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A characterization of a Southeast Florida stony coral assemblage after a  
disease event

By

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## ABSTRACT

Coral reefs have declined globally due to anthropogenic stressors increasing the frequency and severity of bleaching and disease events. In 2014, a stony coral tissue loss disease (SCTLD) outbreak occurred off the coast of southeast Florida and subsequently spread throughout the region. Data collected by the Southeast Florida Reef Evaluation and Monitoring Project (SECREMP) were used to examine the regional impacts of the disease event on the Southeast Florida stony coral assemblage. A long-term annual monitoring project, SECREMP samples permanent sites along the Southeast Florida Reef Tract (SEFRT) from Miami-Dade County north to Martin County. Analysis of stony coral demographic data from 21 sites revealed regional SCTLD prevalence increased significantly, and significant region-wide declines in stony coral diversity and density were observed. From 2014 to 2018, species-specific susceptibility to the disease were evident, with *Meandrina meandrites* and *Dichocoenia stokesi* both losing > 90% of all live tissue by 2016. The reef building, complexity-contributing species *Montastraea cavernosa* and *Orbicella* spp. lost significant tissue (55% and 70% respectively) as a result of this disease event. Overall, up to 64% of all live tissue was lost and at least 11 of 28 total species were impacted by SCTLD. Of the colonies that suffered complete mortality, many were among the largest individuals in the dataset. Loss of large, sexually mature colonies lowers reproductive capabilities and thus severely inhibits the potential for recovery. Juvenile surveys showed many of the large, structurally complex species had little to no juveniles within the sample sites, while eurytopic generalist species made up more than 76% of all juveniles. This disease event resulted in acute mortality and altered ecosystem function to the point where recovery is uncertain. To facilitate recovery, local resource managers need to understand the severity of the disease outbreak on the coral assemblage and mitigate local anthropogenic stressors.

Keywords: disease, coral mortality, long-term monitoring, density, diversity

## INTRODUCTION

Coral reefs are the most diverse of all marine ecosystems, housing almost one third of ocean species and yielding high productivity (Buddemeier et al., 2004). Coral reef systems are valuable in terms of coastal protection and tourism value; where the global value of goods and services is about \$30 billion annually (Moberg and Folke, 1999; Hoegh-Guldberg, 2004). In a constantly changing and dynamic environment, changes in marine conditions may have a direct impact on the future of coral reefs as reef systems face threats from both human mediated and naturally occurring events. On a global scale, rising water temperatures linked to escalating carbon dioxide levels are increasing the frequency and severity of bleaching events (Baker et al., 2008; Manzello, 2015; Hughes et al., 2018). Bleaching events can cause mass mortality and changes to reef composition; there have been 3 mass bleaching events since the 1980s (Heron et al., 2016; NOAA Coral Reef Watch, 2016; Pisapia et al., 2016). In addition to climate change, ocean acidification from absorbed atmospheric carbon dioxide threatens coral reefs by inhibiting their ability to build their calcium carbonate skeletons (Anthony et al., 2008). Coral reefs also face local anthropogenic stressors, including reduced water quality and clarity, nutrient enrichment, and dredging-associated sedimentation (Bruno et al., 2003; Vega Thurber et al., 2013; Miller et al., 2016; van Woesik and McCaffrey, 2017b).

Coral disease outbreaks are emerging as an increasing threat to coral condition and ecosystem function (Harvell et al., 2002; van Woesik, 2002; Maynard et al., 2015). The intensity and frequency of coral disease events has increased during the past few decades (Richardson and Voss, 2005; Sokolow, 2009; Hoegh-Guldberg, 2010; Manzello, 2015). Although the cause of this increase is multifaceted, there is a proposed link between increased disease prevalence and increasing ocean temperatures (Harvell et al., 2002; Miller et al., 2009; Muller and van Woesik, 2012; Precht et al., 2016). Coral disease events reduce fecundity, result in both local and regional population declines, and cause shifts in coral assemblages (Richardson and Voss, 2005; Croquer and Weil, 2009). Climate warming can increase pathogen development and persistence, disease transmission, and susceptibility of the host (Harvell et al. 2002). With rapidly changing climate and anomalously high ocean temperatures becoming a large factor affecting health and resilience of coral reefs, live coral cover and colony density may undergo significant declines (Jones et al. 2004, Bruno et al. 2007).

The chronic disturbances and the high economic value of Southeast Florida reefs require long-term monitoring and comprehensive research to define and quantify change, identify threats to the ecosystem, and develop an effective management plan. This study uses the Southeast Florida Coral Reef Evaluation and Monitoring Project (SECREMP), a long-term monitoring project established in 2003 to monitor status and trends in the Southeast Florida (Miami-Dade, Broward, Palm Beach and Martin counties) reef system. I analyzed 6 years (2013-2018) of stony coral demographic data collected to evaluate the effects of a widespread disease outbreak in the northern portion of the Florida Reef Tract (FRT). The FRT is the third largest barrier reef system in the world and extends 577 km north from the Dry Tortugas (Gilliam et al., 2017). In Florida, coral reefs are important to the local economy and have intrinsic value as part of the only continental United States reef system. The Southeast portion of the Florida Reef Tract (SEFRT) is unique; it contains a linear outer reef structure that is one of the longest continuous reef structures in the western Atlantic and consist of three reef ridges parallel to shore of increasing depth (Banks et al., 2007). The SEFRT reefs span Miami-Dade, Broward, Palm Beach and Martin Counties, are directly adjacent to shore and exist within 3 km of a highly urbanized and developed mainland. Florida reefs related tourism generates \$5.5 billion in sales each year (Gibson et al., 2008; Storlazzi et al., 2019). Broward County's current human population alone is greater than The population of the four counties containing the SEFRT is > 6 million people and is expected to increase to 7.5 million people by 2040 (Acevedo, 2017). Large adjacent populations lead to increased pollution, sedimentation, and coastal development further increasing stressors on the reef tract. Thus, the SEFRT is directly impacted by commercial and recreational fishing activities, marine construction (i.e., dredging and port expansion), sewage outfalls, and ship groundings. These stressors are expected to have an even larger impact on the Southeast Florida reef system in the face of human population growth and global climate change.

A rapidly progressing white disease was first observed in Miami-Dade and Broward counties in 2014 and spread to other portions of the SEFRT by fall 2015 (Precht et al., 2016; Walton et al., 2018). Increased ocean temperatures (Manzello, 2015) followed by coral bleaching were reported in late summer and fall 2014 in the FRT and continued through 2015 (Eakin et al., 2016; van Woesik and McCaffrey, 2017a; Walton et al., 2018). By the summer of 2016, active disease had been reported in all four counties in the SEFRT with multiple species having significant losses in density (Walton et al., 2018). Previously, the majority of non-acroporid



white disease effecting the Caribbean was white plague, first reported in the in 1970s and again in the 1990s (Dustan, 1977) and is now considered to be one of the most serious of coral diseases (Croquer et al., 2003; Richardson and Voss, 2005; Miller et al., 2009). However, this recent disease outbreak has yet to be conclusively identified as the same accepted pathogen known to cause white plague. Due to the unknown etiology of this disease, management agencies have classified it as Stony Coral Tissue Loss Disease (SCTLD) (Florida Keys National Marine Sanctuary, 2018). SCTLD differs from white plague in that lesions may appear in the middle of the colony as opposed to lesions starting at tissue margins or the base of colony; where lesions can be surrounded by bleached tissue (Florida Keys National Marine Sanctuary, 2018). Highly susceptible, intermediately susceptible and low susceptible species have been identified; where highly susceptible species are the first affected during an outbreak, have rapid disease progression and complete colony mortality (Florida Keys National Marine Sanctuary, 2018). Intermediately susceptible species are often affected later, affected in lower quantities, and large colonies can have lesions that last months to years (Florida Keys National Marine Sanctuary, 2018).

In this study, SECREMP data collected between 2013 and 2018 were analyzed to determine the impacts and extent of the disease outbreak and assess the possibility of recovery from this event. Recovery will depend on both growth of existing corals or new corals recruiting into the area. To better evaluate the status of the SEFRT, small colony and juvenile data was added to the SECREMP surveys in 2018. Previous studies have found that coral reproductive output at the colony level is highest when the cover is highest at the species level (Hartmann et al., 2017), and thus low cover after a disturbance event can threaten the chance of recovery. Additionally, reductions in colony size lead to reductions in reproductive output and thus reducing the likelihood of recovery (Connell, 1973; Szmant-Froelich, 1985; Tsounis et al., 2006). Epidemics of coral disease that span anywhere from 10 -1000 km and last for multiple years are estimated to take centuries to recover, if recovery can even occur (Jackson, 1991).

The objectives of this study are to (1) further evaluate the spatial and temporal extent of the outbreak, (2) quantify regional loss to stony coral density and live tissue area, (3) identify species specific effects and recovery, and (4) quantify the density and composition of the juvenile population.

# METHODS

## STONY CORAL DEMOGRAPHIC SURVEYS

To evaluate the impact of this coral disease event along the Southeast Florida Reef Tract, stony coral density and demographic data from 21 SECREMP sites were used. Established in 2003, SECREMP is a long-term coral reef monitoring program which provides resource managers with the annual status as well as spatial and temporal trends along the SFRT. These 21 sites are located along the SFRT from Miami-Dade County in the south to Martin County in the north (Table 1, Figure 1) and encompass multiple reef habitats (Walker, 2012). Sites are identified by county followed by a site number. Each site consists of four, 1 m x 22 m stations demarcated by permanently-installed stainless steel pins. Annual stony coral demographic surveys were conducted during the summer months (May – September) from 2013 to 2018; all stony corals  $\geq 4$  cm were identified to species. Maximum colony diameter and height (defined as the measurement perpendicular to the plane of growth) were recorded along with any visual signs of bleaching, disease or other conditions (i.e., predation, overgrowth interactions, boring sponges, etc.). To assess the effect of the disease outbreak, disease prevalence for SCTLD was assessed and all other diseases were combined to assess an overall ‘other’ disease prevalence. Other diseases included black band disease, yellow band disease, white band disease (for acroporids), and dark spot disease. Percent colony mortality also was assessed. Recent mortality was defined as tissue loss with clearly distinguishable corallite structure and minimal overgrowth by algae or other fouling organisms. Any areas of colony mortality that did not meet these criteria were defined as old mortality. Additionally, to better understand potential recovery after a disease event, smaller size classes were added to the survey. In 2018, demographic data were collected on any colony  $\geq 2$  cm maximum diameter. Any stony corals  $< 2$  cm diameter were identified to the lowest taxonomic level and tallied across all sites. Although not a dedicated juvenile survey, lowering of minimum size was implemented to help better capture species richness and density of smaller colonies.

Table 1. Locations of 21 SECREMP sites with reef type, depth and locations. NRC = Nearshore Ridge Complex, MC = Martin County, PB = Palm Beach County, BC = Broward County, DC = Miami-Dade County

<b>Site</b>	<b>Reef Type</b>	<b>Depth (m)</b>	<b>Latitude (N)</b>	<b>Longitude (W)</b>
MC1	NRC	4.6	27° 07.900'	80° 08.042'
MC2	NRC	4.6	27° 06.722'	80° 07.525'
PB1	NRC	7.6	26° 42.583'	80° 01.714'
PB2	Outer	16.8	26° 40.710'	80° 01.095'
PB3	Outer	16.8	26° 42.626'	80° 00.949'
PB4	Outer	16.8	26° 29.268'	80° 02.345'
PB5	Outer	16.8	26° 26.504'	80° 02.854'
BC1	NRC	7.6	26° 08.872'	80° 05.758'
BC2	Middle	12.2	26° 09.597'	80° 04.950'
BC3	Outer	16.8	26° 09.518'	80° 04.641'
BC4	Inner	9.1	26° 08.963'	80° 05.364'
BC5	Middle	13.7	26° 18.100'	80° 04.095'
BC6	Outer	16.8	26° 18.067'	80° 03.634'
DC1	Inner	7.6	25° 50.530'	80° 06.242'
DC2	Middle	13.7	25° 50.520'	80° 05.704'
DC3	Outer	16.8	25° 50.526'	80° 05.286'
DC4	Outer	12.5	25° 40.357'	80° 05.301'
DC5	Inner	7.3	25° 39.112'	80° 05.676'
DC6	NRC	4.6	25° 57.099'	80° 06.534'
DC7	Middle	16.8	25° 57.530'	80° 05.639'
DC8	NRC	4.6	25° 40.707'	80° 07.111'

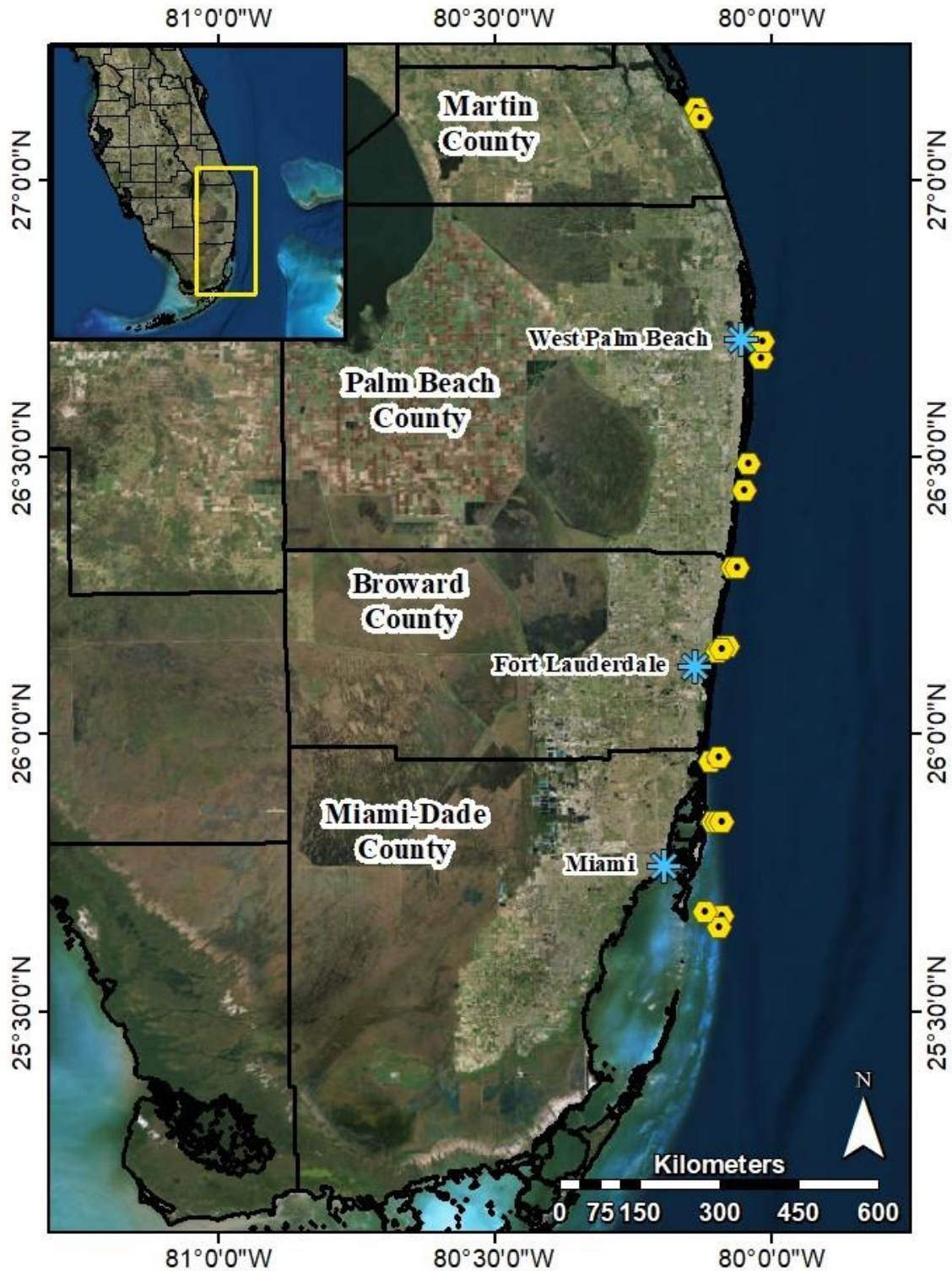


Figure 1. Map of southeast Florida with 21 Southeast Florida Coral Reef Evaluation and Monitoring Project (SECREMP) site locations in yellow. Major cities are denoted with blue asterisks and county lines are outlined in black.

## STATISTICAL ANALYSES

Differences in disease prevalence, coral assemblage diversity, coral density, and coral live tissue area (LTA) were analyzed at the regional level, where regional values were calculated using data from all sites. Assemblage diversity was evaluated using species richness (S), Shannon index ( $H'$ ) and Inverse Simpson's index (D). During the first years of the project *Orbicella annularis*, *O. faveolata* and *O. franksii* were grouped as the *O. annularis* complex and therefore grouped for the purposes of this study.

The metric LTA was utilized to capture the loss of coral tissue that occurred without whole colony mortality. This metric is especially useful because disease often causes partial colony mortality and is thus a more sensitive method for detecting change in the stony coral assemblage. Colony surface areas were calculated using the below modified version of the Knud Thomsen approximation for the surface area of an ellipsoid (Klamkin, 1971; Klamkin, 1976):

$$SA = 2\pi \left( \frac{a^p \left(\frac{1}{2}b\right)^p + a^p \left(\frac{1}{2}b\right)^p + \left(\frac{1}{2}b\right)^p \left(\frac{1}{2}b\right)^p}{3} \right)^{\frac{1}{p}}$$

The surface area was modified to only use one radius measurement and one height measurement. To calculate the surface area of a coral colony, the original equation was multiplied by  $\frac{1}{2}$  to only account for the top half of an ellipsoid. Where  $a$  = maximum colony height,  $b$  = maximum colony diameter and  $p = 1.6075$ , a constant yielding a relative error of at most  $\pm 1.6075\%$ , determined by Knud Thomsen based on Klamkin (1971) work. Total colony mortality was then used with the surface area of the colony to calculate the LTA:

$$LTA = SA \left( 1 - \left( \frac{\% \text{ Old Mortality} + \% \text{ Recent Mortality}}{100} \right) \right)$$

To evaluate regional differences in disease prevalence, colony density, diversity and colony LTA were analyzed using linear mixed-effects models in the nlme package (Pinheiro et al., 2017) in RStudio (RStudio Team, 2015). Year was set as a random effect in these models with disease

prevalence, density or LTA the response variables. Species level disease prevalence, density and LTA were examined using linear mixed-effect models with year as a random effect. For all models if significant effects were found, a Tukey's *post hoc* analysis was performed using the `glht()` (general linear hypothesis) function in the `multcomp` package (Hothorn et al., 2008).

To evaluate the relationship between all disease prevalence and SCTL D as well as all disease prevalence and site LTA and density, a Kendall's rank correlation using tau-b to account for ties was performed. Each metric (disease prevalence, SCTL D prevalence, LTA and density) was calculated by site and tested by year.

## RESULTS

### INCREASED CORAL DISEASE AND CORAL ASSEMBLAGE DECLINES

Regional stony coral disease prevalence increased from 2013 to 2016, peaking at  $3.5 \pm 0.9$  % (mean  $\pm$  SE) colonies affected. Regional disease prevalence then declined to less than 1% in 2017 and 2018 (Figure 2). Disease prevalence previously had increased every year from 2013 to 2016, with 2016 having significantly higher disease prevalence (linear mixed-effects model,  $df=20$ ) than all other years (Figure 2); disease prevalence in 2016 was five times greater than in 2013. This increase in disease prevalence was driven by an increase in stony coral tissue loss disease (SCTL D). This disease presents as tissue loss lesions that either start on the edge of the colony and progress upwards or lesions begin as patches or blotches within intact tissue (Florida Keys National Marine Sanctuary, 2018). In 2013, only three colonies (two *Dichocoenia stokesii* and one *Porites astreoides*) located in Broward and Miami-Dade counties on the Nearshore Ridge Complex (NRC) and the Inner Reef visually presented conditions consistent with SCTL D (Table 2). By 2014, SCTL D prevalence had increased 8-fold ( $0.8 \pm 0.6$  %), and was recorded on six species in three different counties (Table 2). Regional SCTL D prevalence continued to increase in 2015 and by 2016 was  $2.7 \pm 0.8$ %, which was significantly higher than all other years (linear mixed-effects model). By 2016, SCTL D was recorded in all counties within the SEFRT, on all habitat types and on 11 of 28 different species, demonstrating the wide geographic extent of the disease as well as its indiscriminate effect on multiple species (Figure 3). In 2018, SCTL D was only recorded on 2 species: *Montastrea cavernosa* and the *O. annularis* complex.

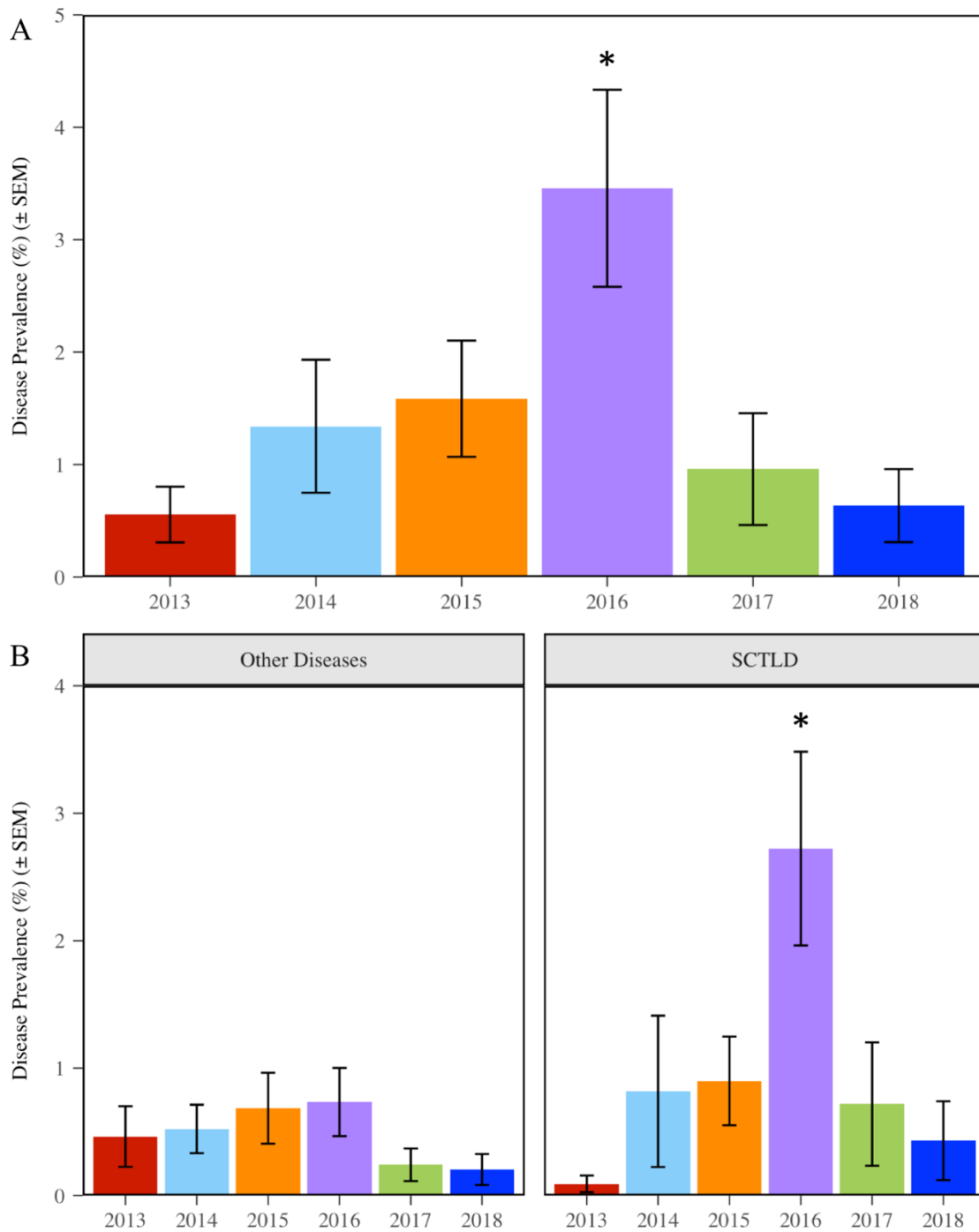


Figure 2. Mean ( $\pm$  SE) annual coral disease prevalence for A) all diseases combined and B) all other diseases and SCTLD. Disease prevalence is the average prevalence per site where all colonies were summed across a site. Asterisks indicate years that significantly differed (linear mixed-effects model, linear mixed-effects model,  $df=20$ ).

Table 2. Annual stony coral abundance, stony coral tissue loss disease (SCTLD) count and prevalence, list of species recorded with SCTLD, abundance and the county the disease was observed in by year for all colonies  $\geq 4$  cm maximum diameter. (NRC = Nearshore Ridge Complex. Regional SCTLD prevalence is mean  $\pm$  SE)

Year	Total Corals	SCTLD Count	SCTLD Regional Prevalence (%)	Species affected	Diseased Colonies	Total colonies	County	Habitat
2013	2280	3	0.09 $\pm$ 0.07	<i>Dichocoenia stokesi</i>	2	75	Broward, Miami-Dade	NRC, Inner
				<i>Porites astreoides</i>	1	528	Miami-Dade	NRC
2014	2382	12	0.82 $\pm$ 0.60	<i>Agaricia agaricites</i>	1	135	Miami-Dade	Inner
				<i>Dichocoenia stokesi</i>	2	78	Broward	Middle
				<i>Meandrina meandrites</i>	1	118	Broward	Outer
				<i>Porites astreoides</i>	1	564	Broward	Outer
				<i>Siderastrea siderea</i>	6	417	Palm Beach, Broward	Middle, Outer
				<i>Stephanocoenia intersepta</i>	1	250	Broward	Outer
2015	2392	18	0.90 $\pm$ 0.35	<i>Dichocoenia stokesi</i>	6	55	Palm Beach, Miami-Dade	NRC, Outer
				<i>Montastraea cavernosa</i>	3	457	Miami-Dade	Inner, Outer
				<i>Montastraea (Orbicella) annularis complex</i>	2	24	Miami-Dade	Inner
				<i>Meandrina meandrites</i>	2	85	Miami-Dade	NRC
				<i>Porites astreoides</i>	1	571	Broward	Inner
				<i>Porites porites</i>	1	115	Miami-Dade	Inner
				<i>Solenastrea bournoni</i>	1	54	Miami-Dade	Inner
				<i>Siderastrea siderea</i>	1	405	Martin	NRC
				<i>Stephanocoenia intersepta</i>	1	258	Miami-Dade	Middle
2016	1936	58	2.72 $\pm$ 0.76	<i>Eusmilia fastigiata</i>	1	4	Palm Beach	Outer
				<i>Montastraea cavernosa</i>	38	248	Miami-Dade, Broward, Palm Beach	NRC, Inner, Middle, Outer
				<i>Montastraea (Orbicella) annularis complex</i>	3	24	Miami-Dade, Broward	NRC, Inner
				<i>Porites astreoides</i>	4	632	Miami-Dade	Inner
				<i>Solenastrea bournoni</i>	5	38	Miami-Dade, Broward, Palm Beach	NRC, Middle
				<i>Siderastrea siderea</i>	6	324	Miami-Dade, Broward, Palm Beach	NRC, Inner, Middle, Outer
2017	2336	19	0.72 $\pm$ 0.48	<i>Montastraea cavernosa</i>	15	231	Miami-Dade, Broward, Palm Beach	NRC, Inner, Outer
				<i>Montastraea (Orbicella) annularis complex</i>	2	21	Broward	NRC
				<i>Porites astreoides</i>	1	789	Broward	Inner
				<i>Stephanocoenia intersepta</i>	1	267	Miami-Dade	Middle
2018	2394	13	0.43 $\pm$ 0.31	<i>Montastraea cavernosa</i>	11	263	Miami-Dade, Broward, Palm Beach	NRC, Inner, Outer
				<i>Montastraea (Orbicella) annularis complex</i>	2	11	Broward	NRC, Inner





Figure 3. Images of nine of the 11 total species recorded with stony coral tissue loss disease.

Other diseases were recorded over the course of this study, however, averaged across all sites, other disease prevalence stayed under 1% and there were no significant increases in prevalence between years (Figure 2). Other diseases recorded in this study included black band disease, yellow band disease, white band disease (only acroporids), dark spot disease, and rapid tissue loss (only acroporids). A significant positive correlation was found between overall disease prevalence and SCTLD prevalence in 2016 (Kendall's rank correlation,  $\tau = 0.38$ ,  $df = 20$ ). No other significant correlations were found between disease prevalence and SCTLD prevalence any other years (Kendall's rank correlation,  $df = 20$ ).

The widespread geographic extent of SCTLD and the species affected was examined by quantifying the coral assemblage diversity and LTA over the six year study period. Across all sites, all three diversity measures were significantly lower in 2017 (S:  $8.4 \pm 0.6$ , H':  $1.5 \pm 0.1$ , D:  $3.5 \pm 0.2$ ) and 2018 (S:  $8.3 \pm 0.6$ , H':  $1.5 \pm 0.1$ , D:  $3.6 \pm 0.3$ ) (mean  $\pm$  SE) compared to 2013-2015 (linear mixed-effects model,  $df=20$ ) (Figure 4). Decreases were seen from 2015 to 2016; however, these reductions were not significant except for species richness. Overall species richness was lowest in 2016 where it was 21% lower than the previous year, while Inverse Simpson's diversity reached a minimum in 2017 and Shannon diversity in 2018 (Figure 4).

From 2013 to 2015, overall LTA increased each year with the highest LTA per site occurring in 2015 with  $1.68 \pm 0.31$  m<sup>2</sup> of tissue per site (Figure 5). From 2015 to 2016, there was a significant 37% loss of LTA across all sites combined (2016;  $1.1 \pm 0.2$ ). Further loss of LTA was seen in 2017, where it reached the minimum over the study period of  $0.9 \pm 0.2$  m<sup>2</sup> of tissue per site. The overall LTA in 2017 and 2018 was significantly lower than in 2013, 2014, and 2015. The species driving this loss include *Montastrea cavernosa*, *Meandrina meandrites*, *Montastrea (Orbicella) annularis* complex, *Dichocoenia stokesi* and *Solenastrea bournoni* (Figure 6, Figure 7). Live tissue area in 2018 did not significantly increase. Live tissue area was found to have a significant positive correlation in both 2017 and 2018 (Kendall's rank correlation; 2017:  $\tau = 0.36$ ,  $df = 20$ ; 2018:  $\tau = 0.42$ ,  $df = 20$ ). No significant relationship was found between LTA and disease prevalence any other year (Kendall's rank correlation,  $df = 20$ ).

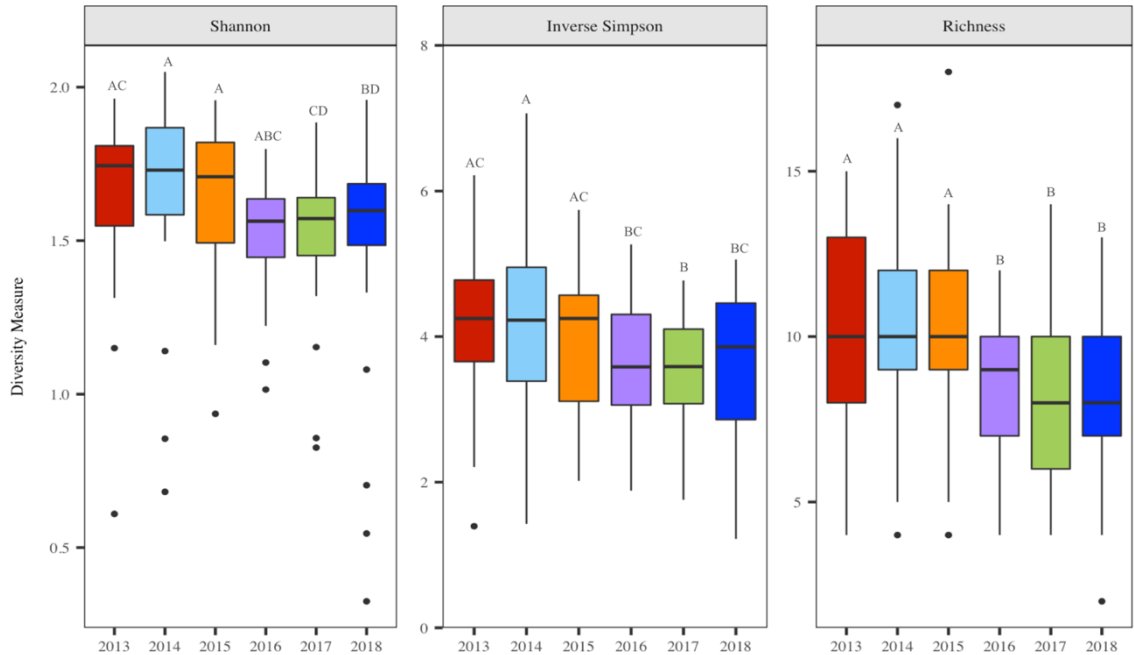


Figure 4. Regional stony coral diversity indices per year for all sites combined. Letters indicate significant difference between years (linear mixed-effects model,  $df=20$ ).

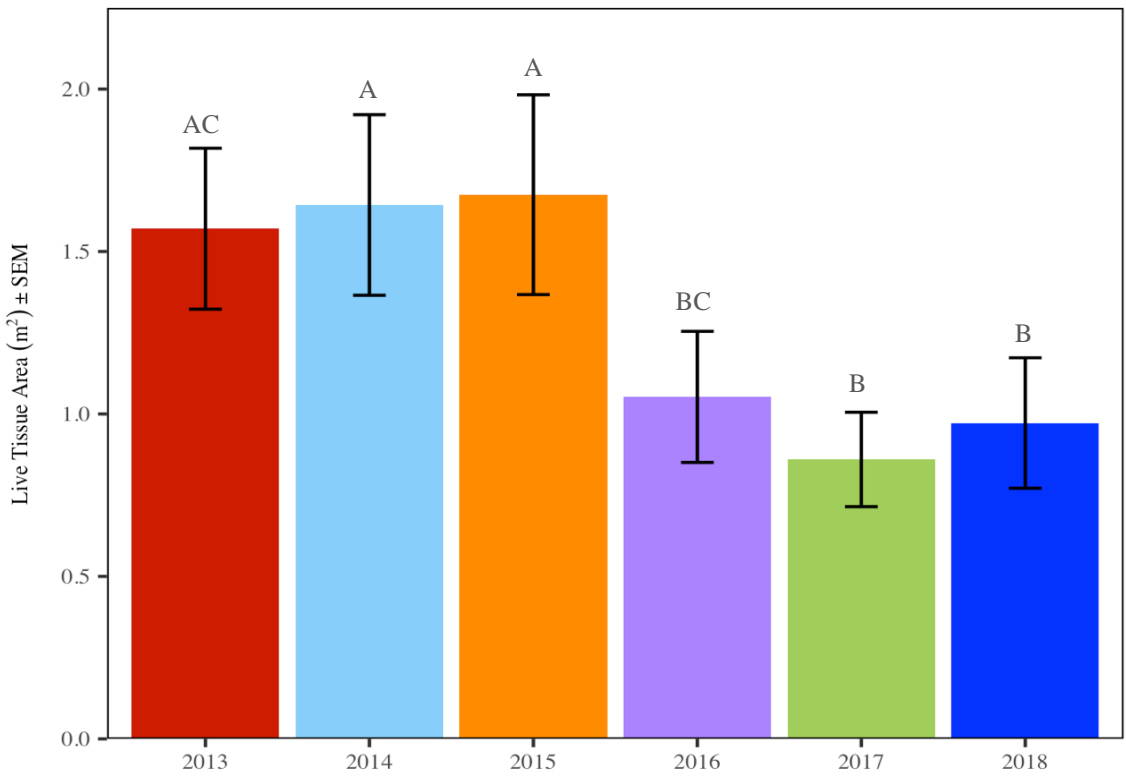


Figure 5. Mean ( $\pm$  SE) annual live tissue area (LTA) for all stony coral species and sites combined. Letters indicate statistical difference (linear mixed-effects model,  $df=20$ ).

## SPECIES-SPECIFIC EFFECTS

While no species affected by SCTLTD were entirely lost from the sample sites, six species' abundances were reduced by over 50% from 2013 to 2018 (Table 3). *Dichocoenia stokesi* peaked in abundance in 2014 with 78 colonies and was reduced to only five colonies across the 21 sites by 2017. Similarly *Meandrina meandrites* also suffered a drastic decline where the highest abundance was observed in 2014 with 118 colonies and by 2016 five colonies were observed; in 2018 *M. meandrites* abundance was only at 22% of what it was in 2014 (Table 3). *Solenastrea bournoni* peaked in abundance in 2014 with 58 colonies, but by 2018 only 19 colonies remained: a loss of 67%. *Orbicella* spp steadily declined in abundance from 2015 to 2018 and only one-half of the colonies recorded in 2013 remained by 2018. Both species of *Pseudodiploria* declined in abundance from 2013 to 2018 with *P. strigosa* declining in abundance by 58% while *P. clivosa* lost 90% of colonies recorded in 2013 (Table 3). *Porites astreoides* and *P. porites* were among the few species that increased in abundance, increasing in abundance by 59% and 115% from 2013 to 2018 respectively (Table 3).

Of the 28 species initially present, seven species had significant decreases in LTA over the course of the study: *M. meandrites*, *S. siderea*, *Orbicella* spp., *P. astreoides*, *D. stokesi*, *S. bournoni*, *Montastraea cavernosa* (linear mixed-effects model, df=20). *Meandrina meandrites* and *D. stokesi* had a significantly lower LTA in 2016, compared to 2013 and 2014 with no significant change through 2018 (Figure 6, Figure 7) (linear mixed-effects model, df=20). Both species lost over 90% of LTA from 2013 to 2018 (Figure 6, Figure 7). *Orbicella* spp. had the lowest LTA in 2018 ( $0.36 \pm 0.09$ ) which was significantly lower than the LTA in 2015 ( $1.34 \pm 0.37$ ), by 2018 only 27% of tissue remained within the sample sites (linear mixed-effects model, df=20). *Solenastrea bournoni* LTA in 2017 and 2018 ( $0.1 \pm 0.0$ ) were significantly lower than 2014 ( $0.2 \pm 0.1$ ; Figure 7) (linear mixed-effects model, df=20). *Montastraea cavernosa* LTA was significantly higher in 2014 ( $3.6 \pm 2.0$ ) and 2015 ( $3.6 \pm 2.1$ ) compared to 2017 ( $1.6 \pm 0.1$ ) (linear mixed-effects model, df=20). Only two species, *S. siderea* and *P. astreoides* had significant increases in LTA. *Siderastrea siderea* had a significant increase from 2016 ( $0.3 \pm 0.1$ ) to 2018 ( $0.4 \pm 0.1$ ), which was the highest LTA recorded for *S. siderea* across study years (linear mixed-effects model, df=20) (Figure 6). *Porites astreoides* significantly increased in LTA from 2013 ( $0.6 \pm 0.2$ ) and 2014 ( $0.6 \pm 0.2$ ) to 2018 ( $0.8 \pm 0.2$ ; Figure 6).

Table 3. Regional stony coral species abundances (# of colonies) for all Southeast Coral Reef Evaluation and Monitoring Program (SECREMP) sites combined

Species	2013	2014	2015	2016	2017	2018	% Change 2013-2018
<i>Acropora cervicornis</i>	8	22	17	19	19	8	0
<i>Agaricia agaricites</i>	133	135	129	125	193	150	13
<i>Agaricia fragilis</i>	3	8	18	12	16	10	233
<i>Agaricia lamarcki</i>	5	4	6	6	3	5	0
<i>Colpophyllia natans</i>	9	7	10	3	2	1	-89
<i>Dichocoenia stokesi</i>	75	78	55	8	5	10	-87
<i>Diploria labyrinthiformis</i>	3	2	2	1	1	2	-33
<i>Eusmilia fastigiata</i>	3	6	6	4	6	5	67
<i>Isophyllia sinuosa</i>	1	1	3	1	8	2	100
<i>Leptoseris cucullata</i>	0	0	0	0	0	1	100
<i>Madracis auretenra</i>	28	43	73	67	67	42	50
<i>Madracis decactis</i>	39	43	41	33	41	46	18
<i>Meandrina meandrites</i>	114	118	85	5	12	14	-88
<i>Montastraea (Orbicella) annularis</i> complex	22	21	24	24	21	11	-50
<i>Montastraea cavernosa</i>	445	472	457	248	231	263	-41
<i>Mycetophyllia aliciae</i>	5	4	6	4	4	7	40
<i>Mycetophyllia lamarckiana</i>	0	0	0	1	0	0	0
<i>Oculina diffusa</i>	8	7	7	5	3	0	-100
<i>Oculina robusta</i>	0	0	0	0	0	1	100
<i>Phyllangia americana</i>	0	0	0	0	1	1	100
<i>Porites astreoides</i>	528	564	571	632	789	838	59
<i>Porites porites</i>	51	79	115	113	147	110	116
<i>Pseudodiploria clivosa</i>	30	27	30	29	30	3	-90
<i>Pseudodiploria strigosa</i>	12	12	10	4	5	5	-58
<i>Scolymia cubensis</i>	3	0	0	1	3	1	-67
<i>Siderastrea siderea</i>	460	421	415	324	434	540	17
<i>Solenastrea bournoni</i>	55	58	54	38	28	19	-65
<i>Stephanocoenia intersepta</i>	240	250	258	229	267	299	25
<b>Total</b>	2280	2382	2392	1936	2336	2394	

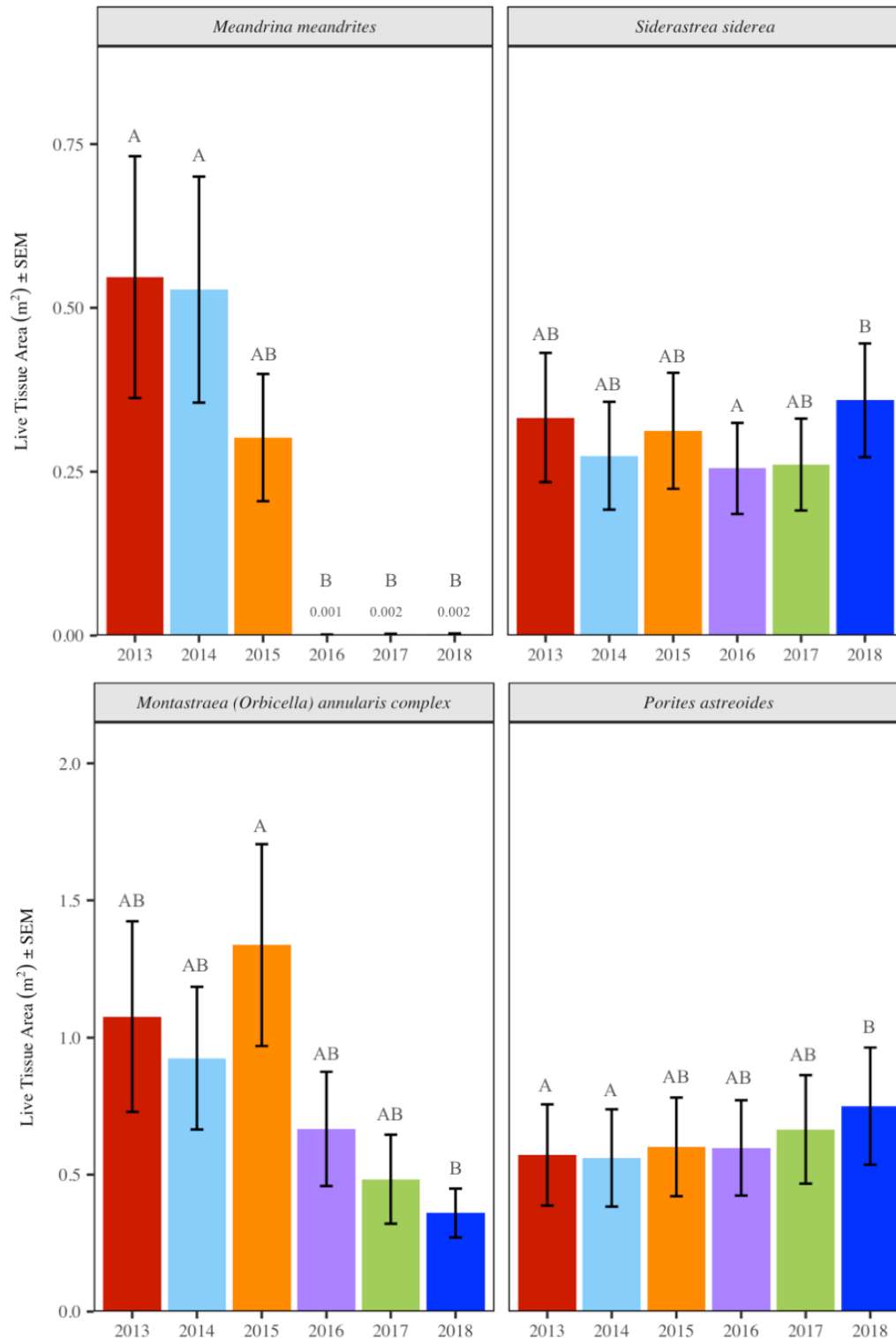


Figure 6. Mean ( $\pm$  SE) regional live tissue area (LTA) ( $m^2$ ) for *Meandrina meandrites*, *Siderastrea siderea*, *Montastraea (Orbicella) annularis complex*, and *Porites astreoides*. LTA is summed across a site and averaged across all sites. Letters indicate significant difference among years (linear mixed-effects model,  $df=20$ ).

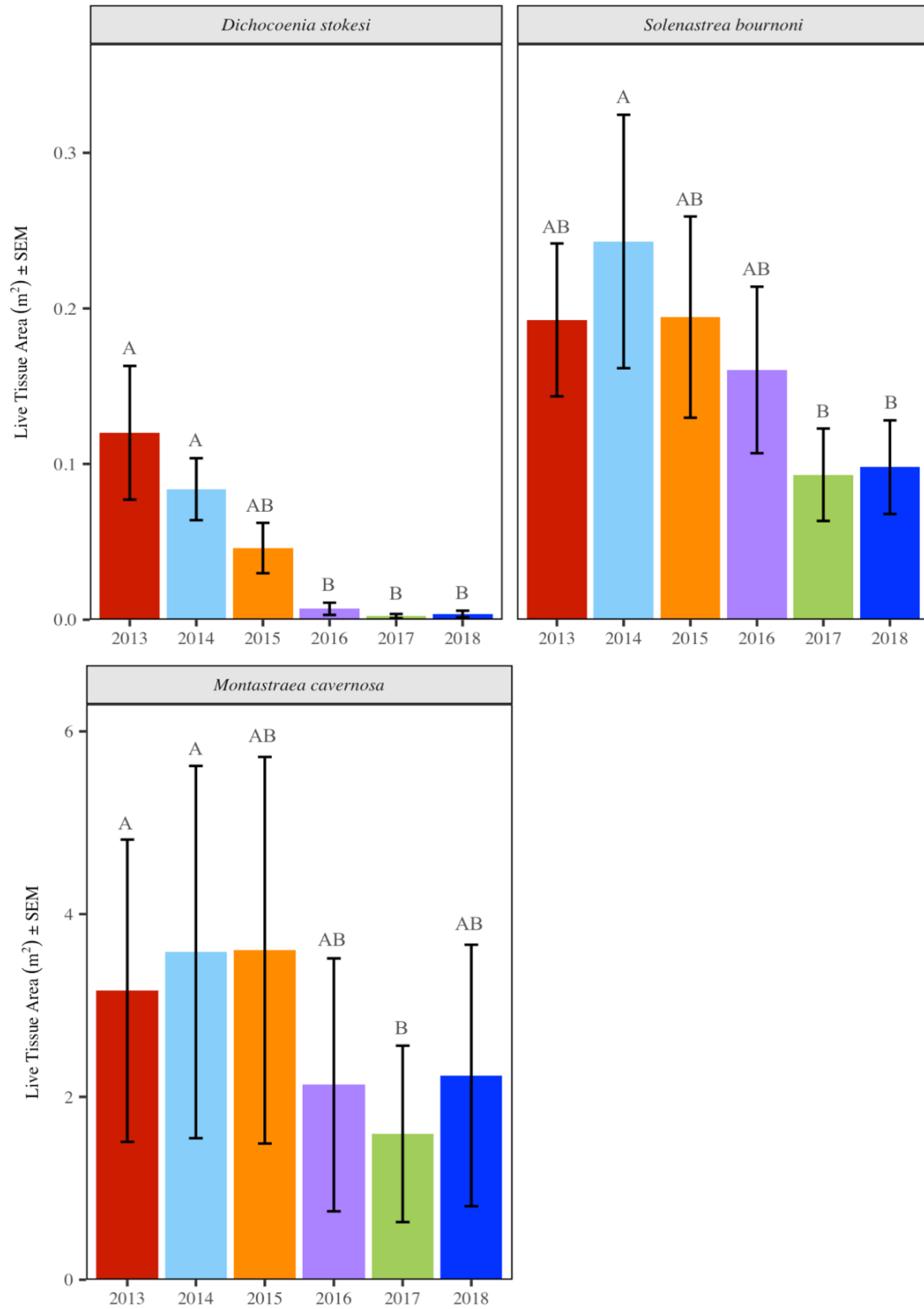


Figure 7. Mean ( $\pm$  SE) regional live tissue area (LTA) ( $m^2$ ) for *Dichocoenia stokesi*, *Solenastrea bournoni* and *Montastraea cavernosa*. LTA is summed across a site and averaged across all sites. Letters indicate significant difference between years (linear mixed-effects model,  $df=20$ ).

The six species and one complex that saw significant changes in LTA had all been recorded with active SCTL D infections during monitoring (Table 2). *Siderastrea siderea* and *P. astreoides* were the only two species affected by the disease to have increases in LTA; however, *S. siderea* had the lowest recorded LTA in 2016 during the peak of the disease outbreak, suggesting a possible effect of the disease on the LTA.

Ten of the 28 species had significant changes in density from 2013 to 2018 (linear mixed-effects model,  $df=20$ ) (Table 4). Seven species had significant declines, and six of the seven were species that were affected by SCTL D. Densities of *Orbicella* spp., *S. bournoni*, *M. meandrites*, *D. stokesi*, and *C. natans* all dropped to or below 0.01 colonies/m<sup>2</sup> by 2018 (Table 4). *Dichocoenia stokesi* had the highest recorded density in 2014 ( $0.04 \pm 0.01$  colonies/m<sup>2</sup>) which had significantly dropped to  $0.00 \pm 0.00$  colonies/m<sup>2</sup> by 2017. *Meandrina meandrites* had a 95% reduction in density from 2014 ( $0.06 \pm 0.01$  colonies/m<sup>2</sup>) to 2016 ( $0.00 \pm 0.00$  colonies/m<sup>2</sup>). *Montastraea cavernosa* also had the highest density in 2014 ( $0.26 \pm 0.07$  colonies/m<sup>2</sup>) that declined to  $0.13 \pm 0.03$  colonies/m<sup>2</sup> by 2017 a loss of over 50% of colonies recorded. Density was found to have a significant positive correlation in both 2017 and 2018 (Kendall's rank correlation; 2017:  $\tau = 0.36$ ,  $df = 20$ ; 2018:  $\tau = 0.45$ ,  $df = 20$ ). No significant relationship was found between density and disease prevalence any other year (Kendall's rank correlation,  $df = 20$ ).

In contrast, three species had significant increases over the study period. Both species of *Porites* within the sample sites significantly increased in density. *Porites porites* increased significantly from 2013 ( $0.03 \pm 0.01$  colonies/m<sup>2</sup>) to 2017 ( $0.08 \pm 0.03$  colonies/m<sup>2</sup>) while *P. astreoides* had a significant increase from 2013 ( $0.29 \pm 0.08$  colonies/m<sup>2</sup>) to 2018 ( $0.45 \pm 0.14$  colonies/m<sup>2</sup>), a 58% increase in density. Density of *Stephanocoenia intersepta* in 2018 ( $0.16 \pm 0.03$  colonies/m<sup>2</sup>) was significantly higher than in 2013 ( $0.13 \pm 0.02$  colonies/m<sup>2</sup>) and 2016 ( $0.12 \pm 0.02$  colonies/m<sup>2</sup>; linear mixed-effects model,  $df=20$ )



Table 4. Regional stony coral species mean density ( $\pm$  SE) for all sites combined and pairwise results (colonies/m<sup>2</sup>) (linear mixed-effects model, df=20; \* p < 0.05; \*\*p < 0.01; \*\*\*p < 0.001; ND = no significant difference)

Species	2013	2014	2015	2016	2017	2018	Pairwise Comparisons
<i>Acropora cervicornis</i>	0.00 $\pm$ 0.00	0.01 $\pm$ 0.01	0.01 $\pm$ 0.01	0.01 $\pm$ 0.01	0.01 $\pm$ 0.01	0.00 $\pm$ 0.00	ND
<i>Agaricia agaricites</i>	0.07 $\pm$ 0.05	0.07 $\pm$ 0.06	0.07 $\pm$ 0.05	0.07 $\pm$ 0.05	0.10 $\pm$ 0.08	0.08 $\pm$ 0.06	ND
<i>Agaricia fragilis</i>	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.01 $\pm$ 0.01	0.01 $\pm$ 0.01	0.01 $\pm$ 0.01	0.01 $\pm$ 0.00	ND
<i>Agaricia lamarcki</i>	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	ND
<i>Colpophyllia natans</i>	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.01 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	*2015 > 2018
<i>Dichocoenia stokesi</i>	0.04 $\pm$ 0.01	0.04 $\pm$ 0.01	0.03 $\pm$ 0.01	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.01 $\pm$ 0.00	***2013 > 2016, 2017, 2018; ***2014 > 2016, 2017, 2018; *2015 > 2016, 2018; **2015 > 2017
<i>Diploria labyrinthiformis</i>	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	ND
<i>Eusmilia fastigiata</i>	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	ND
<i>Isophyllia sinuosa</i>	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	ND
<i>Leptoseris cucullata</i>	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	ND
<i>Madracis auretenra</i>	0.02 $\pm$ 0.02	0.02 $\pm$ 0.02	0.04 $\pm$ 0.04	0.04 $\pm$ 0.04	0.04 $\pm$ 0.04	0.02 $\pm$ 0.02	ND
<i>Madracis decactis</i>	0.02 $\pm$ 0.01	0.02 $\pm$ 0.01	0.02 $\pm$ 0.01	0.02 $\pm$ 0.01	0.02 $\pm$ 0.01	0.02 $\pm$ 0.01	ND
<i>Meandrina meandrites</i>	0.06 $\pm$ 0.01	0.06 $\pm$ 0.01	0.05 $\pm$ 0.01	0.00 $\pm$ 0.00	0.01 $\pm$ 0.00	0.01 $\pm$ 0.00	***2013 > 2016, 2017, 2018; ***2014 > 2016, 2017, 2018; ***2015 > 2016, 2017, 2018
<i>Montastraea (Orbicella) annularis</i> complex	0.01 $\pm$ 0.00	0.01 $\pm$ 0.00	0.01 $\pm$ 0.00	0.01 $\pm$ 0.00	0.01 $\pm$ 0.00	0.01 $\pm$ 0.00	*2013 > 2018; **2015 > 2018; **2015 > 2016
<i>Montastraea cavernosa</i>	0.24 $\pm$ 0.06	0.26 $\pm$ 0.07	0.25 $\pm$ 0.07	0.13 $\pm$ 0.04	0.13 $\pm$ 0.03	0.14 $\pm$ 0.03	2016, 2017, 2018; ***2015 > 2016, 2017; **2015 > 2018
<i>Mycetophyllia aliciae</i>	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	ND
<i>Mycetophyllia lamarckiana</i>	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	ND
<i>Oculina diffusa</i>	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	ND
<i>Oculina robusta</i>	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	ND
<i>Phyllangia americana</i>	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	ND
<i>Porites astreoides</i>	0.29 $\pm$ 0.08	0.31 $\pm$ 0.09	0.31 $\pm$ 0.09	0.34 $\pm$ 0.10	0.43 $\pm$ 0.13	0.45 $\pm$ 0.14	*2018 > 2013
<i>Porites porites</i>	0.03 $\pm$ 0.01	0.04 $\pm$ 0.02	0.06 $\pm$ 0.03	0.06 $\pm$ 0.03	0.08 $\pm$ 0.03	0.06 $\pm$ 0.02	**2017 > 2013
<i>Pseudodiploria clivosa</i>	0.02 $\pm$ 0.01	0.01 $\pm$ 0.01	0.02 $\pm$ 0.01	0.02 $\pm$ 0.01	0.02 $\pm$ 0.01	0.00 $\pm$ 0.00	ND
<i>Pseudodiploria strigosa</i>	0.01 $\pm$ 0.00	0.01 $\pm$ 0.00	0.01 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	ND
<i>Scolymia cubensis</i>	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	ND
<i>Siderastrea siderea</i>	0.24 $\pm$ 0.04	0.23 $\pm$ 0.03	0.22 $\pm$ 0.03	0.18 $\pm$ 0.03	0.23 $\pm$ 0.04	0.29 $\pm$ 0.05	*2013 > 2016; *2018 > 2014; **2018 > 2015; ***2018 > 2016; *2018 > 2017
<i>Solenastrea bournoni</i>	0.03 $\pm$ 0.01	0.03 $\pm$ 0.01	0.03 $\pm$ 0.01	0.02 $\pm$ 0.01	0.02 $\pm$ 0.01	0.01 $\pm$ 0.00	**2015 > 2018
<i>Stephanocoenia intersepta</i>	0.13 $\pm$ 0.02	0.14 $\pm$ 0.03	0.14 $\pm$ 0.03	0.12 $\pm$ 0.02	0.14 $\pm$ 0.03	0.16 $\pm$ 0.03	*2018 > 2013

Density does not provide information on size class changes of species, so colony diameter was used to evaluate the size distribution of the species with significant changes in density. Five species lost all colonies  $\geq 50$  cm in maximum diameter between 2013 and 2018: *S. intersepta*, *S. bournoni*, *M. meandrites*, *D. stokesi*, *C. natans* (Figure 8-Figure 12). *Orbicella* spp. lost all colonies  $> 100$  cm in maximum diameter from 2013 to 2018, and there were no colonies  $< 10$  cm in 2018. By 2018, *Colpophyllia natans* lost all but one colony by 2018. *Montastraea cavernosa* had the largest loss of colonies in the 20-50 cm diameter range, and in 2018 most colonies were  $< 10$  cm. From 2013 to 2018, *M. meandrites* lost all colonies greater than 10 cm diameter. Similarly, *D. stokesi* lost all colonies greater than 15 cm by 2018, including several large colonies  $> 40$  cm. *Solenastrea bournoni* lost colonies across most size classes, including colonies  $< 10$  cm diameter. While *P. porites* and *S. siderea* had increases in the  $< 10$  cm size, increases in colonies  $> 20$  cm were not observed for either species. *Porites astreoides* and *S. intersepta* had increases in colonies  $< 20$  cm; however, for *S. intersepta* all colonies  $> 40$  cm were lost by 2018.

#### JUVENILE SURVEYS

Eight species that had adult colonies in 2018 did not have any juvenile colonies (colonies  $< 4$  cm in diameter) (Table 5). *Dioploria labyrinthiformis*, *Orbicella* spp., and *P. clivosa* were among these species extremely low densities in 2018 (Table 5) and are known to be affected by SCTLD (Florida Keys National Marine Sanctuary, 2018). *D. stokesi*, *M. meandrites* and *S. siderea* had abundances of juveniles greater than or equal to the abundance of adults (colonies  $\geq 4$  cm diameter). *Siderastrea siderea* had 1,162 juvenile colonies contributing to 68% of total *S. siderea* abundance in 2018 (1708). *Montastraea cavernosa* (155) and *S. intersepta* (122) had juvenile colonies contributing to at least 25% of the total species density in 2018. Of the 27 species recorded in 2018 only *P. astreoides* ( $2.47 \pm 0.79$ ) and *S. siderea* ( $3.70 \pm 1.02$ ) had densities  $> 1$  colony/  $m^2$  when colonies of all sizes were included. Total abundance of adult colonies was 2394 across all 21 sites while there were 1924 juvenile colonies.

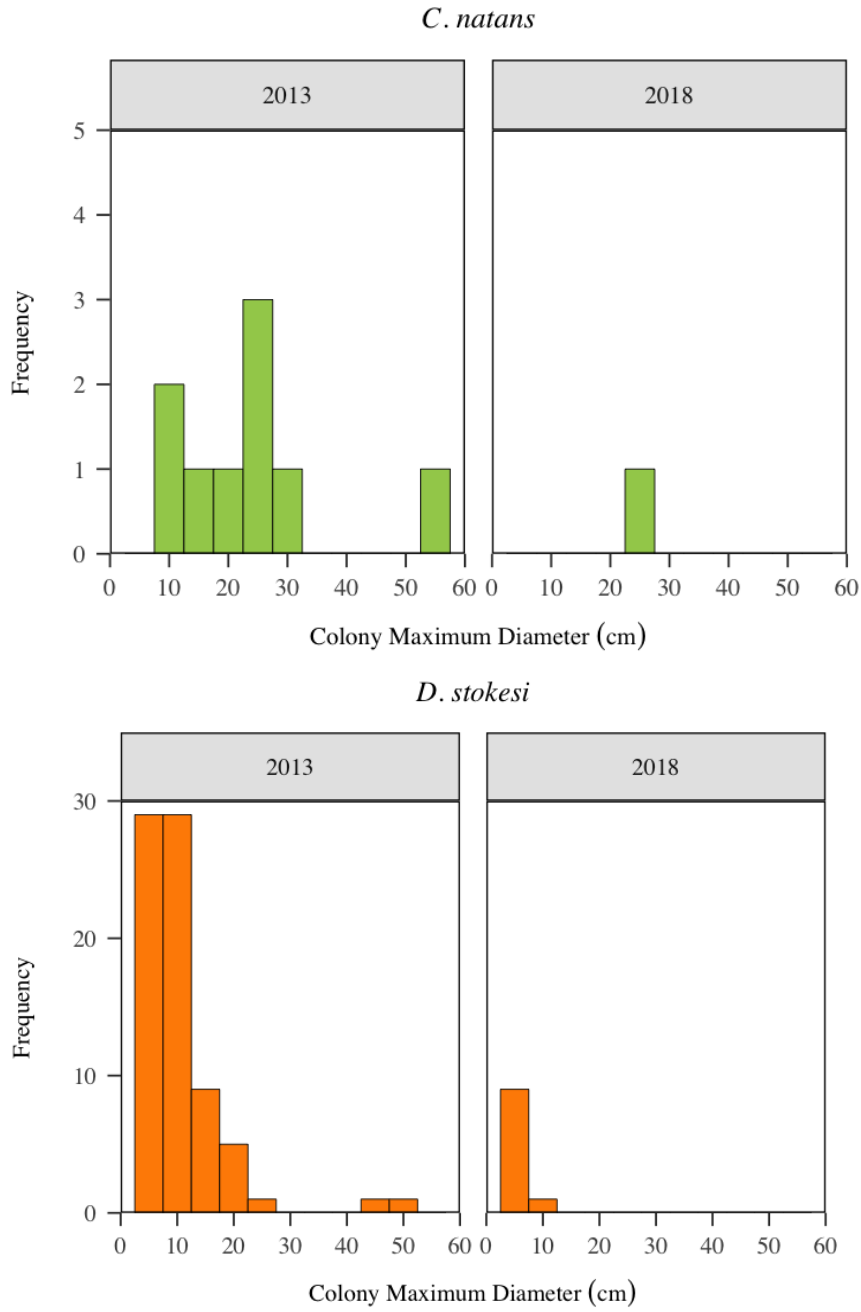


Figure 8. Size frequency distribution of maximum diameter for *Colpophyllia natans* and *Dichocoenia stokesi* across all sites in 2013 and 2018.

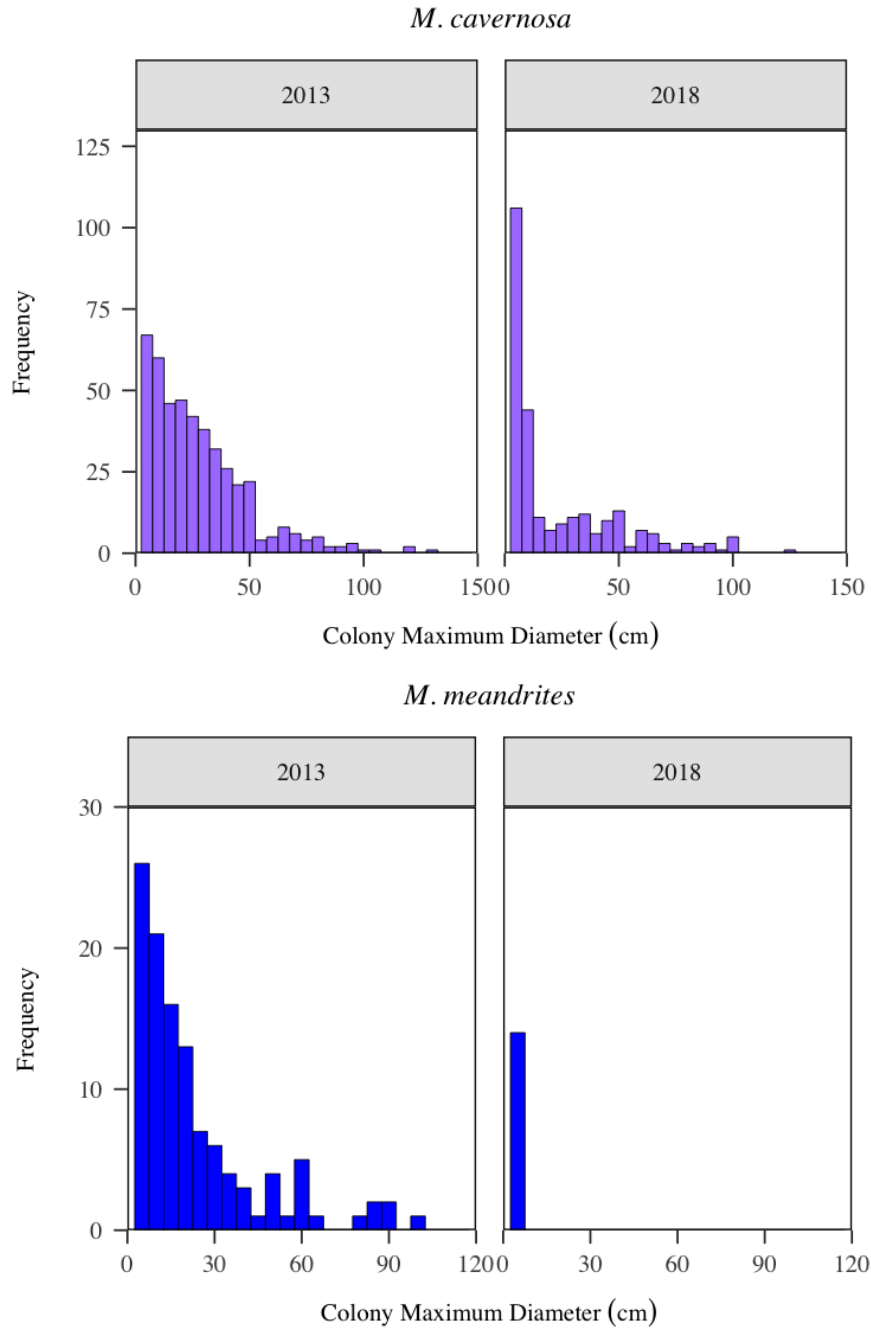
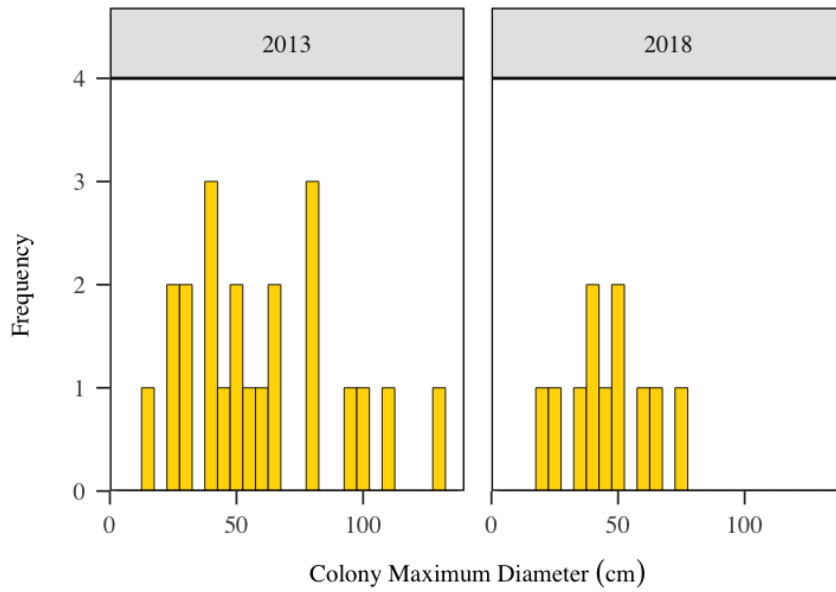


Figure 9. Size frequency distribution of maximum diameter for *Montastraea cavernosa* and *Meandrina meandrites* across all sites in 2013 and 2018.

*Orbicella* spp.



*P. astreoides*

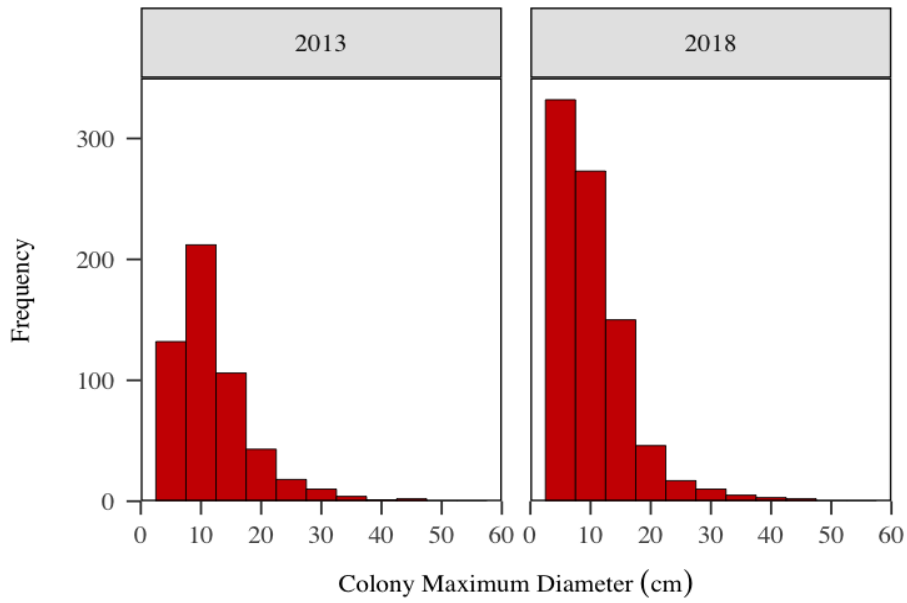


Figure 10. Size frequency distribution of maximum diameter for *Montastraea* (*Orbicella*) *annularis* complex and *Porites astreoides* across all sites in 2013 and 2018.

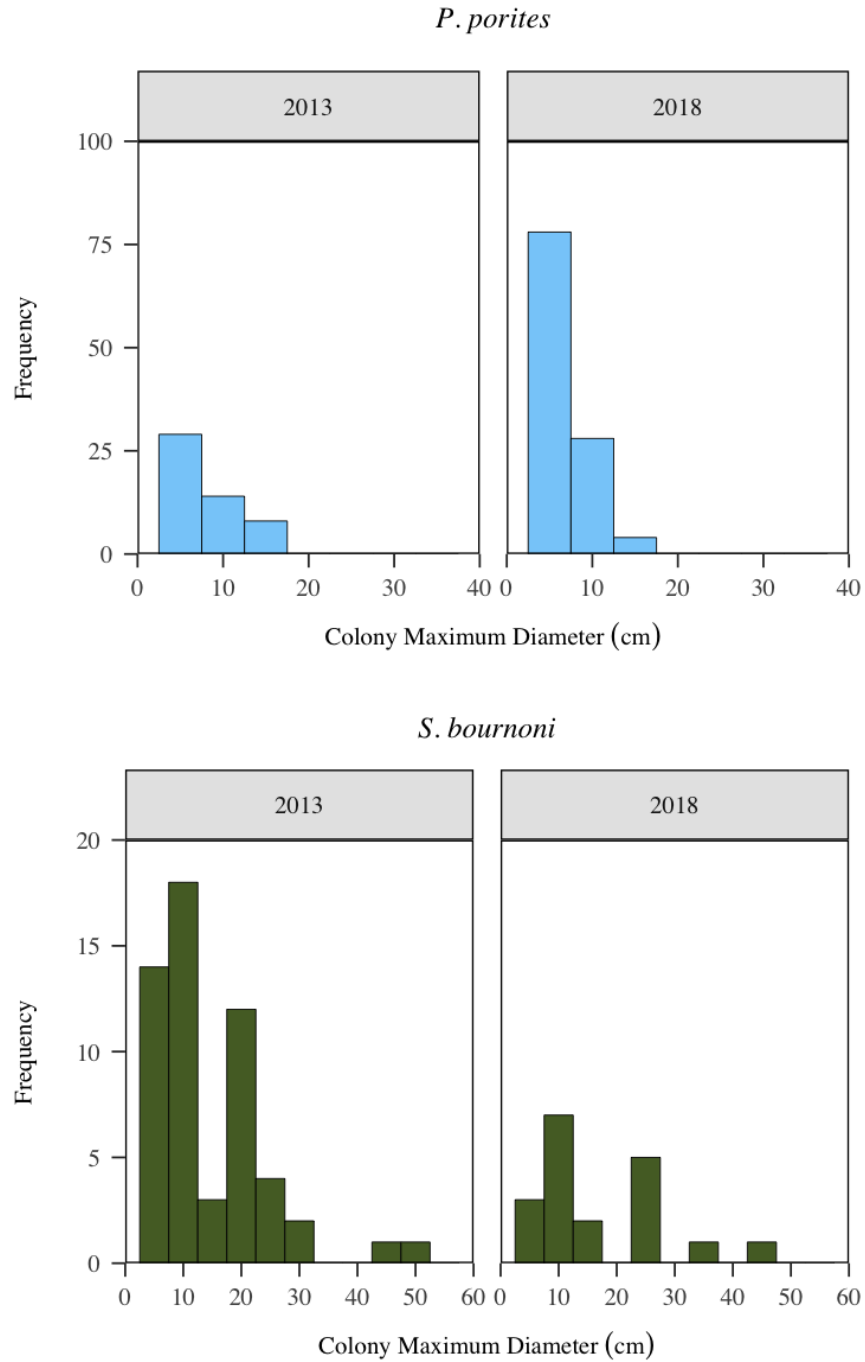


Figure 11. Size frequency distribution of maximum diameter for *Porites porites* and *Solenastrea bournoni* across all sites in 2013 and 2018.

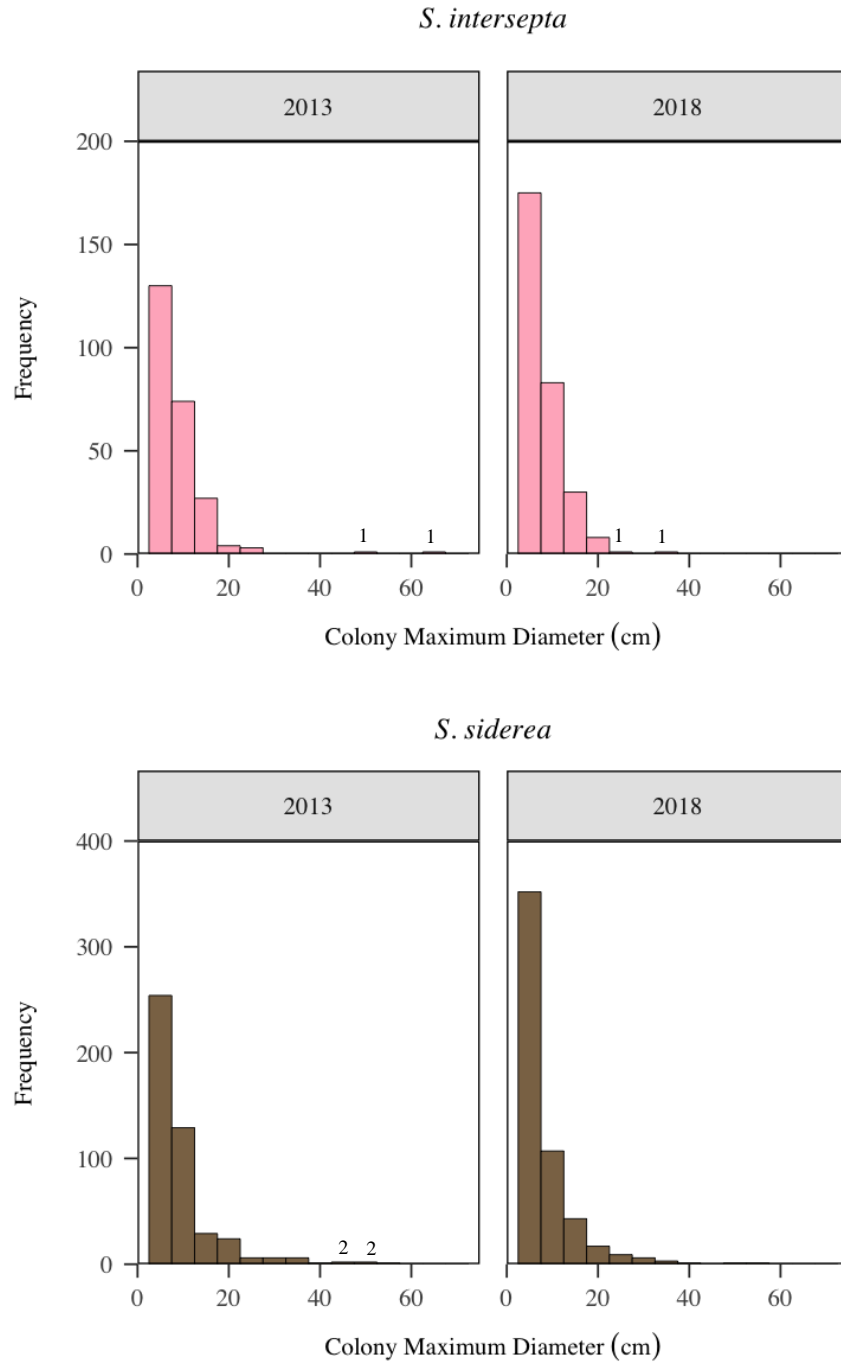


Figure 12. Size frequency distribution of maximum diameter for *Stephanocoenia intersepta* and *Siderastrea siderea* across all sites in 2013 and 2018.

Table 5. Abundance of stony corals in 2018 of adult (colonies  $\geq 4$  cm) and juvenile colonies (colonies  $< 4$ cm) and mean density ( $\pm$  SE) of all colonies.

Species	Adult Abundance (colonies $\geq 4$ cm)	Juvenile Abundance (Colonies $< 4$ cm)	Total Abundance	Total Density
<i>Acropora cervicornis</i>	8	0	8	0.02 $\pm$ 0.01
<i>Agaricia agaricites</i>	150	38	188	0.41 $\pm$ 0.29
<i>Agaricia fragilis</i>	10	4	14	0.03 $\pm$ 0.01
<i>Agaricia lamarcki</i>	5	0	5	0.01 $\pm$ 0.00
<i>Colpophyllia natans</i>	1	1	2	0.00 $\pm$ 0.00
<i>Dichocoenia stokesi</i>	10	33	43	0.09 $\pm$ 0.02
<i>Diploria labyrinthiformis</i>	2	0	2	0.00 $\pm$ 0.00
<i>Eusmilia fastigiata</i>	5	3	8	0.02 $\pm$ 0.01
<i>Isophyllia sinuosa</i>	2	0	2	0.00 $\pm$ 0.00
<i>Leptoseris cucullata</i>	1	0	1	0.00 $\pm$ 0.00
<i>Madracis auretenra</i>	42	16	58	0.13 $\pm$ 0.12
<i>Madracis decactis</i>	46	7	53	0.11 $\pm$ 0.04
<i>Meandrina meandrites</i>	14	14	28	0.06 $\pm$ 0.02
<i>Montastraea (Orbicella) annularis</i> complex	11	0	11	0.02 $\pm$ 0.01
<i>Montastraea cavernosa</i>	263	155	418	0.90 $\pm$ 0.15
<i>Mycetophyllia aliciae</i>	7	0	7	0.02 $\pm$ 0.01
<i>Mycetophyllia lamarckiana</i>	0	1	1	0.00 $\pm$ 0.00
<i>Oculina diffusa</i>	0	0	0	0.00 $\pm$ 0.00
<i>Oculina robusta</i>	1	0	1	0.00 $\pm$ 0.00
<i>Phyllangia americana</i>	1	12	13	0.03 $\pm$ 0.02
<i>Porites astreoides</i>	838	302	1140	2.47 $\pm$ 0.79
<i>Porites porites</i>	110	50	160	0.35 $\pm$ 0.14
<i>Pseudodiploria clivosa</i>	3	0	3	0.01 $\pm$ 0.00
<i>Pseudodiploria strigosa</i>	5	2	7	0.02 $\pm$ 0.01
<i>Scolymia cubensis</i>	1	1	2	0.00 $\pm$ 0.00
<i>Siderastrea siderea</i>	540	1168	1708	3.70 $\pm$ 1.02
<i>Solenastrea bournoni</i>	19	1	20	0.04 $\pm$ 0.01
<i>Stephanocoenia intersepta</i>	299	122	421	0.91 $\pm$ 0.17



## DISCUSSION

The Southeast Florida Reef Tract underwent a temporally (at least 5 years) and geographically (nearly 100 km between affected sites) unprecedented disease event that resulted in drastic changes in the stony coral assemblage including severe declines in stony coral diversity, LTA and density. The disease event began as early as late 2013 or early 2014 and peaked in 2016, with loss of colonies and live tissue continuing in 2017 and 2018. This disease event resulted in acute mortality and altered ecosystem function to the point where recovery is uncertain. Drastic loss of coral colonies, live tissue and colonies of larger size classes may detrimentally decrease fecundity and reproductive potential of remaining corals, thus reducing the potential to recover. Many of the large, structurally complex species lacked juveniles, while eurytopic generalist species had over 76% of all colonies found as juveniles.

Prevalence of SCTL D was within normal population levels (Muller and van Woesik, 2012; Ruiz-Moreno et al., 2012) in 2013 and 2014. However, disease increased 8-fold from 2013 to 2014 and was recorded in three different counties. These data suggest an alternative timeline than suggested by (Precht et al., 2016) who reported elevated white disease starting near Virginia Key, Florida (Miami-Dade County) adjacent to major Port of Miami dredging activities in September 2014. By summer 2014, SCTL D was reported as far north as Palm Beach County on early indicator species, *D. stokesi* and *M. meandrites* (Florida Keys National Marine Sanctuary, 2018). Disease prevalence and the number of species affected both increased in 2015 and 2016. In 2015, nine different species and species complexes had SCTL D including the early indicator species. However in 2016, only intermediately susceptible species had active SCTL D infections. Lack of infections in early indicator species in 2016 was because they were the almost completely lost by 2016. Of the seven early indicator species, five (*C. natans*, *D. stokesi*, *D. labyrinthiformis*, *M. meandrites* and *Pseudodiploria strigosa*) lost > 60% of all colonies. Colonies of *Pseudodiploria clivosa*, another early indicator species, did not succumb to whole colony mortality by 2016, but by 2018 only 10% of colonies remained. By 2018, only *M. cavernosa* and *Orbicella* spp. had active infections. Both species often have lesions, which cause partial mortality lasting months to years (Florida Keys National Marine Sanctuary, 2018).

The number of species and colonies with disease followed the same pattern as overall prevalence. During the peak of the disease event in 2015 and 2016, 9 and 7 species were

affected, respectively. Although the maximum number of species with SCTL D was in 2015, only 18 colonies had the disease, compared to 58 in 2016. Again this was partially attributable to the dramatic loss of the early indicator species before sampling 2016. The number of colonies infected in 2016 was primarily driven by *M. cavernosa*, where 38 of 348 colonies had the disease. The disease event was indiscriminate affecting 11 of 28 species. In addition affecting many species, SCTL D occurred in all habitat types. In 2013, SCTL D was found on the Nearshore Ridge Complex (NRC) and the Inner Reef. By 2014, SCTL D was found on the Inner Reef, Middle Reef and Outer Reef. In 2015, SCTL D was in all four habitat types and all four counties. Prevalence of other diseases remained < 1% across all years and did not significantly change. However, yearly maxima and minima of the disease varied similarly to SCTL D. Other disease prevalence was significantly positively correlated with SCTL D prevalence in 2016; suggesting that all diseases in 2016 were elevated. Prevalence of all other diseases increased every year from 2013 to 2016, then decreased again in 2017 and 2018.

Disease prevalence returned to pre-event levels in 2017, but LTA and diversity quantify loss after the most severe portion of this disturbance event. Live tissue area and diversity are indicators of reef resilience, which is the ability of the system to recover. (Maynard et al., 2017; van Woesik, 2017). All three diversity indices significantly change by or after 2016 (peak of the disease outbreak), demonstrating a trend toward homogeneity. Species richness significantly declined in 2016 and then had no significant change across the next two sample years. Changes in Shannon diversity or Inverse Simpson's indices after 2016 were due to unequal abundance within the already depressed number of species at each site.

With significant declines both in LTA and diversity, the southeast Florida reef system could face associated shifts in ecosystem function and stability, increased susceptibility to selective pressures, and reduced resilience and adaptability (van Woesik, 2002; 2017). The only species with significant increases in LTA or density were small, non-reef building, 'weedy' coral species such as *P. astreoides*, *P. porites* and *S. intersepta* with a concurrent loss of major reef-building species such as *M. cavernosa* and *Orbicella* spp. This shift in species composition towards the fast growing, 'weedy' species can affect structure provided by the reef system as these species typically grow as small flat colonies and result in reduced reef complexity (Knowlton, 2001; Precht and Miller, 2007; Green et al., 2008). Additionally, many other 'weedy'

species of corals such as *A. agricites* had no significant losses in LTA or density. Loss of species and homogenization within sites, demonstrated by the significant change in diversity indices, poses to foster a significant shift in the SEFRT towards eurytopic generalist species, furthering the already previously recorded shift in species dominance along the FRT reported by Burman et al. (2012).

Significant reductions in LTA can be considered equivalent to loss of cover, and these reductions have the potential to affect a systems ability to recover after a disturbance event due to the lower production of larvae. It has been shown that high coral cover populations produce more larvae per square centimeter of tissue, leading to more larvae per square meter of reef (Hartmann et al., 2017). Overall LTA significantly decreased, with 2017 and 2018 having significantly less LTA than 2013 through 2015. Prevalence of SCTL and LTA were significantly positively correlated in 2017 and 2018, and thus sites that had more live tissue in these years also had greater disease prevalence.

This regional decline in LTA was driven primarily by *M. cavernosa* and *Orbicella* spp., with smaller amount of tissue lost from also *M. meandrites*, *S. bournoni* and *D. stokesi*. The reproductive potential of species that saw significant declines in both LTA and density could be inhibited by both the loss of whole colonies and the loss of tissue on still living colonies, lowering reproductive connectivity and reproductive output. The reproductive output may be drastically reduced especially for *D. stokesi* and *M. meandrites* due to having less than 15 colonies across all sites by 2018. Colony size is often directly related to fecundity and changes in colony size can have detrimental effects on reproductive capabilities (Connell, 1973; Szmant-Froelich, 1985; Tsounis et al., 2006). Species that saw significant declines in density often suffered complete colony loss of the largest colonies recorded. Loss of all colonies in the largest size class of each species as seen in *S. intersepta*, *S. bournoni*, *M. meandrites*, *D. stokesi* and *C. natans*, could greatly lower population fecundity within these species, as they now exist as predominantly small colonies. Structural complexity has been shown to predict if a reef will recover or regime shift, reefs containing only smaller colonies, relative to species usual size distribution, decreases the amount of habitat and structural complexity provided by these species (Graham et al., 2015). The drastic loss of coral colonies, live tissue and colonies of larger size

classes has the potential to detrimentally decrease fecundity and reproductive potential of the remaining corals and thus reducing the systems potential for recovery.

Juvenile surveys can provide important insight as to what species have reproduced successfully and had successful settlement onto the reef and provide information on the quality of the environment and substrate for coral reproduction. In previous recruitment and juvenile studies in Southeast Florida, survivorship in the juvenile stage was found to be a critical factor in structuring the spatial structure of adult coral communities (Harper, 2017). Although a dedicated recruitment survey was not performed, the quick method employed still provided a snapshot of the current juvenile population within the sample sites. The complete lack of juveniles found for *D. labyrinthiformis*, *Orbicella* spp., and *P. clivosa* suggest during and previous to the peak of the disease event, these species did not have successful reproduction and settlement on these reefs. As these species now exist at even lower densities in 2018, further successful reproduction seems unlikely. In contrast, *D. stokesi*, *M. meandrites* and *S. siderea*, had more juveniles than adult colonies, demonstrating their successful reproduction and larval settlement. Juvenile density has been found to be a positive predictor of whether a reef will recover or a regime shift will occur (Graham et al., 2015). *Siderastrea siderea* accounted for > 60% of all juveniles recorded in 2018. Although *S. siderea* is considered a reef-building species throughout the Florida Keys and greater Caribbean, in Southeast Florida these colonies rarely are > 50 cm in diameter. This study only recorded a maximum of 5 colonies per year > 50 cm and in 2018, 94% of *S. siderea* colonies were < 20 cm in diameter. Rapidly growing, lower relief species like *P. astreoides* and *S. siderea* comprised > 76% of all juveniles in 2018; these species are persisting after the disturbance event and may dominate these reefs in the future.

## CONCLUSIONS AND RECOMMENDATIONS

The SCTL outbreak on the SEFRT severely and detrimentally impacted the stony coral assemblage, potentially altering the system to the point where recovery is uncertain. Disease prevalence returned to pre-event levels for the region in 2018, and the full effect of the disturbance event on the stony coral assemblage can begin to be quantified: 64% of all live tissue was lost and 11 of 28 stony coral species were affected. The only species with significant increases in LTA or density were small, non-reef building, ‘weedy’ coral species, and major reef

building species were lost. This shift in species composition towards fast growing, ‘weedy’ species can affect structure provided to other organisms, potentially reducing ecosystems services. Species with significant density declines often suffered complete loss of their largest colonies, thereby reproductive capability. Drastic loss of coral colonies, live tissue and large colonies decreases fecundity and reproductive potential, and thus reduces the systems potential for recovery (Figure 13). Additionally, some species with the largest tissue losses had no juvenile colonies demonstrating potentially inhibited reproduction or the complete lack of successful reproduction occurred, which could detrimentally affect the recovery of the reef. As the SEFRT exists directly adjacent to the highly urbanized and developed mainland of south Florida, anthropogenic impacts on the reef could pose additional barriers to recovery.

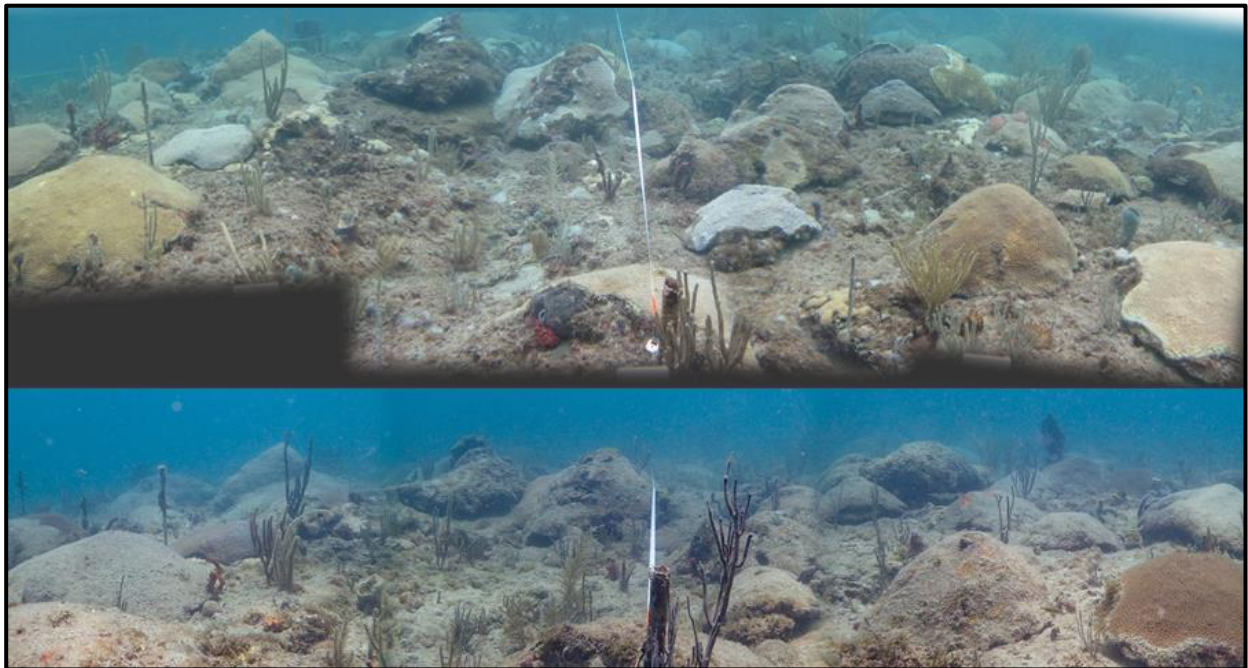


Figure 13. Panoramic image of site BC1 in 2016 (top) and 2018 (bottom). All but three colonies of *Montastrea cavernosa* visible in 2016 the panoramic have completely died by 2018.

With global bleaching and disease events predicted to increase in the future (Maynard et al., 2015), providing conditions to facilitate recovery of the SEFRT is imperative. Local resource managers need to understand the severity of the disease outbreak on the coral assemblage and mitigate local anthropogenic impacts to facilitate recovery. Many of the affected species had juvenile colonies and thus the potential for new, small colonies to grow and contribute to the

assemblage shows potential for recovery. It would be beneficial if management agencies could expand current monitoring efforts to better document recovery. Additionally, these data could be used to investigate the effect of the disease event on much smaller spatial scales to look for patterns at the ecosystem region or site level. The Southeast Florida Coral Reef Evaluation and Monitoring Program was vital in documenting these changes and providing resource managers with reliable data. Further long-term monitoring is imperative to monitor the resource for further loss and to hopefully document recovery.

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