kills corals. A third mechanism involves the use of microbes by the sponge. Tang et al. (2011) reported that when *T. hoshinota* attacked corals, the corals’ microbial communities shifted and became more similar to those found on corals suffering from the black band disease. Their results suggest that harmful bacteria can weaken the coral and thus favor the proliferation of *T. hoshinota*.

We observed four occurrences of a scleractinian coral winning space over *T. hoshinota* (Fig. 2.2a, b). *M. aequituberculata* was more often seen in a foliose form at our study site, however, it was in an encrusting form when it was able to overgrow the sponge. The presence of other invertebrates has been reported to trigger morphological changes in *M. aequituberculata*. For example, the coral will produce fingerlike branches when tube-dwelling invertebrates bore into them (Bergsma 2009). *T. hoshinota* did not appear to counterattack these specific coral colonies. It did not put out tendrils to cover and overgrow them (Fig. 2c). It seemed that these coral colonies were able to outcompete *T. hoshinota* because they did not directly attack the growing fronts, but instead attacked already established sponge colonies that could not grow any bigger because of lack of space at those particular spots. Interestingly, one colony of *M. aequituberculata* that was
overgrowing *T. hoshinota* (Fig. 2.2b) was, at the same time, being overgrown by *T. hoshinota* (Fig. 2b). This highlights how aggressive *T. hoshinota* is as a space competitor on the reef.

A study in Taiwan reported that *Montipora* and *Porites* corals can occasionally overgrow *T. hoshinota* (Wang et al. 2012b). This present report brings additional evidence that some scleractinian corals can actively overgrow the coral-killing sponge and take its space. The high growth rate and morphological plasticity of *M. aequituberculata* no doubt enabled it to compete more efficiently against the sponge. These observations suggest that the equilibrium on reefs highly impacted by *T. hoshinota* may shift in favor of coral species with greater morphological plasticity. Encrusting corals could become more common in the future, which would lead at the same time to a reduction in the 3-dimensional structure of these reefs. Studies on community composition and reef rugosity over time are needed for confirmation.

**Acknowledgements**

We would like to thank the Ministry of Fisheries, Government of Mauritius for allowing us to do this study. Special thanks also go to Attitude Resorts for their support. We are also grateful to Patrice Mason and Katie May Laumann for their help with the SEM and DNA analysis. This is contribution number 325 from the Marine Science Center, Northeastern University.
Figure 2A.1. Reported sightings of *T. hoshinota* (black circles); Mauritius (black star) is the most westerly and southerly report for this species.
Figure 2A.2. Interaction between *Terpios hoshinota* and *Montipora aequituberculata*

(a) and (b) white arrows show *M. aequituberculata* actively overgrowing *T. hoshinota* (gray-black in color); (b) black arrows show *T. hoshinota* overgrowing *M. aequituberculata*; (c) *T. hoshinota* overgrowing *A. austera* – black arrows indicate tendrils that are part of the growing front of *T. hoshinota*. 
Chapter 2B. Investigating the relationship between *Terpios hoshinota* (Porifera) and its photosymbiotic cyanobacteria

**Abstract**

I investigated the relationship between the sponge *Terpios hoshinota* and its photosymbiotic cyanobacteria. Assuming that photosynthate production by the cyanobacterial symbionts benefitted both the symbionts and sponge hosts, I hypothesized that the dark treatment would impact both negatively. I carried out an *ex-situ* experiment where sponge samples were exposed to either a dark or a light treatment for four days. At the end of the experiment, I quantified the impacts of the treatment on the cyanobacterial symbionts by measuring cell density and chlorophyll-a concentration, and on the sponge hosts by measuring wet weight and planar area. The experiment was repeated using a fresh batch of sponge. Additionally, I collected sponge samples that I processed immediately to obtain baseline values for cell density and chlorophyll-a concentration. I used two-way ANOVA, t-tests, and correlation analysis to test for significant effects of treatments. Surprisingly, mean cyanobacterial cell density was significantly higher in the dark than in the light. Although mean chlorophyll-a concentration was higher in the dark, the difference was not significant. Cyanobacterial cell densities and chlorophyll-a concentrations in dark and light were not significantly different from the baseline values. Because of the highly variable cyanobacterial cell densities and chlorophyll-a concentrations in *T. hoshinota*, I was unable to distinguish between treatment effects and the natural variability. I, however, observed an opposite trend in cyanobacterial cell density and sponge host weight; cell density was significantly higher in the dark, and weight change of sponge hosts significantly lower in the dark. This inverse relationship
between the host and symbiont although suggestive was not statistically significant. I thus propose that cyanobacterial symbiont abundance did not drive variation in weight change (growth rate) of the sponge hosts, at least in the short term.

**Introduction**

Sponges can host an abundant and diverse community of symbiotic microbes (Webster and Blackall 2008). The association between the two is often thought to be beneficial. The sponge host can provide the microbial symbionts with a nutrient-rich environment, products of host metabolism, and protection from predation (Usher 2008; Freeman and Thacker 2011). In exchange, it can benefit from supplemental feeding (Wilkinson and Fay 1979; Wilkinson 1983; Friedrich et al. 2001; Yahel et al. 2003), protection against UV radiation (Glover 1985; Regoli et al. 2000), enhanced rigidity of the sponge skeleton (Wilkinson et al. 1981), and secondary metabolites that can act as antibiotics or antifouling chemicals (Unson and Faulkner 1993; Unson et al. 1994; Patterson and Bolis 1997; Flatt et al. 2005). The contribution of microbial symbionts to sponge growth and fitness can, however, vary greatly (Thacker and Freeman 2012).

Although microbial communities can constitute from 40% to over 60% of the sponge total biomass (Friedrich et al. 2001; Yahel et al. 2003), noticeable differences in their abundance and diversity have been observed between sponge species (Weisz et al. 2007; Erwin et al. 2011; Poppell et al. 2013). Based on bacterial abundance, sponges can be classified as either low-microbial abundance (LMA) sponges (10^5 - 10^6 cells g^-1 sponge) or high-microbial abundance (HMA) sponges (10^8 - 10^10 cells g^-1 sponge) (Hentschel et al. 2003). These differences in bacterial abundances are seen to coincide with variation in
sponge morphology (mesohyl density and water vascular system) that could possibly affect filtration rates in HMA and LMA sponges (Vacelet and Donadey 1977). All these could have important implications for the physiology and ecology of sponges.

One very important member group of microbial communities in sponges is the cyanobacteria (Usher 2008). Approximately one third of all coral reef sponges host photosynthetic cyanobacteria (Thacker and Freeman 2012) that can provide up to 50% of the sponge energy budget, and 80% of its carbon (Wilkinson 1983; Cheshire et al. 1997). Sponges with photosynthetic bacteria can be classified as phototrophs or mixotrophs (Wilkinson 1983; 1987). Phototrophs are dependent on photosynthesis to meet the bulk of their energy requirements, and mixotrophs are often assumed to be facultative, however, this may not always be true (Usher 2008). Many sponges that are successful space competitors have also been observed to harbor large quantities of photosynthetic microorganisms (Rützler and Muzik 1993).

*Terpios hoshinota* is a very thin (< 1 mm), encrusting cyanobacteriosponge and a fierce space competitor that can grow on both living and non-living substrates (Plucer-Rosario 1987). The sponge has been observed to change morphology and produce filamentous tips, thick tissue threads or compact edges when it comes into contact with corals (Wang et al. 2012a). A recent study also showed that the sponge edge in contact with corals had a higher metabolic activity when compared to the middle or distal end of the sponge (Wang et al. 2015).

*T. hoshinota* is a threat to coral reefs, and has been observed to be particularly effective at overgrowing and killing several scleractinian coral species across the Indo-Pacific region.
(Bryan 1973; Rützler and Muzik 1993; Fujii et al. 2011; de Voogd et al. 2013; Hoeksema et al. 2014b). A *T. hoshinota* outbreak can extend from a few small patches to areas over several square kilometers (Bryan 1973; Liao et al. 2007). *T. hoshinota* seems to be progressively extending its range, migrating westwards through the Indian Ocean (Montano et al. 2015; Elliott et al. 2015). It is unclear what causes outbreaks of *T. hoshinota*, but they have been linked to pollution (Rützler and Muzik 1993), iron enrichment of seawater, (Schils 2012), and predator release (Pawlik et al. 2007; Loh et al. 2015). Investigating *T. hoshinota*’s interaction with its microbial symbionts is important to better understand what makes this sponge such an efficient space competitor on the reef.

*T. hoshinota* harbors a vast microbiome with both autotrophic and heterotrophic components (Tang et al. 2011). It is thought to be a phototroph due to the high abundance of photosynthetic cyanobacteria that has been observed in its mesohyl (Rützler and Muzik 1993; Hirose and Murakami 2011), but no study has been done to assess how much of its energy budget comes from photosynthesis. The success of *T. hoshinota* as a space competitor has been attributed to its high growth rate aided by its ability to propagate asexually, bridge coral branches, and regrow from fragments (Rützler and Muzik 1993). Using morphological features, the bacteria were initially identified as *Aphanocapsa raspaigellae* (Rützler and Muzik 1993), but more recent genetic studies showed that they belong to a novel group closely related to *Prochloron* (Tang et al. 2011). Freshly hatched larvae of *T. hoshinota* hosted the cyanobacteria (Hirose and Murakami 2011; Wang et al. 2012b), and to date no free-living *Prochloron* cells have
been reported (Münchhoff et al. 2007). These observations suggest that the cyanobacterial symbionts of *T. hoshinota* could be obligate symbionts.

The goal of our study was to investigate the relationship between *T. hoshinota* and its photosymbiotic cyanobacteria. Assuming that photosynthate production by the cyanobacterial symbionts benefitted both the symbionts and sponge hosts, I hypothesized that reduced irradiance would impact both negatively. Reduced irradiance can lead to a reduction in bacterial cell density, chlorophyll-a concentration and biomass in some photosymbiotic sponges (Thacker 2005; Erwin and Thacker 2008; Freeman and Thacker 2011). Therefore, I hypothesized that a dark treatment would also have a negative effect on *T. hoshinota*, leading to loss in biomass and tissue area in the host, and a reduction in cell density and chlorophyll-a concentration in the cyanobacterial symbionts.

**Materials and Methods**

**Study site and sponge identity**

This study was carried out at the southwestern Indian Ocean island of Mauritius (20°10’S, 57°31’E). The island has 240 km² of mostly fringing reef habitats (Turner and Klaus 2005). *T. hoshinota* was first observed in Mauritius in 2010 (Fig. 1a). In June 2013, sponge samples were collected from the lagoon of Anse La Raie to confirm their identity using Scanning Electron Microscopy and DNA analysis (see Elliott et al. 2015 for methods). The examination of spicules (Fig. 1 b-c) and matching of COI mitochondrial DNA sequences in GenBanK (accession number KJ008089) confirmed that the sponge was *T. hoshinota*. 
Sponge collection and acclimation

All *T. hoshinota* samples for our experiments were collected at a depth of 3 m from Anse La Raie lagoon in July 2014. The sponge samples were collected from colonies that were 3-5 m apart. They were all growing on *Acropora austera* Dana 1846, the coral species most affected by *T. hoshinota* at our study site (Elliott et al. 2015). A batch of seven sponge samples and another two of 14 sponge samples each were collected respectively on the 8th, 15th, and 22nd July. The first batch was processed to obtain baseline information on *T. hoshinota* and the other two were used for the experiment. I selected branches of *A. austera* skeleton that were completely overgrown by *T. hoshinota*, and thus devoid of any live coral tissues. These branches were transported to the laboratory in 5-gallon buckets filled with fresh seawater, and were transferred into two 12-gallon aquaria. They were then cut so that they would be 7-9 cm tall, and attached to a plastic base (3x3 cm egg crate material) using zip ties. The extra pieces of sponge were discarded.

The seawater temperature in the aquaria was kept at 23°C, the mean lagoon temperature for July at our study site. During acclimation, the samples received a photosynthetically active radiation of 140 µmoles m⁻² s⁻¹ (Hamilton HQI Reefstar pendant metal halide lamp) for 10 hours per day, an irradiance level similar to previous studies (Klöppel et al. 2008; Wang et al. 2012b). Each aquarium was supplied with bubblers to ensure adequate oxygenation. The sponge samples were left to acclimate for two days prior to the start of the experiment. A 25% seawater change was done for each aquarium at intervals of 3 hours for the period of 6 AM to midnight local time during those 2 days. After each water change, the temperature of seawater in the aquaria would change by < 0.5°C, and would
stabilize to 23°C within the first hour. Seawater was collected from the adjacent lagoon, and filtered using a 50 µm mesh sieve to remove all coarse particles prior to each water change.

The experiment

I carried out an ex-situ experiment to test the effects of darkness on T. hoshinota. I had a light and a dark treatment. The light and temperature conditions during the experiment were similar to those of the acclimation period, with the exception of the dark treatment not receiving any light. I used two waterbaths (60x40x25cm) filled with seawater to maintain the temperature constant during the experiment. In each one, I placed seven experimental units (n = 7), which were 1.5 L plastic containers filled with 1.3 L of seawater. Each experimental unit was supplied with its own air supply. The experiment began at the end of the acclimation period, when each experimental unit received one sponge sample randomly picked from the aquaria. Each sample was weighed and photographed before it was placed in the experimental unit. The sponge samples were left in their respective experimental units in the light or dark treatment for a total of four days, and seawater was not changed during this period. Daily checks were made, and about 15-20 ml of seawater was added to compensate for evaporation and maintain the volume of 1.3 L at all times. At the conclusion of the experiment, samples were weighed and photographed before they were processed for cyanobacteria cell density and chlorophyll-a concentration. This experiment was repeated using a fresh batch of sponge samples that were acclimated as described in the previous section.

Cyanobacteria cell density
Five subsamples were collected from each sample using a stratified random method: the sample was visually divided into 5 sections and a subsample was randomly collected per section. Each subsample consisted of a 2 mm x 2 mm surface area of sponge removed from the dead coral skeleton using a scalpel. The result was homogenized in 300 μl of distilled water using a pellet pestle to extract cyanobacterial cells. Two 10 μl of the homogenate were then pipetted onto a hemocytometer and viewed under a compound microscope at a magnification of 400X to calculate cell densities (Maldonado et al. 2010; Guidi-Rontani et al. 2014). The cyanobacteria were as described by Rutzler and Muzik (1993) that is perfectly circular and 5-7 μm in diameter. I found that the cells had a distinctive greenish brown color. This counting procedure was repeated for each subsample. A total of 10 counts (5 subsamples x 2) were done per sample and averaged. The original cell density in each sponge samples was back-calculated based on total homogenate volume and I report the density as mm² of sponge surface area.

**Chlorophyll-a concentration**

The remaining sponge tissues (after subsamples were collected for cell counts) were used for chlorophyll-a measurements. A brush was used to scrape all remaining sponge tissue off the dead coral skeletons. The sponge tissues were dried and weighed to the nearest 0.05 g. Chlorophyll-a was extracted in accordance with Parsons et al. (1984). Chlorophyll-a concentration was then standardized to μg chl-a g⁻¹ sponge.

**Planar area and sponge biomass**

A photo of each sponge sample were taken at the start and end (prior to any processing) of each experiment to investigate changes in planar area due to the treatments. I
positioned the camera and sample on the same plane and at a fixed distance apart. One side of the square plastic base was marked and always placed facing the camera so that I would always take the picture from the same side. The photos were imported into ImageJ software (Abràmoff et al. 2004), and the planar area of the sponge samples were measured before and after the treatments.

In addition for batch 2, I measured the blotted wet weight (to the nearest 0.05 g) of each sponge sample at the start and end of the experiment to investigate changes in sponge biomass relative to changes in their respective cyanobacterial density.

**Baseline information on T. hoshinota**

Seven samples collected on the 8th July were processed immediately after they were collected and brought back to the laboratory. Cyanobacteria density and chlorophyll-a concentration were obtained as described above. I compared our experimental results of cyanobacteria density and chlorophyll-a concentration to those obtained from these fresh samples.

**Statistical analysis**

All statistical tests were done using R (R Core Team 2015). I performed individual two-factor analysis of variance (Type III) on cyanobacteria density, chlorophyll-a concentration, and planar area using treatment (light, dark and reef) and batch as factors. Post-hoc comparisons of each treatment pair were also done using a Tukey test to determine which were significantly different.
For batch 2, t-tests were done to test for significant changes in (1) cyanobacterial density and (2) weight change of sponge hosts due to the treatments. A Pearson’s product-moment correlation test was also done between the sponge host changes in weight and their respective cyanobacterial density to determine if cyanobacterial density was correlated to weight change in sponge host.

Results

Treatment effects on the cyanobacteria

Mean cyanobacteria densities and chlorophyll-a concentrations of *T. hoshinota* for the dark treatment, light treatment and fresh samples are shown in Figure 2. See Supplemental Tables 1 and 2 for measured values.

The two-factor analysis of variance on cyanobacteria cell density showed a significant effect of the treatment (ANOVA, F(2, 35) = 4.57, p =0.02; Fig. 2a), but no significant effect of batch or interaction between treatment and batch. The post-hoc Tukey test showed that the mean cell density in the dark was significantly different from that of the light treatment (p < 0.05; Fig. 2a). There were no significant differences between reef and dark or reef and light treatments (Fig. 2a). The two-factor analysis of variance on chlorophyll-a concentration showed no significant effects of treatment or batch or interaction between treatment and batch (Fig. 2b).

Treatment effects on the sponge host

Planar area changes were very small and insignificant. Changes in the dark and light treatments were respectively 0.04 ± 0.01 cm² and 0.16 ± 0.07 cm². These represented <
3% loss in mean planar area.

For batch 2, there were significantly more cyanobacteria in the dark than in the light (p < 0.05; Fig. 3a). Sponge hosts in the light also lost significantly more weight than those in the dark treatments (Fig. 3b). Results from figures 3a and 3b suggested that there might be an inverse relationship between cyanobacterial density and weight change in the sponge hosts. However, there was no significant correlation between the changes in weight of sponge hosts and their respective cyanobacterial density (r = 0.04, p = 0.90). This lack of correlation provided evidence that cyanobacterial abundance did not drive variation in weight change (growth rate) of the sponge hosts, at least in the short term.

**Discussion**

Although it is thought that *T. hoshinota* benefits from photosymbiont nutrition (Rützler and Muzik 1993), no study has been done to assess the energetic contribution of the cyanobacterial symbionts to the host sponge. Shading experiments have been used before to test whether photosymbiotic cyanobacteria benefit their sponge hosts; loss of weight by the host kept in the shade/dark would suggest that the host relied on photosymbiont nutrition (Thacker 2005; Freeman and Thacker 2011). Our 4-day ex-situ experiment where I tested the effects of reduced irradiance on *T. hoshinota* showed that cyanobacterial abundance did not drive variation in weight change (growth rate) of the sponge hosts, at least in the short term. *T. hoshinota* can use heterotrophic pathways to acquire energy. Energy sources such as particulate organic matter (Wilkinson 1987; Freeman and Thacker 2011) and dissolved organic matter (Reiswig 1981; Yahel et al. 2003; de Goeij et al. 2013), and important elements such as phosphorus (Zhang et al. 2015) and nitrogen (Wilkinson and Fay 1979; Mohamed et al. 2008; Hoffmann et al.
2009) could be obtained by the sponge by filtering seawater. However, our experiment was of short duration. Further studies are needed to elucidate *T. hoshinota’s* energy budget and the contribution of its diverse symbionts (Tang et al. 2011).

While the mean chlorophyll-a concentration in the dark treatment was not significantly different from the light treatment, the cyanobacterial cell density was significantly higher in the dark treatment than in the light treatment. This was surprising as I expected the opposite with the dark treatment reducing availability of photosynthate, and hence energy available for reproduction. It appears that the initial response of the cyanobacteria to reduced irradiance/photosynthate production was to compensate by producing more cells. This could have been achieved by using their stored carbon sources (Baulina 2012). The host sponge can also control the abundance of symbionts within its tissues (Thacker 2005), but at times it is unable to do so when changes in local environmental conditions lead to a very high growth rate of the symbionts (Rützler 1988). Consequently, the increase in cells that I observed could be due to the host sponge not being able to control the density of its symbionts in prolonged darkness, possibly due to a reduced supply of energy/photosynthate. The fact that chlorophyll-a concentration did not increase significantly with the increase in cells also suggests that light energy may be necessary for chlorophyll biosynthesis in the cyanobacterial symbionts of *T. hoshinota* (Hunsperger et al. 2015).

Shading experiments done in-situ using different species of photosymbiotic sponges report a decrease in symbiont cell density (Freeman and Thacker 2011) and chlorophyll-a concentration after 2-6 weeks (Thacker 2005; Erwin and Thacker 2008; Freeman and Thacker 2011). An in-situ experiment done on an ascidian harboring *Prochloron* sp.,
which is similar to the cyanobacterial symbiont of *T. hoshinota*, also resulted in a decrease of chlorophyll content by > 80% after nine days of 0% sunlight (Olson 1986). It is therefore possible that I would have obtained similar results had our experiments lasted longer. Shading experiments lasting four weeks in-situ have also shown a loss in biomass in a few sponge species harboring photosymbiotic cyanobacteria

The mean cell density and chlorophyll-a concentration in the light and dark treatments were generally lower than those from the reef treatment (Fig. 2.2). The possible accumulation of wastes (Reiswig 1971) and small volume of water per experimental unit, which was not changed during the whole duration of the experiment, could have contributed to these lower mean values.

Larger sample sizes should be used in the future to fully capture the natural distribution of cyanobacterial density and chlorophyll-a concentration in *T. hoshinota*. In-situ shading experiments measuring rates of photosynthesis to respiration are needed to better understand the impacts of reduced irradiance on *T. hoshinota* and its cyanobacterial symbionts. All these will further our understanding of the energy budget of *T. hoshinota* and ultimately what makes the coral-killing sponge such an effective space colonizer on the reefs.

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Ministry of Fisheries, Government of Mauritius to collect samples of *T. hoshinota*, a marine sponge species that is not protected or endangered. Funding was provided by the US National Science Foundation, Integrative and Organismal Systems, under Award #1412462. This is contribution number XXX from the Marine Science Center, Northeastern University.
Figure 2B.1. *Terpios hoshinota* characteristics.

(a) Sponge (gray) overgrowing *Acropora* sp., (b) spicule, and (c) detail of tylostyle spicule with quadrilobate end characteristic of this species.
Figure 2B.2. Comparing light, dark and reef (fresh samples) treatments.

(a) Cyanobacteria cell density (mean ± SE). (b) Chlorophyll-a concentration (mean ± SE). Samples sizes for the light, dark and reef treatments were respectively 14, 14 and 7.
Figure 2B.3. Batch 2.

(a) Cyanobacterial density, (b) Weight change by sponge hosts, (c) Comparing weight change in sponge hosts to density of cyanobacteria.
Chapter 3. 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 five 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. australis*. 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. australis* at irradiance > 500 µmol photons m\(^{-2}\) s\(^{-1}\), a possible explanation for its high spreading rate. We discuss the long-term implications of proliferation of *T. hoshinota* on the community structure and dynamics of our study site.

**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 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 the photosynthetic capacity 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, deprive the coral polyps of support and afterwards 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; for example, tissue damage in stony corals can increase their susceptibility to overgrowth by encrusting sponges (Aerts 2000).

The sponge *Terpios hoshinota* Rützler and Muzik 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 the few species 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 community composition was observed to shift and become more similar to those found on corals suffering from the 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 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 (Céline Miternique pers. comm.) . 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 three-fold 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 on 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 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. 3.2a). 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. 3.2a; Turner and Klaus 2005). The lagoonal reefs consist mainly of branching and tabular *Acropora*, massive *Porites*, foliaceous *Montipora* and *Pavona* and consolidated seagrass (Turner and Klaus 2005). Our principal field site was at Anse La Raie lagoon (ALR; Fig. 3.2a), 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. 3.2b). The total area of the lagoon surveyed was 6.53 km². We calculated that there was a total 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 km$^2$ of seagrass, 0.81 km$^2$ of algae, 0.46 km$^2$ of dead coral/rubble, 0.41 km$^2$ of reef crest, 0.06 km$^2$ of rocks, and 0.1 km$^2$ of old coral platform. Sand was the most abundant type of substrate with 4.08 km$^2$. 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. 3.2b; 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 m$^2$ 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. The following measurements were taken for each *T. hoshinota* colony: (1) the sector of circular plot 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; measuring the exact size of each sponge colony would have required extra underwater time that we did not have; and (4) the coral species on which it was growing. Because of the high
abundance of the *T. hoshinota* colonies, we could not assign an exact bearing to each colony, which would have enabled us to do a more accurate mapping of the sponge colonies. 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*. We looked at a histogram of the calculated surface areas and decided on three breaks that allowed us to have four size categories (< 0.05, 0.05–0.15, 0.15–0.30, > 0.30 m²) with roughly equal number of observations. This choice was made for clarity of presentation. The surface area of the sponge colonies was represented as circles on the polar plot figure. 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. 3.2b). 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 0.7 to 1.1 m². A total area of 99 m² was analyzed (all four transects included). Overlays at resolutions of 150, 200, and 250 points per m² were tested on three
individual pictures, and percent cover estimates compared using Pearson’s product-moment correlation (Guinan et al. 2009). We aimed for the lowest resolution that would provide a correlation coefficient ($r$) $\geq 0.95$. The $r$ was 0.92 ($p < 0.001$) for the 150 versus 200 points per m$^2$, and 0.97 ($p < 0.001$) for the 200 versus 250 points per m$^2$. Therefore, we chose a resolution of 200 points per m$^2$ to extract the percent cover for the entire dataset. 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, a rapid presence/absence survey was done with the goal of determining the extent of spread of $T. hoshinota$ around Mauritius. A total of nine shallow back reef lagoons were surveyed (Fig. 3.2a): 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. To ensure a consistent sampling effort at each surveyed site, all surveys were done by the same person and lasted 60 minutes each. Major coral patches were targeted along the way and the presence/absence of $T. hoshinota$ growing on living and non-living surfaces was recorded. 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. Each coral patch was surveyed by snorkeling for five minutes, and the presence-absence of $T. hoshinota$ was recorded.
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. Using a 25 × 25 cm PVC quadrat that was equally divided into 16 parts, 15 quadrats having 20–40 % cover (3–6 parts of the 25 × 25 cm quadrat) of *T. hoshinota* were set up. Another 15 quadrats that did not have any *T. hoshinota* at the start of the experiment were also set up as controls. All quadrats were at least 2–3 m apart. Similarly, thirty 25 × 25 cm quadrats were set to measure the spreading rate of *A. austera* with (n =15) and without (n =15) *T. hoshinota* over a 5-month period.

A photo of each quadrat was taken at the time of setup and again five months later (December 2014). The corners of each quadrat were marked with metal pegs, and photos were always taken such that the northwest corner of the quadrats would be in the top left corner. The distance between the camera and the quadrat was kept the same by using a PVC frame that supported the camera. 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 (Abràmoff et al. 2004). One-way ANOVAs were used to test how 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. austera, 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. austera*, and (3) *A. austera* 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 (*F*′). Samples were exposed to eight incremental steps of irradiance ranging from 0 to 2346 µmol photons m\(^{-2}\) 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 = \(\phi_p\) x PAR where \(\phi_p\) was the effective quantum yield of PSII and PAR was the photosynthetically available irradiance reaching the sponge/coral (µmol photon m\(^{-2}\) s\(^{-1}\)). From the rETR, the maximal rETR at light saturation (rETR\(_{max}\)) and the initial slope of the light-limited relationship (\(\alpha\)) were calculated by fitting the observed data to the following negative exponential curve: rETR = rETR\(_{max}\) x (1 – e\(^{-\alpha \times PAR/rETR_{max}}\)) (Finelli
et al. 2007). Curve fitting was achieved using a non-linear least squares model. A 95% confidence interval band was also plotted for each curve. All measurements were done 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. australa* 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 using 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 0.7–1.1 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 3.1). The polar plots showed that *A. austera* was the most impacted by *T. hoshinota*, followed by *A. formosa* and *M. aequituberculata* (Fig. 3.3). Other taxa overgrown by the sponge include *M. digitata, M. spongiosa, Pocillopora damicornis* and crustose coralline algae (CCA), all of which are grouped under ‘other’ (Fig. 3.3). Overall, out of the 1256 m$^2$ surveyed, there was an estimated 416 m$^2$ of available hard coral substrate of which 55 m$^2$ had been overgrown by *T. hoshinota* (Table 3.1; Fig. 3.3). 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 m$^2$ in size, respectively. The maximum colony size recorded was 0.75 m$^2$.

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. (Fig. 3.4a). Overall, of the 2000 m$^2$ surveyed, there was an estimated 588 m$^2$ of available hard coral substrate of which an estimated 59 m$^2$ 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. 3.4b). Moreover, *T. hoshinota* was observed to primarily overgrow *A. austera* (92% of all *T. hoshinota* observed; Fig. 3.4c).
**Terpios hoshinota around Mauritius**

The island-wide survey revealed only one other site where *T. hoshinota* was present, namely Roches Noires (Fig. 3.1). A solitary *T. hoshinota* colony of about 15 x 15 cm was observed on a colony of *Porites lutea*.

**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 five 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 (*χ*² = 16.84, df = 1, p-value = 4.1 x 10⁻⁵), and preferentially overgrew *A. austera* more than any other stony coral species at ALR (*χ*² = 18.372, df = 2, p-value = 1.0 x 10⁻⁴).

**Photosynthetic capacity of *T. hoshinota***
There was no significant difference in the fitted slope ($\alpha$) for *T. hoshinota* ($\alpha = 0.19$), healthy *A. austera* ($\alpha = 0.20$) and partially overgrown *A. austera* ($\alpha = 0.27$) (Fig. 3.5). However, there was a significant difference in the relative ETR maximum for *T. hoshinota* ($r\text{ETR}_{\text{max}} = 102.19$) compared to both healthy *A. austera* ($r\text{ETR}_{\text{max}} = 57.72$) and partially overgrown *A. austera* ($r\text{ETR}_{\text{max}} = 59.19$), which is $>40\%$ higher for *T. hoshinota*. This implies that *T. hoshinota* had a significantly higher photosynthetic capacity than *A. austera* when irradiance $> 500 \, \mu\text{mol photons m}^{-2} \, \text{s}^{-1}$ ($p < 0.05$; Fig. 3.5). There were no significant differences in photosynthetic capacity of healthy and partially overgrown *A. austera*.

**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. 3.6). 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 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. 3.1). 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 five 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 towards 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 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*

*Terpios hoshinota*, as we predicted, 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 µmol photons m$^{-2}$ s$^{-1}$ in December at ALR (11 am – 12 pm, clear sunny sky, 3.0 m deep). At irradiance levels > 500 µmol photons m$^{-2}$ s$^{-1}$, *T. hoshinota* had a greater rETR than *A. austera*. This ability to better take advantage of high levels of irradiance could potentially explain *T. hoshinota*’s higher competitive ability against the coral at ALR. However, it is important to realize that rETR only measures only one component of the photosynthetic process. Photosynthetic and respiration rates should be measured to fully capture the photosynthetic capacity of *T. hoshinota*. 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 for two years 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.

**Acknowledgements**

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Table 3.1. Community composition in the circular plots at the putative outbreak center of *T. hoshinota* based on the Braun-Blanquet estimate.

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<th>Cover (%)</th>
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<td>Plot 2</td>
<td>Plot 3</td>
<td>Plot 4</td>
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<td>42</td>
<td>38</td>
<td>23</td>
<td>33</td>
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<td>12</td>
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<tr>
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<td>22</td>
<td>27</td>
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<tr>
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<td>4</td>
<td>6</td>
<td>10</td>
<td>6</td>
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<tr>
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<td>2</td>
<td>3</td>
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<td>5</td>
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*a* Scleractinian corals with and without *T. hoshinota* grouped together
Figure 3.1. *Terpios hoshinota* and *Montipora aequituberculata* at Anse La Raie lagoon.

(a) The coral-killing sponge *T. hoshinota* overgrowing *Acropora* corals. (b) *T. hoshinota* overgrowing *M. aequituberculata*. (c) *M. aequituberculata* overgrowing *T. hoshinota*. 
Figure 3.2. The island of Mauritius with its surrounding reefs and lagoons.

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 position of 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.
Figure 3.3. 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 coral species they overgrew. Sector color represents percent of available substrate.
Figure 3.4. Community composition at the area adjacent to the putative outbreak center of *Terpios hoshinota*.

(a) Overall community composition (b) composition of stony corals, and (c) identity of stony corals overgrown by *T. hoshinota*.
Figure 3.5. Photosynthetic capacity of *Terpios hoshinota* and *Acropora austera*.

Photosynthetic capacity (rETR$_{\text{max}}$) of *Terpios hoshinota* (black) compared to healthy (blue) and partially overgrown *Acropora austera* (green). Shaded areas represent 95% confidence interval band for each curve.
Figure 3.6. Non-metric multidimensional scaling (nMDS) plot for the benthic community at Anse La Raie lagoon.

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 score. 2-D stress = 0.12.
Recommendations

To protect the coral reefs of Mauritius, conservation managers should focus on reducing the overall impacts of the local stressors around the island. However, evenly redistributing the impacts of these different stressors across the island will not be an effective mitigation strategy. Moreover, reducing the impacts of the local stressors will only benefit coral communities on the back-reefs and not those on the fore-reefs. Therefore, working with the international community to curb global warming remains one of the most important conservation strategy to protect both the back- and fore-reefs coral communities of Mauritius. Another interesting factor that came out from this study was that study sites on the windward side of the island appeared to have a higher carrying capacity for the stressors measured. More studies are needed to tease apart which physical characteristics of particular sites are driving the difference in response to the same stressors.

Tourism was the second most important stressor after sea surface temperature on the back-reefs. Conservation of coral reefs in Mauritius would therefore highly benefit from mitigating the impacts of the growing tourism industry. Ultimately, determining the island’s carrying capacity for tourism would allow policy makers to make informed decisions regarding the trade-offs associated with increasing tourist arrivals. Fish abundance was the second local stressor that significantly impacted the benthic communities. Long-term studies on the impacts of fishing on coral reefs would allow policy makers to pursue ecosystem based fishing management.

The coral-killing sponge *Tepios hoshinota* should be treated as an invasive species. Conservation management should focus on preventing its spread from Anse La Raie.
lagoon to other lagoons. The single colony of *T. hoshinota* observed at Roches Noires lagoon should be removed while this is still possible to prevent further spread. Educating the general public about this threat is also very important as they can participate in the early detection of the spread of *T. hoshinota*, and alert the local authorities that can then take immediate action. Ultimately, long-term monitoring is needed to better understand the effects of *T. hoshinota* on community structure, composition and topographic complexity over time.
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Appendix

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